

Floristic and faunal Cape biochoria: do they exist?

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4.1 Introduction

'There is no dispute that in the south of the continent there are found numerous species, genera and even families . . . that do not occur north. The question that we have to answer is whether these forms constitute a separate . . . unit which is distinct, as a whole, from the other complexes of forms on the African continent?' (Balinsky 1962).

Many authors, over a long period, have remarked on the biotic distinctiveness of the southwestern corner of Africa, both in terms of its flora (Bolus 1886; White 1976; Goldblatt 1978) and its fauna (Moreau 1952; Stuckenberg 1962; Carcasson 1964; Poynton 1964; Holt et al. 2013). Climatically the region is defined by predominantly cool-season (autumn to spring) rainfall and mild temperatures (Chapter 2), and its plant species richness is unmatched in the rest of Africa (Manning and Goldblatt 2012; Snijman 2013). The Cape Floristic Region (CFR; or core Cape flora of Manning and Goldblatt 2012) is a distinctive phytogeographic feature (Goldblatt and Manning 2000), previously recognized as one of six global floral kingdoms on account of its high species richness and endemism (Marloth 1908; Good 1974; Takhtajan 1986; but see Cox 2001 who considered this ranking untenable). More recently, the concept of a Greater Cape Floristic Region (GCFR), incorporating both the CFR and the succulent karoo region, has found favour as a more coherent biogeographical unit (Bayer 1984; Jürgens 1991, 1997; Born et al. 2007). Bayer (1984) contends that once a larger, cool-season rainfall zone is considered, then similarities in floristic composition and their patterns can be better understood 'within which other

factors, such as geology, altitude, latitude, and longitude can operate'. As such, proponents of a GCFR argue for a shared evolutionary and ecological history, largely attributed to a cool-season moisture regime.

It is not clear, however, whether a Greater Cape Region is sensible only in the context of floristic data, or whether the cool-season moisture zone shows biogeographic coherence across a broader sampling of taxonomic groups (i.e. a Greater Cape Biochorion (*sensu* Werger 1978)). A phytochorion or zoochorion is defined geographically as an unranked area with a uniform composition of plant or animal species, respectively (Linder et al. 2005; Olivero et al. 2012). Several studies have explored the chorological divisions across southern Africa using individual taxonomic groups (e.g. plants (Born et al. 2007), frogs (Poynton 1964; Crowe 1990), insects (Carcasson 1964; Endrödy-Younga 1978), and birds (Crowe 1990; De Klerk et al. 2002)). While these studies have generally highlighted the distinctiveness of the predominantly mesic winter rainfall Cape (see also Stuckenberg 1962), some have demonstrated strong faunal links between the Cape and neighbouring succulent karoo areas (e.g. Endrödy-Younga 1978; Vernon 1999), while others have shown a stronger arid link, between areas of succulent karoo and Nama karoo (e.g. Carcasson 1964; De Klerk et al. 2002). Synthesizing the results of these studies to test the hypothesis of shared biotic regions has, however, been complicated by methodological inconsistencies across these plant and animal studies.

Establishing whether both fauna and flora are aligned within core regions of a cool-season moisture zone, and whether the floristic distinctness of the GCFR

is reflected in the biogeographic patterns of other lineages, is of great importance when seeking to understand the historical and ecological development of the biota of the CFR and the adjacent succulent karoo region (Rueda et al. 2010). Delineating and mapping of biogeographic regions utilizing a standardized method provides ‘units of area’ (Hausdorf 2002) to work with when searching for shared historical and evolutionary patterns across taxa—the ‘biogeographic homology’ of Morrone (2001). Biogeographic regions are likely to represent areas of unique evolutionary history and ecological process (Morrone 2009) and, as such, may be areas of high conservation importance (Kreft and Jetz 2010; Olivero et al. 2012). These areas can be interpreted in terms of historical events, such as geomorphic change and climate stability (Chapter 8), or ecological pattern (Wiens and Donoghue 2004; Beck et al. 2012), and they represent appropriate areas within which to investigate drivers of diversification and clade origin (Chapters 5, 7, Rosen 1988; Jetz et al. 2004). Furthermore, by highlighting the biotic diversity and uniqueness of different areas, they can be used to inform conservation and management strategies (Chapter 14), and to assess the threats posed to biodiversity by invasive species (Chapter 12) and climate change (Chapter 13).

