The use of incidence data to estimate bat (Mammalia: Chiroptera) species richness and taxonomic diversity and distinctness within and between the biomes of South Africa, Lesotho and Swaziland

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Submitted for partial fulfillment of Master of Sciences Degree by Course Work

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DECLARATION

I declare that this research report is my own, unaided work. It is being submitted for the Degree of Masters of Science by course work in Resource Conservation Biology in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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Ernest Seamark

Date: ___17 June 2013____

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ABSTRACT

Species richness and estimates of species richness were calculated based on assemblages of bats, within the biomes of South Africa, Lesotho and Swaziland following the vegetation classification of Mucina and Rutherford (2006). Similarity indices were used to explore the various relationships between the assemblages between the various biomes. Taxonomic diversity and distinctness examined the various assemblages within each of the biomes to investigate which biomes contained assemblages that were taxonomically diverse and/or taxonomically distinct compared to all species known to occur within South Africa, Lesotho and Swaziland.

The Desert biome had the lowest recorded species richness (5 species), and there was insufficient data to calculate estimates of species richness for this biome. While the Albany had 11 species recorded with species estimates (*Est.*) ranging between 11-12, then in increasing order - Nama-Karoo (12 species, *Est.* 13-25 species), Succulent-Karoo (13 species, *Est.* 15-30 species), Fynbos (17 species, *Est.* 18-25 species), Indian Ocean Coastal Belt (31 species, *Est.* 32-36 species), Forest (32 species, *Est.* 37-46 species), Grassland (39 species, *Est.* 42-54 species), Azonal (45 species, *Est.* 49-63 species) and Savanna (57 species, *Est.* 59-67 species). The mean recorded estimates (based on the averages of all models) and rounding up to a full species indicates that the Albany biome contains the lowest expected species richness of 12 species, then Fynbos and Nama-Karoo (21 species), Succulent-Karoo (22 species), Indian Ocean Coastal Belt (34 species), Forest (43 species), Grassland (49 species), Azonal (54 species) and Savanna (64 species).

Sample completeness was calculated for each of the biomes which indicates in ascending order that the Albany biome is 93.2% complete followed by the Indian Ocean Coastal Belt biome (91.1%), Savanna biome (89.9%), Azonal biome (84.1%), Fynbos biome (81.5%), Grassland biome (80.7%), Forest biome (75.8%), Succulent-Karoo biome (61.3%), and Nama-Karoo biome (59.9%). This showed that the Albany biome was found to be the only biome that has been sufficiently sampled.

The Jaccard and Sørensen pair wise indices resulted in the clustering of the biomes with similar species richness, due to the large range in species richness (5-57 species) between the biomes. The Lennon *et al.* (2001) index which is not affected by large species richness between the samples indicated that the Desert and Nama-Karoo assemblages were most dissimilar to one another, while the Indian Ocean Coastal Belt assemblage was the most similar to the remaining biome assemblages. The Albany biome assemblage and Azonal biome assemblage were shown to the most dissimilar to one another.

The Grassland, Nama-Karoo and Savanna biomes contribute to higher taxonomic diversity, while the Albany, Azonal, Fynbos, Nama-Karoo and Succulent-Karoo biomes contain lower species richness generally but represent a higher taxonomic distinctness from the chiroptera assemblages in the Grassland and Savanna biomes. The Desert, Forest and Indian Ocean Coastal Belt biomes do not contain bat assemblages that are neither taxonomically distinct nor diverse when compared to the taxa of South Africa, Lesotho and Swaziland.

The bat assemblage within the Nama-Karoo are both taxonomically diverse and distinct from chiroptera assemblages found within the other nine biomes, requiring a greater focus on conservation actions for the bat species assemblage located within this biome.

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INTRODUCTION

Diversity has a variety of meanings, whether the perspective is ecological or taxonomic, local or global, political, cultural, agricultural or scientific (Williams *et al.*, 1991). Areas of high species richness (hotspots) have been suggested for the designation of protected areas at the broad scale of biogeographic regions (Myers *et al.* 2000; Hurlbert and Jetz 2007). Sechrest *et al.* (2002) showed that these hotspots across the world contain greater amounts of evolutionary history than would be expected based on purely species richness (Mace *et al.* 2003). These differences in the evolutionary history of taxa in these hotspots result in a diversity of morphological, physiological, and behavioral characters (Williams and Humphries, 1996) and of their features (Faith, 1992). Faith (1992) defines features of taxa as a measure of cladistic or phylogenetic diversity, which is an effective indicator of underlying feature diversity. Many of the characters may represent functional traits (Woodward and Cramer, 1996; Lavorel *et al.*, 1997; Díaz and Cabido, 2001), and the character richness of an area or region may be closely related to the functional diversity of the area or region (Tilman *et al.*, 1997; Petchey and Gaston, 2002; Petchey *et al.*, 2004; Petchey and Gaston, 2006).

However, would species richness alone be sufficient at the broad scale biogeographic / bioclimatic region for long-term conservation of a complementarily of species (Pressey *et al.* 1993; Williams *et al.* 1996; Margules and Pressey 2000; Gotelli and Colwell 2001; Rondinini *et al.* 2006)? If two different communities have identical numbers of species and the equivalent patterns of species abundance, but differ in the evolutionary history, it seems intuitively appropriate that the most taxonomically varied community is more diverse (Magurran, 2004). Pielou (1975) pointed out that diversity would be higher in a community in which species are divided amongst many genera as opposed to one where the majority of species belong to the same genus. Heard and Mooers (2000) demonstrated that phylogenetic relationships are one of the most important factors determining species extinction. Therefore, phylogenetic information may be a better indicator of conservation value than species richness alone (Webb *et al.* 2002; Mace *et al.* 2003; Schweiger *et al.* 2008). As with diversity the term conservation value has a variety of meanings depending on the scale of perspectives. Winston and Angermeier (1995) questioned conservation value in that many cases it ignored existence and value of other components of biotic diversity, such as genetic diversity and ecosystem diversity. To overcome this failure to measure conservation value, Pressey *et al.* (1994) viewed conservation value in terms of irreplaceability. Where irreplaceability is the potential contribution of a site to a conservation goal by virtue of the features it contains (Pressey *et al.* 1994; Margules and Pressey 2000). Identifying areas for conservation on the basis on species richness only, may therefore bias conservation in favor of communities that have evolved and radiated recently (Krajewski, 1994; Sechrest *et al.*, 2002). Therefore, species richness, and, or the estimates thereof, may not give a representative indication of area for setting of conservation priorities (Vane-Wright *et al.*, 1991; Williams *et al.*, 1991; Williams and Gaston, 1994; Williams, 1996;

Vane-Wright, 1996) or environmental monitoring (Warwick and Clarke, 1995; Clarke and Warwick, 1998; Clarke and Warwick, 1999).

Several authors have proposed a variety of indices other than species richness, which also take into account phylogenetic diversity; however, these differ greatly in their method of calculation (Vane-Wright *et al.*, 1991; Faith, 1992; Solow *et al.*, 1993; Faith, 1994; Warwick and Clarke, 1998; Izsak and Papp, 2000; Clarke and Warwick, 2001b; Rodrigues and Gaston, 2002). These indices can be separated in two categories, topology based and distance based (Krajewski, 1994).

Vane-Wright *et al.* (1991) was the first to propose the application of topology-based methods, which reflect the phylogenetic branching order within a monophyletic group. In this approach, the diversity contribution of a particular species is inversely proportional to the number of nodes (hypothetical ancestors) between that species and the root of the tree. Therefore, members of recent or speciose clades tend to contribute less to group diversity than do ancient or species-poor clades. Community distinctness (as a measure of phylogenetic diversity) is then obtained simply by summing the weights of the species (Keith *et al.*, 2005; Schweiger *et al.*, 2008).

Distance-based methods use either a minimum spanning path or a pairwise distance approach. The minimum spanning path measures the phylogenetic diversity of a community by summing up the branch lengths of the subtree that includes the community's species (Faith, 1992). Branch lengths indicate the expected number of molecular "features" accumulated over evolutionary history. Common branches reflect shared molecular information inherited from common ancestors, while the branch length of a single species not shared by others reflects exclusive information (Faith, 1992). While the minimum spanning path approach measures overall phylogenetic information of a community, the pairwise distance approach is based on a distance matrix between all species of a community (Schweiger *et al.*, 2008). Distances can be based on morphological or functional differences (Izsak and Papp, 1995), on Linnean taxonomy (Warwick and Clarke, 1995), on branch lengths of phylogenies based on molecular data (Solow *et al.*, 1993; Pavoine *et al.*, 2005) or, if branch lengths are not known, on the number of nodes separating each pair of species (Faith, 1992).