In this chapter we provide a systematic and consistent biogeographic evaluation, at the species level, of five very different taxonomic groups (plants, birds, butterflies, reptiles, and frogs). For each taxonomic group, we group units of area together, based on their species similarity, and map these chorological patterns. We use these patterns to test the hypotheses of: (a) a primary (biotic) break dividing South Africa into western (predominantly cool-season rainfall) and eastern (predominately summer rainfall) regions; (b) an extended Greater Cape Biochorion, grouping the CFR and the succulent karoo region; and (c) a more restricted Cape Biochorion, centred on the CFR.

4.2 The biotic uniqueness of the southern tip of Africa

The biogeographic regionalization of an area is determined by its species composition and how different this composition is to that of other regions (Croizat et al. 1974). The GCFR is particularly rich in both species and endemics (Picker and Samways 1996; Kuhlmann 2009; Linder et al. 2010; Manning and Goldblatt 2012; Snijman 2013). The elevated levels of endemism seen for many plant and animal groups suggest narrow ranges for many taxa, and imply a strongly regionalized biota (Rueda et al. 2010). Before we explore common patterns

of regionalization for a Cape Biochorion, we briefly introduce the biotic elements that make the broader Cape region so different from the rest of southern Africa.

4.2.1 Plants

The GCFR, comprising fynbos, renosterveld, thicket, succulent karoo, and enclaves of afrotemperate forest vegetation (Chapter 1), has a documented vascular plant flora of 11 423 species, with species endemism estimated at 77.9%, and generic endemism at 22.2% (248 endemic genera in 1119 genera; Snijman 2013). The region includes four endemic or near-endemic plant families, all confined to fynbos. These are dicots of diverse affinity: Penaeaceae (Myrtales; 23 species), Grubbiaceae (Cornales; three species), Roridulaceae (Ericales; two species), and Geissolomataceae (Crossomatales; one species); ordinal classification following APG3 2009). Asteraceae, typically the largest family in floras of arid and semi-arid regions, is the most richly represented in the region, but the extraordinarily high contributions of Iridaceae, Ericaceae, and Aizoaceae is unique to this region, and consequently in southern Africa as a whole (Manning and Goldblatt 2012; Snijman 2013). Ericaceae, Proteaceae, Restionaceae, and Rutaceae have diversified greatly on the impoverished sandstone soils of the Cape mountain ranges (Manning and Goldblatt 2012). Geophytes comprise an exceptionally high proportion of the flora (c.20%), possibly higher than in any other flora globally. Most geophytes are monocots (notably Iridaceae, Hyacinthaceae, and Amaryllidaceae) but several dicot genera contribute large numbers of geophytes as well, namely *Oxalis* (Oxalidaceae), *Pelargonium* (Geraniaceae), and *Othonna* (Asteraceae; Manning and Goldblatt 2012; Snijman 2013).

4.2.2 Animals

Although less well appreciated, the GCFR harbours diverse and endemic-rich vertebrate and invertebrate faunas. Snakes and lizards represent the largest group of endemic vertebrates in southern Africa (Bauer 1999). The GCFR has 191 reptile species (16 families, 60 genera), of which 45 are considered endemic or near endemic to the region. Amongst these, three groups stand out as having large numbers of endemic taxa: geckos, cordylids, and chameleons. All three appear to be substrate specific, with the geckos and cordylids having distributions that are strongly correlated with particular rocky substrates and the distributions of chameleons being aligned to vegetation types (Chapter 7, Tolley et al. 2006; Herrel et al. 2011).