Studies on patterns of species richness and endemism among mammals in South Africa have not comprehensively included the second most diverse order of mammals; Chiroptera (bats) (Siegfried and Brown 1992; Turpie and Crowe 1994). Gelderblom *et al.* (1995) was the first to attempt to identify areas of importance for inadequately protected taxa, which included the Chiroptera. Only a few studies have been published on the numerical richness of bat species within Africa, and these have mainly focused on protected areas (Dixon, 1966; Bourquin and Mathias, 1984; Bourquin and Mathias, 1995; Seamark and Kearney, 2008; Kearney *et al.*, 2008; Kearney *et al.* 2010; Kearney and Seamark 2011) or regions, South African biomes (Gelderblom *et al.*, 1995); or provincial vegetation (Rowe-Rowe and Taylor, 1996).

Historically most reports of species richness have been based on the number of species recorded from a specific area or region (Magurran, 2004).

To date only six papers have been published that have attempted to report some form of diversity measure for bats other than just the species richness, within southern Africa (Rautenbach *et al.* 1996; Keith *et al.* 2005; Kearney *et al.* 2010; Kearney and Seamark 2011; Schoeman and Jacobs 2011; Schoeman *et al.* 2013), and for East Africa (Webala *et al.*, 2004). Preliminary work by the ACR (2010; 2011) included a map that showed Chao2 estimates of species richness calculated for quarter degree grid cells throughout Africa, yet it provided no interpretation or suggestions as how these results can be used by conservationists or researchers.

Gelderblom *et al.* (1995) examined Chiroptera within the context of biomes following the biomes of Rutherford and Westfall (1986), where they recorded 18 species' from the Fynbos; 31 species' from the Grassland, 17 species' from the Nama-Karoo, 12 species' from the Succulent Karoo and 51 species from the Savanna biomes. However, they do not indicate the total number of species occurring within the study area. Monadjem *et al.* (2010) recognizes 58 species, from South Africa, Lesotho and Swaziland, while the ACR (2011) recognizes 65 species from this same region. The difference of 7 species between the two publications is mainly due to differences in the taxonomic nomenclature followed in the two publications, and the ACR (2011) also includes four species that are possible vagrants or misidentifications.

Keith *et al.* (2005) focused on the phylogenetic and taxonomic distinctiveness of the various Chiroptera taxa occurring in South African region however did not look at the regional assemblage distinctness within South Africa. Schweiger *et al.* (2008) define "distinctiveness" as the relation of a particular species to the rest of the species within the assemblage, whereas "distinctness" represents the relation of one assemblage of species to another assemblage of species.

No additional published studies are known to have tested or updated the results of Gelderblom *et al.* (1995). Since 1995, there has been additional papers that have documented/described additional species, distributions as well as correcting previous misidentifications of bat species within South Africa (Rautenbach *et al.* 1996; Rowe-Rowe and Taylor 1996; Kearney and Taylor 1997; Taylor 1998, 2000; Jacobs and Fenton 2001; Taylor *et al.* 2004; Miller-Butterworth *et al.* 2005; Seamark 2005; Seamark and Kearney 2006; Kearney *et al.* 2008a, 2008b; Monadjem *et al.* 2010). A revision of the work by Gelderblom *et al.* (1995) with special reference to the Chiroptera will provide valuable insight to provide information to update the strategic plan for the preservation of South Africa's biodiversity, and South Africa's commitment to the Convention on Biological Diversity (DEAT, 2005a; DEAT, 2005b). Such a revision will also provide a critically required understanding of the broad scale bat assemblages within the southern African context.

Broad scale understanding is usually undertaken at a biome (Rutherford and Westfall 1986, 1994), ecoregion (Olson and Dinerstein 2002; Burgess *et al.* 2004) and bioregion (Mucina and Rutherford, 2006) and are becoming increasingly used by those concerned with management and conservation of natural resources (Rutherford *et al.*, 2006). These terms of units have broad-scale applications to those who have to develop conservation and management strategies over large areas (Rutherford *et al.*, 2006). A biome is viewed as a high-level hierarchical unit having a similar vegetation structure exposed to similar macroclimatic patterns, often linked to characteristic levels of disturbance such as grazing and fire (Rutherford *et al.*, 2006). The biome can be considered a kind of 'sub continental biotic super community' (Rutherford *et al.*, 2006), while Cox and Moore (2000) refer to it as a 'large-scale ecosystem'. O'Neill *et al.* (1986) defines the biome as a high-level hierarchical unit, which are not characterized by individual species but mainly by the emergent properties of vegetation structure and associated climate or any other applicable broad-scale environmental factors. Hierarchy theory also suggests that higher-level spatial hierarchy scales are associated with longer-term time scales although there is a complex interplay between evolutionary (long-term) and ecological (short-term) time scales (Rutherford *et al.*, 2006). Strictly speaking the term biome includes both plant and animal communities (Clements and Shelford, 1939), but due to the dominant nature of vegetation cover, biomes have been based only on vegetation characteristics (Rutherford *et al.*, 2006).

The two most cited works on biomes in southern Africa, are (Rutherford and Westfall 1986, 1994) which emphasize that:

1. A biome is the largest land community unit recognized at a continental or sub continental scale and therefore does not recognize any subsets of a biome as a 'biome of lower rank'.
2. Biome patches should be of viable and minimum size (also to acknowledge the zoological components of a biome – about 20 km in shortest cross distance).
3. Biomes are defined primarily on combinations of dominant life or growth forms, and not on the basis of taxonomic characteristics (floristic nor faunal) or non dominant elements.
4. Biomes are defined primarily on the basis of major climatic features that most affect the biota.

Rutherford and Westfall (1994) recognized seven biomes – Savanna, Nama-Karoo, Grassland, Succulent-Karoo, Fynbos, Desert and Forest biomes. While, Low and Rebelo (1996a) also recognized seven biomes, they did not distinguish the Desert biome of Rutherford and Westfall (1994) and introduced a new biome termed Thicket in their classification. More recently Mucina and Rutherford (2006) identified 10 biomes in South Africa, Lesotho and Swaziland (Table 1). They recognized the seven biomes of Rutherford and Westfall (1994) and the Thicket biome recognized by Low and Rebelo (1996), which they termed the Albany Thicket, and also introduced two new biomes; Indian Ocean Coastal Beltand Azonal vegetation.

Table 1. Biomes of South Africa, Lesotho and Swaziland after Mucina and Rutherford (2006)**.**

Biome	South Africa	Lesotho	Swaziland
Fynbos	X	-	-
Succulent Karoo	X	-	-
Desert	X	-	-
Nama-Karoo	X	-	-
Grassland	X	X	-
Savanna	X	-	X
Forest	X		
Albany Thicket	X	-	-
Indian Ocean Coastal Belt	X	-	-
Azonal	X	-	-

Here we aim to obtain a better understanding of the use of incidence data to estimate bat (Mammalia: Chiroptera) species richness, taxonomic diversity and distinctness within and between the biomes of South Africa, Lesotho and Swaziland landscape. This will be achieved through the examination and comparison of various methods that have been developed for use with incidence data (presence and absence). These methods include the calculation of species richness, and estimates thereof, together with taxonomic diversity and distinctness within and between the various biomes of South Africa, Lesotho and Swaziland.

MATERIAL AND METHODS

Geographic distribution records for 65 bat species from South Africa, Lesotho and Swaziland (downloaded from the website of the African Chiroptera Report (ACR, 2011)) were used in this analysis. Only records identified to species level were included, those taxa identified to genus or higher taxonomic levels were excluded from the analysis, therefore only verified museum voucher specimens were included in the analysis. The records in the African Chiroptera Report data are based on museum voucher specimens housed in valid repositories around the world. Each data record (voucher specimen) contains information on museum accession number, species identification, age, sex, collector, collector date, collection locality, and in some cases where known the geographic coordinates of the locality. These records with geographic coordinates were used, and provided us with 9,387 records (9,055 records for South Africa, 119 records for Lesotho and 204 records for Swaziland).

Four species identified in the ACR (2011) were removed from analysis, as these were single records and are suspected as being possible misidentifications or vagrants. These species were – *Epomophorus labiatus* (American Museum of Natural History – AMNH 200225); *Mormopterus acetabulous* (Museum

Natural History, Paris – MNHN 1984-1201); *Rousettus obliviosus* (Humbolt Museum, Berlin – ZMB 3891) and *Tadarida ventralis*, which is known only from the holotype collected within the old Transvaal province with no further locality information (British Museum of Natural History – BMNH 1875.11.1.9.1).