As has been highlighted repeatedly, the mesic winter rainfall area of the GCFR is globally unique in terms of its amphibian fauna. It has over 57 species, 31 of which are endemic, and two endemic genera. Poynton's (1964) seminal study laid the foundation for future work, emphasizing the high incidence of endemics, and the Gondwanan connections of the amphibian fauna in the mesic winter rainfall area. This area has continued to be of interest to a number of faunal researchers (see Poynton and Broadley 1978; Poynton 1980, 1987, 1992, 1994; Drinkrow and Cherry 1995; Seymour et al. 2001; Alexander et al. 2004; Poynton 2013; Schreiner et al. 2013), and most recently, the mesic winter rainfall area has again been singled out as especially significant for amphibians (Linder et al. 2012; Holt et al. 2013), with high levels of phylogenetic turnover between the mesic winter rainfall area and much of the rest of sub-Saharan Africa.

Although the CFR is relatively depauperate in terms of its bird diversity and endemism (seven endemic species), the endemics that do occur are remarkable with respect to their evolutionary affinities. Two of Africa's oldest songbird lineages (40–55 Ma; Barker et al. 2004; Beresford et al. 2005; Fjeldså and Bowie 2008; Johansson et al. 2008; Jetz et al. 2012), namely the sugarbirds (Promerops: Promeropidae) and rockjumpers (Chaetops: Chaetopidae), each have one of their two species restricted to fynbos (Hockey et al. 2005). Additionally, the orange-breasted sunbird (*Anthobaphes violacea*) is one of Africa's most divergent sunbird lineages (Fjeldså and Bowie 2008) and Victorin's warbler (*Cryptillas victorini*), once thought to be a warbler in the genus *Bradypterus*, is now convincingly placed as a divergent monotypic lineage in the Macrosphenidae (Alström, Olsson et al. 2013). The succulent karoo has few endemics, but shares many bird species with the CFR and the Nama karoo, and, together with the latter, supports one of the greatest regional concentrations of endemic birds in Africa (Allan et al. 1997; Hockey et al. 2005). These arid areas have several endemic larks (Alaudidae), chats (Muscicapidae), and cisticolid warblers (Cisticolidae). They also support three monotypic genera, comprising the cinnamon-breasted warbler (*Euryptila subcinnamomea*), the Namaqua warbler (*Phragmacia substriata*), and the rufous-eared warbler (*Malcorus pectoralis*). The larks and chats comprise some important in situ radiations (e.g. in *Cercomela*, *Certhilauda*, and *Calendulauda*; Chapter 7, Outlaw et al. 2010; Alström, Barnes, et al. 2013), and show strong linkages with species restricted to the north east arid zone of Africa (van Zinderen Bakker 1969; Verdcourt 1969).

The invertebrates, including insects, show exceptional richness and endemism within the GCFR, and

the region is considered as a global centre of diversity and adaptive radiation for several insect groups (see Box 4.1). Moreover, the invertebrate fauna has various unusual components, including a large palaeoendemic element (Stuckenberg 1962; Bowden 1978; Endrödy-Younga 1978, 1988; Picker and Samways 1996; Stuckenberg 2000; Day 2005; Kirk-Sprigs and McGregor 2009; van Noort and Shaw 2009) and a diversity of neoendemics, associated with the adaptive radiations of various pollinator groups (e.g. bees (Kuhlmann 2009), wasps (Gess 1992), flies (Hesse 1969; Usher 1972; Greathead and Evenhuis 2001; Sinclair 2003; Barraclough 2006; Stuckenberg and Kirk-Sprigs 2009), nemopterid lacewings (Tjeder 1967; Sole et al. 2013), Hopliini beetles (Peringuey 1902; Colville 2009), and jewel beetles (Holm 1978; Holm and Gussmann 2004)).