DATA PREPERATION

A point shape file, of all the specimens for the 61 bat species for South Africa, Lesotho and Swaziland records was created in DIVA-GIS 7.4.0.1 (www.diva-gis.org). The accuracy of the shape file depended on the accuracy of the co-ordinates obtained from original data source (ACR, 2011) which did not exceed a 25 km^2 (Quarter Degree Squared – QDS) accuracy. The 'extract values by points' function in DIVA-GIS was used to obtain information on the biomes of the South African Vegetation types (Mucina and Rutherford, 2006). The 'point to grid' – richness and Presence/Absence output variable was selected; the grid size was defined at a Quarter Degree Grid Cell size (0.25° by 0.25°) and the point to grid procedure was set as simple. The simple setting allows for all species points within the grid to be pooled, without information from a neighbouring grid cell to be incorporated, which is the alternative setting. The parameter selected for presence/absence being the taxon name. For each of the 61 species the total number of QDS in each biome were used, these values were used in further analysis as frequency (abundance) of the species within each biome (Table 2).

Table 2. List of the taxa found in South Africa, Lesotho and Swaziland (ACR, 2011), arranged by family, genus and species rank, together with the frequency/abundance (number of Quarter Degree Squares that the taxa was recorded in within each of the 10 biomes of South Africa, Lesotho and Swaziland). Al – Albany biome, Az – Azonal biome, D – Desert, Fo – Forest biome, Fy – Fynbos biome, G – Grassland biome, IO – Indian Ocean vegetation biome, NK – Nama Karoo biome, S – Savanna biome, SK – Succulent Karoo biome, Tot – Total number of QDS that the taxa is recorded in across South Africa, Lesotho and Swaziland.

Family	Genus	Species	Al	Az	D	Fo	Fy	G	IO	NK	S	SK	Tot
Pteropodidae	*Eidolon*	*helvum*	0	1	0	0	0	8	1	3	6	1	20
Pteropodidae	*Epomophorus*	*crypturus*	0	0	0	1	0	0	2	0	19	0	22
Pteropodidae	*Epomophorus*	*wahlbergi*	2	3	0	6	3	16	14	0	42	1	87
Pteropodidae	*Rousettus*	*aegyptiacus*	4	2	0	4	3	5	4	0	8	2	32
Hipposideridae	*Cloeotis*	*percivali*	0	0	0	0	0	1	0	0	10	0	11
Hipposideridae	*Hipposideros*	*caffer*	0	3	0	3	0	8	6	0	47	0	67
Hipposideridae	*Hipposideros*	*vittatus*	0	2	0	0	0	0	0	0	1	0	3
Rhinolophidae	*Rhinolophus*	*blasii*	0	1	0	0	0	7	0	0	7	0	15
Rhinolophidae	*Rhinolophus*	*capensis*	5	3	0	2	12	1	0	0	2	6	31
Rhinolophidae	*Rhinolophus*	*clivosus*	3	1	0	4	16	63	3	1	49	6	146
Rhinolophidae	*Rhinolophus*	*darlingi*	0	4	1	1	0	5	0	8	35	1	55
Rhinolophidae	*Rhinolophus*	*denti*	0	0	0	0	0	1	0	0	5	0	6
Rhinolophidae	*Rhinolophus*	*fumigatus*	0	1	0	0	0	1	0	0	2	0	4
Rhinolophidae	*Rhinolophus*	*hildebrandtii*	0	3	0	0	0	3	0	0	10	0	16
Rhinolophidae	*Rhinolophus*	*landeri*	0	1	0	0	0	1	0	0	2	0	4

Family	Genus	Species	Al	Az	D	Fo	Fy	G	IO	NK	S	SK	Tot
Rhinolophidae	*Rhinolophus*	*simulator*	0	2	0	1	0	12	5	0	43	0	63
Rhinolophidae	*Rhinolophus*	*swinnyi*	0	2	0	2	0	7	1	0	3	0	15
Embalonuridae	*Taphozous*	*mauritianus*	0	2	0	1	1	4	2	2	22	0	34
Nycteridae	*Nycteris*	*hispida*	0	0	0	1	0	0	2	0	1	0	4
Nycteridae	*Nycteris*	*thebaica*	4	9	1	2	6	17	9	11	79	8	146
Nycteridae	*Nycteris*	*woodi*	0	2	0	0	0	0	0	0	2	0	4
Molossidae	*Chaerephon*	*ansorgei*	0	1	0	0	0	0	0	0	3	0	4
Molossidae	*Chaerephon*	*nigeriae*	0	0	0	0	0	0	2	0	2	0	4
Molossidae	*Chaerephon*	*pumilus*	0	2	0	6	0	3	14	0	51	0	76
Molossidae	*Mops*	*condylurus*	0	1	0	4	0	1	7	0	26	0	39
Molossidae	*Mops*	*midas*	0	2	0	0	0	0	0	0	5	0	7
Molossidae	*Otomops*	*martiensseni*	0	0	0	0	0	0	5	0	1	0	6
Molossidae	*Sauromys*	*petrophilus*	0	0	1	0	3	1	0	5	13	3	26
Molossidae	*Tadarida*	*aegyptiaca*	7	4	0	4	10	39	3	10	50	4	131
Molossidae	*Tadarida*	*fulminans*	0	1	0	0	0	0	0	0	1	0	2
Miniopteridae	*Miniopterus*	*fraterculus*	0	0	0	3	2	14	2	0	11	0	32
Miniopteridae	*Miniopterus*	*inflatus*	0	0	0	0	0	1	0	0	2	0	3
Miniopteridae	*Miniopterus*	*natalensis*	4	4	0	2	12	26	5	0	56	1	110
Cistugoidae	*Cistugo*	*lesueuri*	0	1	0	0	5	14	0	1	0	0	21
Cistugoidae	*Cistugo*	*seabrae*	0	1	1	1	0	0	0	1	0	1	5
Vespertilionidae	*Eptesicus*	*hottentotus*	0	1	1	1	6	7	0	1	9	0	26
Vespertilionidae	*Glauconycteris*	*variegata*	0	2	0	1	0	0	2	0	3	0	8
Vespertilionidae	*Hypsugo*	*anchietae*	0	0	0	1	0	1	4	0	6	0	12
Vespertilionidae	*Kerivoula*	*argentata*	0	1	0	0	0	0	1	0	1	0	3
Vespertilionidae	*Kerivoula*	*lanosa*	1	2	0	0	1	2	2	0	7	0	15
Vespertilionidae	*Laephotis*	*botswanae*	0	0	0	0	0	0	0	0	4	0	4
Vespertilionidae	*Laephotis*	*namibensis*	0	0	0	0	1	0	0	0	0	0	1
Vespertilionidae	*Laephotis*	*wintoni*	0	0	0	0	0	2	0	0	0	0	2
Vespertilionidae	*Myotis*	*bocagii*	0	3	0	2	0	0	0	0	4	0	9
Vespertilionidae	*Myotis*	*tricolor*	1	2	0	2	3	21	1	0	17	1	48
Vespertilionidae	*Myotis*	*welwitschii*	0	0	0	0	0	4	1	0	8	0	13
Vespertilionidae	*Neoromicia*	*capensis*	7	9	0	5	17	119	8	22	99	11	297
Vespertilionidae	*Neoromicia*	*nana*	0	3	0	5	0	5	15	0	38	0	66
Vespertilionidae	*Neoromicia*	*rendalli*	0	0	0	0	0	0	0	0	1	0	1
Vespertilionidae	*Neoromicia*	*somalica*	0	2	0	0	0	1	0	0	2	0	5
Vespertilionidae	*Neoromicia*	*sp_aff_melckorum*	0	2	0	0	0	0	0	0	1	0	3
Vespertilionidae	*Neoromicia*	*zuluensis*	0	2	0	1	0	0	0	0	22	0	25
Vespertilionidae	*Nycticeinops*	*schlieffenii*	0	2	0	1	0	1	0	0	27	0	31
Vespertilionidae	*Pipistrellus*	*hesperidus*	0	3	0	6	0	4	9	0	15	0	37
Vespertilionidae	*Pipistrellus*	*rueppellii*	0	2	0	0	0	0	0	1	1	0	4
Vespertilionidae	*Pipistrellus*	*rusticus*	0	2	0	1	0	2	0	0	28	0	33

Family	Genus	Species	Al	Az	D	Fo	Fy	G	IO	NK	S	SK	Tot
Vespertilionidae	*Scotoecus*	*albofuscus*	0	0	0	0	0	0	2	0	0	0	2
Vespertilionidae	*Scotophilus*	*dinganii*	2	5	0	6	1	8	13	0	74	0	109
Vespertilionidae	*Scotophilus*	*leucogaster*	0	1	0	0	0	0	0	0	1	0	2
Vespertilionidae	*Scotophilus*	*nigrita*	0	0	0	0	0	0	0	0	1	0	1
Vespertilionidae	*Scotophilus*	*viridis*	0	5	0	4	0	2	2	0	24	0	37
		Species richness	**11**	**44**	**5**	**31**	**17**	**39**	**30**	**12**	**56**	**13**	**61**

ESTIMATES OF SPECIES RICHNESS

The program Species Prediction And Diversity Estimation (SPADE) (Chao and Shen, 2010), was used to calculate species estimates. Seven models were calculated - Homogeneous model (Lee and Chao, 1994), Chao2 estimator (Chao, 1987), Chao2-bc (Chao *et al.*, 2005), and Incidence-based Coverage Estimators (Colwell and Coddington, 1994), but adapted by Chao and Shen (2010) - Model(h), Model(h)-1, Model(th), and Model(th)-1.