Stuckenberg (1998, 2000) and others (Usher 1972; Barraclough 2006; Karolyi et al. 2012) have highlighted the adaptive responses in mouthpart morphology of anthophilic genera found in at least seven fly families. The high frequency of these adaptations in species from the winter rainfall zone is significant because it indicates that the diversification of the GCFR flora has exerted strong selection on diverse anthophilic insect groups. Other insect and invertebrate taxa, which are either directly (e.g. phytophagous) or indirectly (e.g. predators) linked to plants, also show high biogeographic distinctiveness and/or signatures of adaptive radiation; for example Orthoptera (Dirsch 1965; Naskrecki and Bazelet 2009), Mantophasmatodea (Klass et al. 2003), Coleoptera (Sole et al. 2004), weevils (see Box 4.1), and scorpions (Prendini 2005).

The rich insect diversity of the GCFR is yet to be comprehensively explored (Hesse 1969; Bowden 1978; Kuhlmann 2009); recent research, however, has yielded the discovery of a new insect order whose global centre of diversity is the winter rainfall zone (Picker et al. 2002), as well as the documentation of species radiations (Naskrecki and Bazelet 2009; Sole et al. 2013) and unique adaptive forms (Picker et al. 2012).

4.3 Assessment of the validity of a Cape Biochorion

'The first step toward . . . generalization is to determine what major types of coincident distributions (generalized tracks) recur'. (Croizat et al. 1974)

Early historical biogeographic studies were largely based on the intuitive, often subjective, and non-replicable approach of examining the distribution maps of selected species (Drège 1843; Bolus 1875; Marloth

Box 4.1 Insect elements unique to the Greater Cape Biochorion

Monkey beetles (Scarabaeoidea: Hopliini)

Approximately 1040 described species (51 genera) of monkey beetles are currently known from South Africa, the centre of adaptive radiation for the world's Hopliini. Roughly 63% of the world's species and 38% of the genera are concentrated here. Remarkably, >50% of the world's species occur in the Greater Cape. Two dominant genera, *Heterochelus* (c.300 South African species, 70% of which occur in fynbos vegetation types and 40% in succulent karoo vegetation types) and *Peritrichia* (c.90 South African species, 77% of which occur in fynbos vegetation types and 64% in succulent karoo vegetation types; Box 4.1 Fig 1a), make up approximately 35% of the South African monkey beetle fauna. A remarkably high percentage of species (98%) and genera (80%) are national endemics. Of equal significance is the huge (and globally unique) functional diversity seen in the South African monkey beetles. They pollinate a wide diversity of plants in the winter rainfall zones, with pollination guild structure based on flower colour, shape, and floral resources (Picker and Midgley 1996). The extreme sexual dimorphism in both colour (c.82% of species) and hind-leg size and shape (c.76%) suggests that sexual selection may be a strong driver explaining the huge diversity of species in the Greater Cape (Colville 2009).

Lacewings (Nemopteridae)

The 72 South African species of spoon- and thread-wing lacewings (Box 4.1 Fig 1b) represent 57% of the world's species, 79% of which occur in the Greater Cape and Nama karoo regions. This represents almost half of the world's species (Sole et al. 2013), an indicator of the extensive radiation of the family in the western parts of southern Africa. Approximately 94% of the South African species are endemic (Tjeder 1967). As adults feed on pollen and nectar, they are considered important pollinators in the arid and semi-arid regions.

Heelwalkers (Mantophasmatodea)

This is the most recently discovered order of insects (Klass et al. 2002; Picker et al. 2002), with all 20-odd species restricted to Africa. The majority (12 species) occur in the winter rainfall zone of South Africa (Eberhard et al. 2011). The Austrophasmatidae (Box 4.1 Fig 1c) is endemic to the Greater Cape, and contains nine species (Klass et al. 2003). The recent discovery of these fairly large nocturnal predators in southern Africa underlines the need for more intensive

collection and taxonomic work of the entomofauna of the Greater Cape region in general.