SAMPLE COMPLETENESS

To estimate the relative completeness of the sampling within the various biomes the species richness is divided by the estimated species richness for the same biome. Further investigations may also be made by comparing the species richness by the estimated range (minimum and maximum from the various estimators) to obtain a percentage range of inventory completeness (Magurran 2004). The closer the minimum range is to 100, the more complete the inventory and the smaller the range between the minimum and maximum percentages calculated for completeness the more robust the estimates of completeness. Comparing these completeness estimates are useful to prioritize which biomes are in need of further sampling (Magurran 2004).

SIMMILARITIES INDEXES

To examine the similarity between the various biomes, a pair wise comparison was calculated using the Jaccard (1908), Sorensen (1948) and Lennon *et al.* (2001) similarity indices, between each assemblage within each biome. Southwood and Henderson (2000) regard the Sørensen's measure one of the most effective presence/absence similarity measures, as it is identical to the Bray-Curtis present/absence coefficient (Magurran, 2004). Lennon *et al.* (2001) note that if samples differ markedly in terms of species richness the Sørensen measure will always be large, therefore introduced a new turnover measure that focuses more precisely on differences in composition.

Magurran (2004) indicates that one of the great advantages of the above three indices measures (Jaccard, Sørensen and Lennon *et al.* (2001)) is their simplicity. However, this virtue is also a disadvantage in the sense that the coefficients take no account of the relative abundance or frequency of species therefore the Bray-Curtis (Chao *et al.*, 2005; Chao *et al.*, 2006) was used to examine abundance between the various assemblages.

DendroUPGMA (http://genomes.urv.es/UPGMA/) (Garcia-Vallve *et al.*, 1999); was used to plot the above similarity matrixes to obtain a visual representation of the similarity between the various biomes. DendoUPGMA transforms similarity coefficients into distances and makes a clustering using the Unweighted Pair Group Method with Arithmetic mean (UPGMA) algorithm. The results of the above four similarity measures were examined and compared, to gain a better understanding of the possible relationships between the biomes and the Chiroptera assemblages contains within these biomes.

TAXONOMIC DIVERSITY AND DISTINCTNESS

The program PAST version 2.11 (Hammer *et al.*, 2001) was used to calculate the taxonomic diversity and taxonomic distinctness up to the family level for each biome. Taxonomic distinctness index (Clarke and Warwick, 1998) is a natural extension of the Simpson's index, which is robust in the face of variable or uncontrolled sampling effort (Price *et al.*, 1999). 'Taxonomic diversity' or Δ (appropriate for species abundance data), takes account of species abundance as well as taxonomic relatedness. It measures the average path length between two randomly chosen individuals (which may belong to the same species) (Clarke and Warwick, 2001a). The second form, 'taxonomic distinctness' or Δ^* represents the special case where each individual is drawn from a different species. Δ^*, a pure measure of taxonomic relatedness, is equivalent to dividing Δ by the value it would take if all species belonged to the same genus, that is in the absence of a taxonomic hierarchy (Clarke and Warwick, 2001a). When presence/absence data are used both measures reduce to the same statistic, Δ^*, which is the average taxonomic distance between two randomly selected species (Magurran 2004). To interpret the taxonomic diversity (Δ) and distinctness (Δ^*) the following null hypothesis (H_o) that the taxonomic distinctness and or taxonomic diversity of a biome is not significantly different from the total list. While the alternate hypothesis (H_A) is the taxonomic distinctness and or taxonomic diversity is significant from the total list (Clarke and Warwick, 2001a). This is tested by repeatedly sub sampling species lists of size *m* at random from the total list and used to construct an approximate 95% confidence interval across a *m* value, if the estimated Δ or Δ^*fall below or above the confidence interval then I will reject H_o, and accept H_A. If the values fall between the 95% confidence interval as suggested by Clarke and Warwick (2001a), then H_o is accepted that the biome is not significantly different from the total list.

RESULTS

SPECIES RICHNESS

The Savanna biome reported the highest bat species richness with 57 species being recorded from this biome, which comprises 93% of the total species richness recorded from South Africa, Lesotho and Swaziland. This was followed by the Azonal biome which recorded 45 species comprising 73% of the bat species richness for South Africa, Lesotho and Swaziland. The Grassland biome recorded 39 species comprising 63% of the total species richness. The Forest biome recorded 32 species comprising 52% of the total species richness for South Africa, Lesotho and Swaziland. The Indian Ocean Coastal Belt recorded 31 species comprising 50% of the species richness for South Africa, Lesotho and Swaziland.

ESTIMATES OF SPECIES RICHNESS

There was insufficient data to calculate species richness estimates for the Desert biome. Therefore, species richness estimates were calculated for nine of the 10 biomes. The estimated species richness for the nine biomes ranged between 11 species in the Albany to a maximum of 91 species in the Savanna biome. The large range difference in the species estimates indicated above is due to reporting the range of all models combined. Chao and Shen (2010) suggest that for the Incident-based Coverage estimate (ICE) that if the covariant is above 0.8 then the bias corrected form of the model should be used. Rejecting the data from those models where the covariant are above 0.8 (Table 3), the estimated mean species richness for the nine biomes ranged from 11 in the Albany to a maximum of 67 in the Savanna biome. The Albany had 11 species recorded with species estimates ranging between 11 – 12, then in increasing order the Nama-Karoo biome with 12 species being recorded and species estimates ranging between 13 – 25, Succulent-Karoo biome with 13 species being recorded and species estimates ranging between 15 – 30, Fynbos biome with 17 species being recorded and estimates ranging between 18 – 25, Indian Ocean Coastal Belt biome with 31 species being recorded and estimates ranging between 32 – 36, Forest biome with 32 species being recorded and estimates ranging between 37 – 46, Grassland biome with 39 species being recorded and estimates ranging between 42 – 54, Azonal biome with 45 species being recorded and estimates ranging between 49 – 63 and the Savanna biome with 57 species being recorded and estimates ranging between 59 – 67.

The results of the homogeneous model (Table 3), where it is assumes that the detection probabilities of the species are equal, indicate that the Albany biome (*Est*: 11.6 species) had the lowest species richness, then Nama-Karoo (*Est*: 13.8 species), Succulent-Karoo (*Est*: 15.5 species), Fynbos (*Est*: 18.3 species), Indian Ocean Coastal Belt (*Est*: 32.9 species), Forest (*Est*: 37.9 species), Azonal (*Est*: 51.2 species) and the highest species richness being recorded from the Savanna (*Est*: 59.8 species).

The results of the Chao2 and Chao2-bc (Table 3) indicated that the lowest species richness estimator based on undetected species was the Albany (*Est*:11.9 species), then Nama-Karoo (*Est*: 16.9 species), Succulent-Karoo (*Est*: 20.2 species), Fynbos (*Est*: 24.8 species), Indian Ocean Coastal Belt (*Est*: 32.9 species), Forest (*Est*: 45.6 species), Azonal (*Est*: 49.5 species), Grassland (*Est*: 54.1 species) and the highest being the Savanna (*Est*: 64.1 species). The Chao2-bc is used for the Nama-Karoo and Succulent-Karoo as the covariant is above 0.8 therefore these two biomes were highly heterogeneous and Chao and Shen (2010) suggest that the Chao2-bc should be used.

The Incident-based Coverage estimates (Model(h)) (ICE) assume that the detection probabilities are heterogeneous among species. The covariant for ICE for the Nama-Karoo and Succulent-Karoo were above 0.8 (Table 3), therefore these two biomes were highly heterogeneous. Due to this the Model(h)-1 outputs were used (Chao and Shen, 2010). The lowest ICE species richness estimator based on the Model(h) was the Albany (*Est*: 11.8 species), Fynbos (*Est*: 20.0 species), Succulent-Karoo (*Est*: 24.3 species), Nama-Karoo (*Est*: 24.4 species), Indian Ocean Coastal Belt (*Est*: 35.0 species), Forest (*Est*: 42.4 species), Grassland (*Est*: 48.0 species); Azonal (*Est*: 54.5 species), and the highest Savanna (*Est*: 64.7 species) (Table 3).