Jumping cockroaches

The world's only jumping cockroach (*Saltoblattella montistabularis*; Box 4.1 Fig 1d) occurs in fynbos (Picker et al. 2012). This remarkable cockroach shows parallel evolution with grasshoppers, in terms of body plan and biomechanics of jumping. In spite of its very unusual appearance, many of the features that make it unique amongst cockroaches are locomotory adaptations, and the insect is probably a close relative of the cosmopolitan and modern subfamily Blatellinae (Djernæs et al. 2011). This evolutionary novelty is likely to be an adaptation for improved locomotion in a vertically stratified habitat such as stands of restios.

Weevils

The largest insect superfamily, Curculionoidea, has an estimated 12 000 species in southern Africa, and a large number of interesting groups in the GCFR. Radiations have occurred in multiple lineages, some mirroring those of their host plants. Examples are: *Sibinia* (Tychiini) and Urodontidae (both on Aizoaceae); *Apioninae* (Apionidae; Box 4.1 Fig 1e) on *Aspalathus* and *Indigofera* (Fabaceae); Gymnetrini on Scrophulariaceae; and Ceutorhynchini on Bruniaceae, *Leucodendron* (Proteaceae), and *Heliophila* (Brassicaceae). These are mostly small weevils (1–3 mm) which associate with the plants' reproductive structures. Although host specificity may still play an important role, radiation also appears to be driven by abiotic factors such as geology. This is the case in the large (mostly 1–3 cm), ground-inhabiting weevils *Brachycerus* (Brachycerinae) and *Epsus* (Microcerinae). There are also ancient lineages of Gondwanan affinity, mostly associated with Proteaceae (Tanaonini, several lineages in Entiminae sensu lato).

Palaeorelictual insect groups

Of great evolutionary and biogeographical interest is the presence of numerous palaeorelictual insect groups in the winter rainfall Cape (e.g. *Leptonyma sericea*; Box 4.1 Fig 1f). These survivors of ancient Gondwanan lineages allow insights into the palaeohistory of the region, helping to explain current speciation patterns of both the fauna and flora of the GCFR. Palaeorelictual insects are mostly strong endemics, typically being confined to temperate habitats, especially forest, high-altitude fynbos, mountain streams

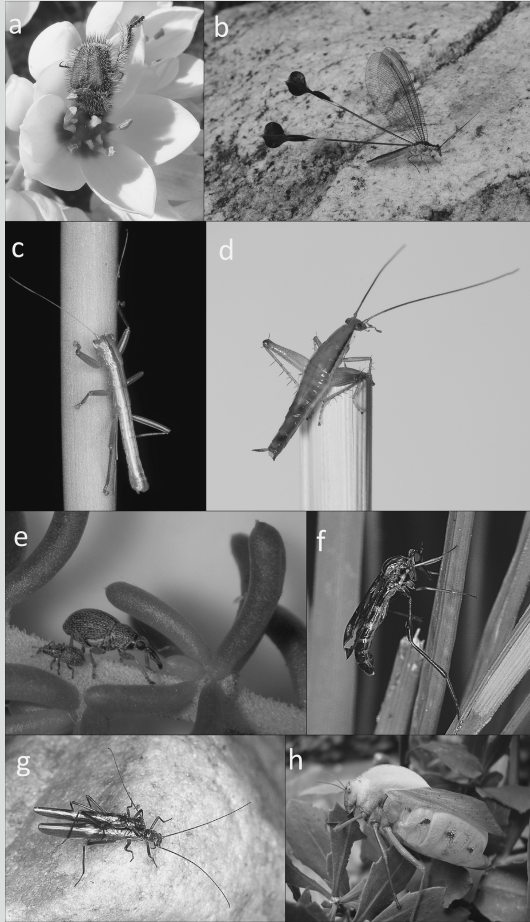
Box 4.1 *Continued*

(e.g. *Aphanicerca capensis*; Box 4.1 Fig 1g), and caves. Due to these attributes, they are considered of high conservation importance. They are best represented on the Table Mountain chain (147 species per quarter degree square), but have

secondary hotspots in the Hottentots Holland Mountains (80 species per quarter degree square) and the southern Cape forests (36 species per quarter degree square; Day 2005).