The Incident-based Coverage estimates Model(th) (ICE) assumes that the detecting probability varies not only among species but also among samples. The Model(th) analysis (Table 3), yielded high covariant values for the Nama-Karoo and Succulent-Karoo biomes again (< 0.8), indicating the two biomes were highly heterogeneous, requiring the adoption of the Model(th)-1 outputs (Chao and Shen, 2010). The lowest species richness estimator calculated for the Model(th) was the for the Albany biome (*Est*: 11.9 species), with the Succulent-Karoo (*Est*: 24.8 species), Nama-Karoo (*Est*: 25.0 species), Indian Ocean Coastal Belt (*Est*: 35.2 species), Forest (*Est*: 42.9 species), Grassland (*Est*: 48.3 species), Azonal (*Est*: 58.8 species) biomes increasing, and again the highest detecting probability was for the Savanna (*Est*: 64.9 species) (Table 3).

The results of the various models (Table 3) consistently showed that the Albany biome had the lowest estimates of species richness. While the Nama-Karoo and Succulent-Karoo, shared second lowest species richness estimates and the Fynbos third across the various incident based estimate (ICE) models. The Azonal and Savanna biomes consistently had the highest estimates of species richness, but swapped places depending on the model used.

Using the estimates (*Est*) (Table 3) from the various applicable models, and applying the bias corrected model data only when covariant were above 0.8 (Chao and Shen, 2010). A mean estimate was derived and rounded up to create a full species. This indicates that the Albany biome contains the lowest species richness with 12 species expected, then Fynbos and Nama-Karoo (21 species), Succulent-Karoo (22 species), Indian Ocean Coastal Belt (34 species), Forest (43 species), Grassland (49 species), Azonal (54 species) and Savanna (64 species).

SAMPLE COMPLETENESS

Based on calculations of mean sample completeness in ascending order the Albany biome is 93.2% complete followed by the Indian Ocean Coastal Belt biome (91.1%), Savanna biome (89.9%), Azonal biome (84.1%), Fynbos biome (81.5%), Grassland biome (80.7%), Forest biome (75.8%), Succulent-Karoo biome (61.3%), and Nama-Karoo biome (59.9%). These results suggest that additional sampling is needed in the Nama-Karoo and Succulent Karoo biomes as these are under sampled. Keeping in mind that the Desert biome had insufficient data to compute estimates of species richness therefore sample completeness could not be calculated. Therefore the Desert biome is in urgent need of further sampling. Further breakdown per biome on the sample results are given in the discussion on each of the biomes.

Table 3. Species richness recorded for each of the 10 biomes together with the results of incident estimators calculated in SPADE, where SE: Standard error, CI: Confidence interval, ICE: Incidence Coverage Estimation, CV: Covariance. Model results in bold should be ignored (see notes below table for further information). See Chao and Shen (2010) for additional descriptions of the various models computed.

Biome	**Species richness**	**Homogeneous Model Est (±SE) 95% CI**	**Chao2 Est (±SE) 95% CI**	**Chao2-bc Est (±SE) 95% CI**	**Model(h) or ICE Est (±SE) 95% CI Est. CV (rare)**	**Model(h)-1 or ICE-1 Est (±SE) 95% CI Est. CV**	**Model(th) or ICE Est (±SE) 95% CI Est. CV**	**Model(th)-1 or ICE Est (±SE) 95% CI Est. CV**
Number Obs (*D*)	-	11	45	-	32	17	39	31
Number of QDS (*t*)	-	20	26	-	31	47	205	27
CV$_{infreq}$	-	0.37	0.527	-	0.559	0.64	0.657	0.598
Albany	11	11.6 (±0.9) 11.1-16.1	11.9 (±1.8) 11.1-21.6	11.3 (±1.2) 11.0-19.2	11.8 (±0.8) 11.2-15.3 0.370	**11.9 (±0.9)** **11.2-15.4** **0.407**	11.9 (±1.4) 11.1-19.1 0.447	**12.0 (±1.6)** **11.1-20.2** **0.494**
Azonal	44	51.2 (±3.4) 47.2-61.9	49.5 (±3.5) 46.2-62.1	48.9 (±3.3) 46.0-62.1	54.5 (±3.6) 49.7-64.4 0.527	**56.0 (±4.6)** **50.0-69.1** **0.617**	58.8 (±7.4) 50.2-81.9 0.756	**62.6 (±10.5)** **51.0-96.7** **0.911**
Desert	5	-	-	-	-	-	-	-
Forest	31	37.9 (±3.4) 34.0-48.9	45.6 (±10.6) 35.7-81.8	42.8 (±8.4) 34.8-73.4	42.4 (±2.7) 38.4-49.1 0.559	**45.0 (±3.1)** **40.1-52.7** **0.692**	42.9 (±6.7) 35.6-64.9 0.587	**45.8 (±9.3)** **36.2-77.8** **0.730**
Fynbos	17	18.3 (±1.4) 17.2-24.4	24.8 (±11.4) 18.0-80.5	19.9 (±4.8) 17.3-44.8	20.0 (±1.6) 18.2-25.0 0.640	**20.8 (±1.9)** **18.5-26.5** **0.766**	20.3 (±3.3) 17.6-34.0 0.678	**21.2 (±4.6)** **17.7-41.1** **0.816**
Grassland	39	42.7 (±2.5) 40.1-51.4	54.1 (±12.4) 42.7-100.8	49.9 (±9.3) 41.6-85.6	48.0 (±2.7) 44.1-55.0 0.657	**51.0 (±3.3)** **46.0-59.4** **0.816**	48.3 (±6.0) 41.9-68.8 0.676	**51.5 (±9.0)** **42.5-83.2** **0.843**
Indian Ocean	30	32.9 (±1.7) 31.4-39.5	32.9 (±2.2) 31.3-42.5	32.4 (±2.0) 31.2-41.9	35.0 (±1.8) 32.7-40.5 0.598	**35.6 (±2.0)** **33.1-41.5** **0.683**	35.2 (±3.4) 32.1-47.8 0.636	**36.0 (±4.2)** **32.2-52.0** **0.729**
Nama-Karoo	12	13.8 (±1.9) 12.3-21.8	24.2 (±16.8) 13.6-103.9	16.9 (±6.7) 12.7-48.7	**19.2 (±2.6)** **15.6-26.3** **0.960**	24.4 (±5.7) 17.2-41.3 1.344	**19.4 (±7.1)** **13.5-48.1** **0.983**	25 (±15.1) 14.1-91.5 1.384
Savanna	56	59.8 (±2.1) 57.8-67.2	64.1 (±5.9) 58.7-86.3	62.6 (±5.1) 58.2-82.7	64.7 (±2.6) 61.0-71.7 0.675	**66.8 (±3.1)** **62.4-74.8** **0.806**	64.9 (±5.0) 59.5-81.8 0.688	**67.1 (±7.0)** **60.0-91.5** **0.823**
Succulent-Karoo	13	15.5 (±2.3) 13.5-24.5	30.3 (±22.7) 15.4-136.1	20.2 (±8.7) 14.1-59.2	**20.3 (±2.4)** **16.9-26.6** **0.817**	24.3 (±4.4) 18.4-36.7 1.107	**20.5 (±6.8)** **14.6-47.4** **0.838**	24.8 (±12.7) 15.1-78.9 1.139

[1] CV_{infreq} is greater than 0.8, which require corrected Chao2 and Model(h)-1 models to reduce bias (Chao and Shen, 2010).

PAIR WISE SIMILARITY INDICES

The results of the Jaccard and Sørensen pair wise indices (Table 4 and Figure 1) show similar results to each other. Three distinct clusters are presented, with the Albany, Fynbos and Succulent-Karoo cluster, the Desert and Nama-Karoo cluster are separated, while the third major cluster can be split into two additional sub clusters namely the Azonal, Savanna and Grassland, and the other the Forest and Indian Ocean Coastal Belt clusters. This clustering pattern supports the suggestion by Lennon *et al.* (2001) who suggested that the patterns observed in the Jaccard and Sorensen indices may be based on the species richness than on actual similarity between the assemblages. This is observed when comparing the species richness for each of the biomes, and how they cluster together on the dendogram (Figure 1). This clustering pattern follows the species richness of the various biomes and does not necessarily give a true reflection of similarity between the biomes. Therefore, the use of the Jaccard and Sørensen measures may not be showing similarity between the biomes but rather an artifact of the species richness between the various biomes, therefore the patterns observed may be based more on the species richness than on actual similarity between the assemblages. To overcome the issue of marked differences in species richness between the samples the Lennon *et al.* (2001) similarity measure (but is interpreted as dissimilarity (Magurran 2004)), which focuses on differences in the composition of the samples being compared was used. The Lennon et al (2001) dendogram (Figure 2) shows the Desert and Nama-Karoo create a very clear cluster being most dissimilar to one another, while the Indian Ocean Coastal Belt is clearly similar to the remaining biomes. The Albany and Azonal are shown to be the most dissimilar to one another in the Lennon *et al.* (2001) dendogram (Figure 2). The clustering of the Desert biome to the Nama-Karoo may be an artifact of under sampling of this biome, or alternatively this biome together with the Nama-Karoo may be the most similar in both species richness (Jaccard and Sørensen) and dissimilar in composition (Lennon *et al.* (2001)).

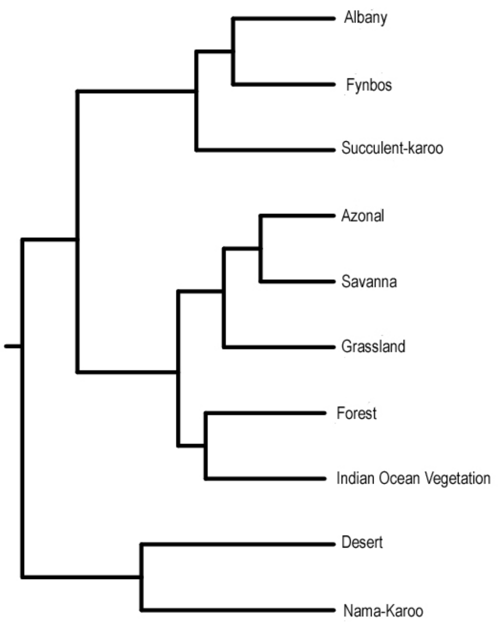

Figure 1. Dendogram based on the pair wise similarity matrix for the Jaccard and Sørensen (Table 4) for each of the biomes types.

Table 4. Pair wise similarity matrix for the Jaccard and Sørensen incidence comparing each biome to one another, calculated in SPADE.

		Jaccard incidence									
		Albany	**Azonal**	**Desert**	**Forest**	**Fynbos**	**Grassland**	**Indian Ocean**	**Nama-Karoo**	**Savanna**	**Succulent-Karoo**
Sørensen	**Albany**	1.0000	0.2500	0.0667	0.3030	0.6471	0.2821	0.3125	0.2105	0.1964	0.6000
	Azonal	0.4000	1.0000	0.0889	0.5833	0.2979	0.5962	0.4151	0.2444	0.7241	0.2667
	Desert	0.1250	0.1633	1.0000	0.1212	0.1579	0.1000	0.0286	0.4167	0.0702	0.2857
	Forest	0.4651	0.7368	0.2162	1.0000	0.3611	0.5435	0.5750	0.2222	0.5439	0.3235
	Fynbos	0.7857	0.4590	0.2727	0.5306	1.0000	0.4000	0.3333	0.3810	0.2586	0.5000
	Grassland	0.4400	0.7470	0.1818	0.7042	0.5714	1.0000	0.4583	0.2439	0.6379	0.3000
	Indian Ocean	0.4762	0.5867	0.0556	0.7302	0.5000	0.6286	1.0000	0.1622	0.5000	0.2571
	Nama-Karoo	0.3478	0.3929	0.5882	0.3636	0.5517	0.2439	0.2791	1.0000	0.1724	0.4706
	Savanna	0.3284	0.8400	0.1311	0.7045	0.4110	0.7789	0.6667	0.2941	1.0000	0.2105

	Jaccard incidence									
	Albany	**Azonal**	**Desert**	**Forest**	**Fynbos**	**Grassland**	**Indian Ocean**	**Nama-Karoo**	**Savanna**	**Succulent-Karoo**
Succulent-Karoo	0.7500	0.4211	0.4444	0.4889	0.6667	0.4615	0.4091	0.6400	0.3478	1.0000

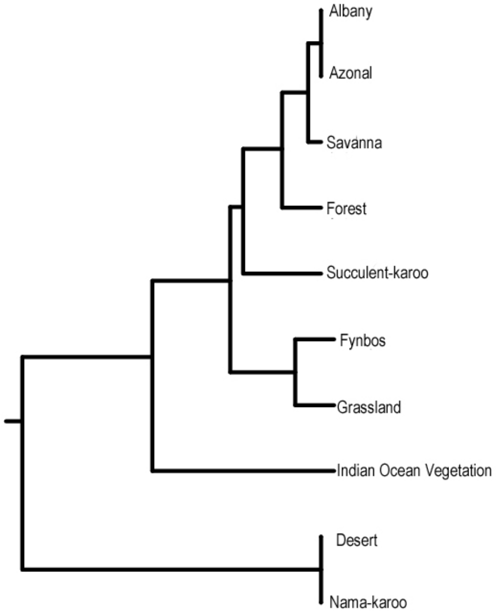

Figure 2. Dendogram based on the similarity matrix (Table 5) for the Lennon *et al.* (2001) indices' for each of the biomes types.

Table 5. Pair wise similarity matrix for the Lennon *et al.* (2001) indicies comparing each biome.

	Albany	**Azonal**	**Desert**	**Forest**	**Fynbos**	**Grassland**	**Indian Ocean**	**Nama-Karoo**	**Savanna**	**Succulent-Karoo**
Albany	1.0000	1.0000	0.2000	0.9091	1.0000	1.0000	0.9091	0.3636	1.0000	0.8182
Azonal	-	1.0000	0.8000	0.8750	0.8235	0.7949	0.7097	0.9167	0.9545	0.9231
Desert	-	-	1.0000	0.8000	0.6000	0.8000	0.2000	1.0000	0.8000	0.8000
Forest	-	-	-	1.0000	0.7647	0.7813	0.7419	0.6667	0.9688	0.8462
Fynbos	-	-	-	-	1.0000	0.9412	0.7059	0.6667	0.8824	0.7692
Grassland	-	-	-	-	-	1.0000	0.7097	0.8333	0.9487	0.9231

	Albany	Azonal	Desert	Forest	Fynbos	Grassland	Indian Ocean	Nama-Karoo	Savanna	Succulent-Karoo
Indian Ocean	-	-	-	-	-	-	1.0000	0.5000	0.9355	0.6923
Nama-Karoo	-	-	-	-	-	-	-	1.0000	0.8333	0.6667
Savanna	-	-	-	-	-	-	-	-	1.0000	0.9231
Succulent-Karoo	-	-	-	-	-	-	-	-	-	1.0000

MULTIPLE INCIDENCE-BASED CALCULATION

The multiple incidence-based calculations take into account relative abundance or frequency data between the assemblages. Biomes that have similar survey or sampling effort (e.g. number of QDS sampled), would cluster closer together. This is observed in the pair wise similarity matrix for the Bray-Curtis (Table 6) and the associated dendogram (Figure 3) which shows that the assemblages within the Desert biome are least similar (lowest sample effort/relative abundance) to other biomes, while those of the Albany, Succulent-Karoo, Fynbos and Nama-Karoo biomes have similar relative abundance (based on number of QDS within the biome assemblage (Table 2), and these are lower than the relative abundance within the Azonal, Forest, Indian Ocean Coastal Belt biome clade. The Grassland and Savanna biomes relative abundance were most similar to one another, and were the most distinct from the other biome assemblages.

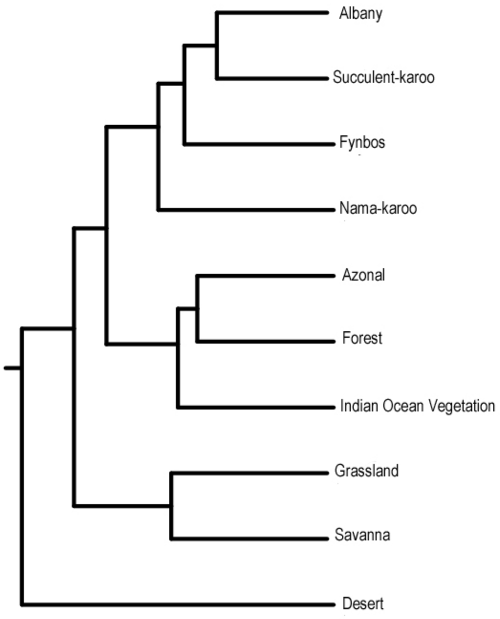

Figure 3. Dendogram of the similarity matrix for the data contained in (Table 6) for the Bray-Curtis multiple incidence-based calculations

Table 6. Pairwise similarity matrix for the Bray-Curtis multiple incidence-based calculations, comparing each of the biomes.

	Albany	**Azonal**	**Desert**	**Forest**	**Fynbos**	**Grassland**	**Indian Ocean**	**Nama-Karoo**	**Savanna**	**Succulent-Karoo**
Albany	1.0000	0.4218	0.0444	0.4355	0.5352	0.1506	0.3298	0.3585	0.0707	0.6512
Azonal		1.0000	0.0714	0.5864	0.3732	0.2899	0.4784	0.3931	0.1815	0.4314
Desert			1.0000	0.0899	0.0561	0.0181	0.0131	0.1408	0.0079	0.1569
Forest				1.0000	0.3441	0.2490	0.5776	0.2133	0.1523	0.3692
Fynbos					1.0000	0.3259	0.2960	0.4762	0.1552	0.5541
Grassland						1.0000	0.3038	0.2262	0.5194	0.1570
Indian Ocean							1.0000	0.2243	0.2426	0.2887
Nama-Karoo								1.0000	0.1194	0.5357
Savanna									1.0000	0.0779
Succulent-Karoo										1.0000

TAXONOMIC DIVERSITY AND DISTINCTNESS

The Grassland, Nama-Karoo and Savanna biomes contribute to higher taxonomic diversity, while the Albany, Azonal, Fynbos, Nama-Karoo and Succulent-Karoo biomes contain lower species richness generally but represent a higher taxonomic distinctness from the chiroptera taxa in the Grassland and Savanna biomes (Table 7). The Desert, Forest and Indian Ocean Coastal Belt biomes were found to be neither taxonomically distinct nor diverse when compared to the remaining biomes. The bat assemblage within the Nama-Karoo biome are both taxonomically diverse and distinct from chiroptera species found within the other nine biomes, requiring a greater focus on conservation actions for bat species located within this biome.

Table 7 Taxonomic diversity (Δ) and taxonomic distinctness (Δ*), with the 95% confidence intervals'. Bold indicates where the H_o is rejected and H_A accepted. H_o: Taxonomic diversity (Δ) and or taxonomic distinctness (Δ*) is not significantly different from the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland). H_A: The taxonomic diversity (Δ) and or taxonomic distinctness (Δ*) is significant from the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

	Diversity Δ 95% CI	**Distinctness Δ^* 95% CI**
Albany	2.621 2.442 - 2.723	**2.899** **2.638-2.869**
Azonal	2.636 2.544 - 2.701	**2.702** **2.712-2.831**

	Diversity **Δ** **95% CI**	**Distinctness** **Δ^*** **95% CI**
Desert	3 1.800-3.000	3 2.000-3.000
Forest	2.656 2.530-2.703	2.75 2.692-2.838
Fynbos	2.577 2.550-2.697	**2.845** **2.710-2.825**
Grassland	**2.482** **2.596-2.665**	2.803 2.746-2.804
Indian Ocean	2.634 2.554-2.682	2.777 2.717-2.817
Nama-Karoo	**2.426** **2.510-2.719**	**2.936** **2.676-2.849**
Savanna	**2.649** **2.607-2.646**	2.772 2.758-2.786
Succulent-Karoo	2.524 2.511-2.728	**2.864** **2.677-2.857**

The Nama-Karoo was the only biome that was significantly different for both diversity and distinctness measures. While the Desert, Forest and Indian Ocean biomes were not significantly different for either taxonomic diversity or taxonomic distinctness (see methods or Table 3 for further information on how significance is established).

BIOME ASSESSMENT

Albany biome

Eleven species have been recorded as occurring within the Albany biome, comprising 18% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland (Table 2). The estimates of species richness ranged between 11 and 12 species (Table 3), which indicates that a single additional species may be recorded, from within this biome. The Albany and Fynbos biomes were the most similar based on species richness (Figure 1 and Table 4). While the Albany and Azonal were the most different in composition (Figure 2 and Table 5). The relative abundance of assemblages was most similar to the Succulent-Karoo, Fynbos, and Nama-Karoo biomes (Figure 3 and Table 6). The Albany biome was found to be taxonomically distinct, but not taxonomically diverse when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

Azonal biome

Forty-five species have been recorded as occurring within the Azonal biome comprising 73% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland (Table 2). The estimates of species richness calculated in this study ranged between 49 and 63 species (Table 3), indicating a potential of 4 -18 additional species still to be recorded from this biome. This indicates that the estimates based on current ACR (2011) data for the Azonal biome is likely only 71 -91% complete. The Azonal and Savanna biomes were the most similar based on species richness, then the Grassland biome (Figure 1 and Table 4). The Azonal and Albany biomes were the most different in composition (Figure 2 and Table 5). The relative abundance of species assemblages was most similar to the Indian Ocean Coastal Belt biome (Figure 3 and Table 6). The Azonal biome was found to be taxonomically distinct, but not taxonomically diverse when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

Desert biome

Five species have been recorded as occurring within the Desert biome comprising 8% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland (Table 2). The estimates of species richness could not be calculated due to insufficient data. The Desert and Nama-Karoo biomes were the most similar based on species richness and were unique from the other biomes (Figure 1 and Table 4). Interestingly, the Desert and Nama-Karoo biomes were also shown to be the most different in composition (Figure 2 and Table 5). The Desert biome was found to be neither taxonomically distinct, nor taxonomically diverse when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

Forest biome

Thirty-two species have been recorded as occurring within the Forest biome comprising 52% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland (Table 2). The estimates of species richness ranged between 37 and 46 species (Table 3), indicating a potential of 5 - 14 additional species that may still be recorded from this biome. This indicates that the sampling within the Forest biome is only 69 -86% complete. The Forest and Indian Ocean Coastal Belt biomes were the most similar based on species richness (Figure 1 and Table 4). While the Forest biome composition, was different to those of the Albany, Azonal and Savanna biomes (Figure 2 and Table 5). The Forest biome was found to be neither taxonomically distinct nor taxonomically diverse when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

Fynbos biome

Seventeen species have been recorded as occurring within the Fynbos biome comprising 27% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland (Table 2). Gelderblom *et al* (1995) recognized 18 species as occurring in the Fynbos biome, the lower species richness in this study is due to the misidentification of *Chaerophon pumila* by Rautenbach and Nel (1978) and corrected by Jacobs and Fenton (2001) as *Sauromys petrophilus*. The estimates of species richness ranged between 18 and 25 species (Table 3), indicating a potential of 1 - 8 additional species that may still be recorded from this biome. This indicates that the sampling within the Fynbos biome is only 68 - 94% complete. The Fynbos and Albany biomes were the most similar based on species richness, then with the Succulent-Karoo biome (Figure 1 and Table 4). While the Fynbos biome showed most difference in composition with the Grassland biome (Figure 2 and Table 5). The relative abundance of species assemblages was most similar to the Albany, Succulent-Karoo and Nama-Karoo biomes (Figure 3 and Table 6). The Fynbos biome was found to be taxonomically distinct, but not taxonomically diverse when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

Grassland biome

Thirty-nine species have been recorded as occurring within the Grassland biome comprising 63% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland (Table 2). Gelderblom *et al* (1995) recognized 31 species as occurring in the Grassland biome, unfortunately Gelderblom *et al.* (1995) did not indicate what species occurred; therefore no comparisons may be made between the two studies. The estimates of species richness ranged between 42 and 54 species (Table 3), indicating a potential of 3 -15 additional species that may still be recorded from this biome. This indicates that the sampling within the Grassland biome is only 72 - 92% complete. The Grassland biome were the most similar based on species richness with those of the Azonal and Savanna biomes (Figure 1 and Table 4). While the Grassland biome showed the most difference in composition with the Fynbos biome (Figure 2 and Table 5). The relative abundance of species assemblages was most similar to the Savanna biome (Figure 3 and Table 6). The Grassland biome was found to be taxonomically diverse but not taxonomically distinct when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

Indian Ocean Coastal Belt biome

Thirty-one species have been recorded as occurring within the Indian Ocean Coastal Belt biome, comprising 50% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland (Table 2). The estimates of species richness ranged between 32 and 36 species (Table 3), indicating a potential of 1 - 5 additional species that may still be recorded from this biome. This indicates that the sampling within the Indian Ocean Coastal Belt biome is only 86 - 96% complete. The Indian Ocean Coastal Belt biome were the most similar based on species richness with the Forest biome (Figure 1 and Table 4). The composition of the Indian Ocean Coastal Belt biome showed that it was not different in composition from the other biomes, except those of the Desert and Nama-Karoo biomes (Figure 2 and Table 5). The relative abundance of species assemblages was most similar to the Azonal biome (Figure 3 and Table 6). The Indian Ocean Coastal Belt biome was found to be neither taxonomically diverse nor taxonomically distinct when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

Nama-Karoo biome

Twelve species have been recorded as occurring within the Nama-Karoo biome, comprising 19% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland (Table 2). Gelderblom *et al*

(1995) recognized 17 species as occurring in the Nama-Karoo biome. The loss of 5 species from the Nama-Karoo is due to records that were attributed to this biome by Gelderblom *et al.* (1995), but in this study were reassigned to another biome (Azonal biome) following the classification of Mucina and Rutherford (2006). The estimates of species richness ranged between 13 and 25 species (Table 3), indicating a potential of 1 - 13 additional species that may still be recorded from this biome. This indicating that the sampling within the Nama-Karoo biome is only 48 -92% complete. The Nama-Karoo and Desert biomes were the most similar based on species richness and were unique from the other biomes (Figure 1 and Table 4). The Nama-Karoo and Desert biomes were also the most different in composition (Figure 2 and Table 5). The relative abundance of species assemblages was most similar to the Albany, Succulent-Karoo and Fynbos biomes (Figure 3 and Table 6). The Nama-Karoo biome was found to be both taxonomically diverse and taxonomically distinct when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

Savanna biome

Fifty-seven species have been recorded as occurring within the Savanna biome, comprising 93% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland. Gelderblom *et al* (1995) recognized 51 species as occurring in the Savanna biome. The estimates of species richness ranged between 59 and 67 species (Table 3), indicating a potential of 2 - 10 additional species that may still be recorded from this biome. This indicates that the sampling within the Savanna biome is only 85 - 96% complete. The Savanna and Azonal biomes were the most similar based on species richness then with the Grassland biome (Figure 1 and Table 4). The Savanna biome was most different in composition from those of the Albany and Azonal biomes (Figure 2 and Table 5). The relative abundance of species assemblages was most similar to the Grassland biome (Figure 3 and Table 6). The Savanna biome was found to be taxonomically diverse but not taxonomically distinct when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

Succulent-Karoo biome

Thirteen species have been recorded as occurring within the Succulent-Karoo biome, comprising 21% of the total chiropteran species diversity for South Africa, Lesotho and Swaziland. Gelderblom *et al* (1995) recognized 12 species as occurring in the Succulent-Karoo biome. The loss of 1 species from the Succulent-Karoo is due to records that were attributed to this biome by Gelderblom *et al.* (1995), but in this study were reassigned to another biome (Azonal biome) following the classification of Mucina and Rutherford (2006). The estimates of species richness ranged between 15 and 30 species (Table 3), indicating a potential of 2 and 17 additional species still from this biome. This indicates that the sampling within the Succulent-Karoo biome is only 43 - 86% complete. The Succulent-Karoo biome was the most similar based on species richness with both the Albany and Fynbos biomes (Figure 1 and Table 4). The Succulent-Karoo biome was the most different in composition from those of the Albany, Azonal, Savanna and Forest biomes (Figure 2 and Table 5). The relative abundance of species assemblages was most similar to the Albany, Fynbos and Nama-Karoo biomes (Figure 3 and Table 6). The Succulent-Karoo biome was taxonomically distinct, but not taxonomically diverse when compared to the total list (being all species occurring across all biomes within South Africa, Lesotho and Swaziland).

DISCUSSION

Knowledge of species distributions and process that drive them facilitate conservation (Gelderblom *et al.* 1995). Productivity, area, climatic and evolutionary history have been identified as possible factors that influence species richness (Hurlbert and Haskell 2003; Thuiller *et al.* 2006; Schoeman *et al.* 2013). But there is little consensus about relative importance of these factors (Pianka 1966; Rohde 1992; Ricklefs and Schluter 1993; Hurlbert and Haskell 2003; Thuiller *et al.* 2006; Field *et al.* 2009). In South Africa it has been suggested that patterns of species richness are largely determined by rainfall as mediated by vegetation (Turpie and Crowe 1994; Rutherford *et al.* 2006; Qian *et al.* 2009). Nel (1975) found a positive correlation between rainfall and species richness for mammalian taxa in South Africa on a latitudinal basis. While, Findley (1993) showed that species richness is correlated with area surveyed. This would support the Savanna biome having the highest bat species richness (Rautenbach, 1978, 1982; Gelderblom *et al.*, 1995; this study), as this is the largest biome in South Africa (Mucina and Rutherford 2006a). But, it does not explain the Azonal biome which is one of the smallest biomes in South Africa (Mucina and Rutherford 2006a), but contained the second highest bat species richness, after the Savanna biome. Species-energy theory suggests that sites with greater available energy are able to support more individual organisms and, hence species (Connell and Orias 1964; Brown 1981; Wright 1983; Hurlbert and Haskell 2003). This may explain the high species richness of the Azonal biome.

The Azonal biome is associated with major river systems and their associated flood plains and extends in both a longitudinal and latitudinal direction within South Africa (Mucina and Rutherford 2006a). Majority of bat surveys focus capture along rivers or near water (Kunz *et al.* 2009). Monadjem and Reside (2008) showed that riverine systems in Swaziland had higher species richness than that of the surrounding landscape. This higher species richness of riparian vegetation compared to the surrounding landscape has also been reported in other studies; USA (Ober and Hayes 2008; Johnson *et al.* 2010), Europe (Lundy and Montgomery 2009) and Japan (Akasaka *et al.*, 2009, 2010).

Patten (2004) found that for North American bat families there was a strong correlation with productivity, than that of size of area. There has been much debate in the literature around the relationship of productivity and species richness (Waide *et al.* 1999; Mittelbach *et al.* 2001). Riverine systems generally have a higher productivity than the surrounding landscape (Schiemer *et al.* 2001; Mitsch *et al.* 2005), therefore this may explain the reason for high species richness within the Azonal biome. Schoeman *et al.* (2013) found strong support for habitat heterogeneity and climate/productivity/energy hypotheses as predictors' of bats species richness in Southern Africa. Further investigations at different scales may be needed to examine productivity and bat species richness within the various biomes, as it may be found that areas of higher productivity will support a greater number of species (Waide *et al.* 1999; Mittelbach *et al.* 2001; Schoeman *et al.* 2013). Direct comparison with the results of Gelderblom *et al.* (1995) was not possible. The main issue being that Gelderblom *et al.* (1995) used the classification and spatial distribution of the biomes following Rutherford and Westfall (1987), while this study followed Mucina and Rutherford (2006). The recognition of an addition of three biomes (Mucina and Rutherford, 2006) within the South African, Lesotho and Swaziland landscape meant that some of the biomes recognized by Rutherford and Westfall (1987) were split. The Azonal biome recognized by Mucina and Rutherford (2006) is a case in point. It is likely that in the three dryer biomes of Desert, Nama-Karoo and Succulent-Karoo, survey sites were selected along perennial or non-perennial watercourses. The majority of the major river systems within these dryer biomes are recognized by Mucina and Rutherford (2006) as a distinct biome (Azonal biome). Further investigations are needed to examine the relationship of the Azonal biome within the dryer regions, with a focus on the species richness of the adjacent biomes (Azonal vs Nama-Karoo and Azonal vs Succulent-Karoo).

Results from this study suggest that the Albany biome was the only biome within South Africa, Lesotho and Swaziland that has been sufficiently sampled for its bat assemblage. This is possibly due to a higher heterogeneity across the samples within the Albany biome, which is not observed within the other biomes. Additional surveys are needed within the Desert biome, as there was insufficient data to calculate species richness estimates, therefore could not determine the completeness of the bat species found within this biome. In all pair wise calculations the Desert biome is an outlier, and this may be an artifact of insufficient sampling and therefore should be interpreted with some caution. The Nama-Karoo and Succulent Karoo are also in need of additional surveys as these two biomes had the least known confidence (greatest range of estimates based on the minimum and maximum estimates across the various models), where more than 50% of the species present may only be known. This supports the recommendations of Gelderblom *et al.* (1995), that greater sampling effort was needed in the dryer interior of South Africa (Desert, Nama-Karoo and Succulent-Karoo).

No endemic bat taxa (taxa only recorded within a single biome) were observed for any of the 10 biomes reported within this study. Gelderblom *et al.* (1995) found higher endemism in other mammalian taxa from isolated biomes (e.g. Fynbos), than that found in the larger Savanna biome.

CONCLUSIONS

The establishment of protected areas within the Grassland, Nama-Karoo and Savanna biomes will contribute to securing higher taxonomic diversity (DEAT 2008), while the Albany, Azonal, Fynbos, Nama-

Karoo and Succulent-Karoo biomes contain lower species richness but represent a higher taxonomic distinctness from the chiroptera taxa in the Grassland and Savanna biomes. Conservation efforts within the Desert, Forest and Indian Ocean Coastal Belt biomes, would not contribute significantly to the conservation of bat species within South Africa.

It is recommended that more effort be given to the conservation of areas within the Nama-Karoo biome, and gaining a better understanding of the species within this region, as the species contained within the Nama-Karoo are both taxonomically diverse and distinct from those chiroptera species found within the remaining nine biomes.

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