Bladder grasshoppers (Pneumoridae)

This is an ancient family largely endemic to South Africa; all 17 species and nine genera (Dirsch 1965) occur in the region, with two forest species extending into East Africa (Dirsch 1965). The Greater Cape has a distinctive and rich fauna of bladder grasshoppers (Box 4.1 Fig 1h), with at least 12 species found here, all of these endemic to this region (Dirsch 1965).



Box 4.1 Figure 1 (a) *Peritrichia* monkey beetles belong to a guild of monkey beetles that feed almost exclusively on white, pink, and blue flowers (Photo: Sarah-Leigh Hutchinson); (b) the spoon-wing lacewing (*Sicyoptera dilatata*) was only known from a single specimen captured in 1836, and thought extinct until its recent rediscovery in the Riviersonderend mountain range (Photo: Mike Picker); (c) *Austrophasma caledonense* is a fynbos member of the insect order Mantophasmatodea, an order entirely restricted to Africa (Photo: Mike Picker); (d) the jumping cockroach (*Saltoblattella montistabularis*) shows convergence in body plan with grasshoppers (Photo: Mike Picker); (e) adaptive radiation of fynbos apionid weevils, with two species co-occurring on one *Aspalathus* species (Fabaceae) (Photo: Şerban Procheş); (f) the wormlion fly (*Leptonyma sericea*), showing elongated mouthparts for nectar feeding, is considered to belong to a relictual family with extensive radiation in the Greater Cape (Photo: Mike Picker); (g) the stonefly (*Aphanicerca capensis*) is a representative of South Africa's Gondwanan fauna, occurring only in temperate mountain streams (Photo: Mike Picker); (h) a male *Bullacris* showing the unique resonating bladder characteristic of this basal grasshopper family (Photo: Mike Picker).

1908; Nordenstam 1969; Hengeveld 1992). In the Cape, these early studies mostly used limited datasets, and retrieved broad-scale regional patterns (e.g. Bolus 1905; Marloth 1908). As the flora of the Cape became better known, the numbers of taxa analysed and the resolution of biogeographic detail improved (Weimarck 1941; Dahlgren 1963), as did the resolution of subcontinental studies for both floristic (e.g. White 1976) and faunal datasets (e.g. Carcasson 1964; De Klerk et al. 2002). It is

only relatively recently that the essentially comprehensive lists of the Cape flora have been synthesized into meaningful phytogeographical patterns (Goldblatt and Manning 2000). The combination of modern analytical techniques, increased computational power, and large multi-species distributional datasets has also given rise to a more objective means to identify biogeographic patterns (e.g. Kreft and Jetz 2010; Linder et al. 2012; Holt et al. 2013; Bradshaw et al. submitted).

Table 4.1 Summary of the numbers of records and species richness of the South African plant and animal datasets analysed in this study.

Group	Dataset(s)	Approximate number of records	Number of species	Reference
Plants	PRECIS including Protea Atlas Project	1.79 million	20 657	Germishuizen et al. (2006) South African Botanical Diversity Network Report No. 41; < http://www.proteaatlas.org.za/index.htm >
Birds ¹	South African Bird Atlas Projects (SABAP)	>5 million	627	< http://sabap2.adu.org.za/index.php >
Reptiles	Southern African Reptile Conservation Assessment (SARCA)	61 300	409	Bates et al. (2014) <i>Suricata</i> 1, 1–482; < http://sarca.adu.org.za/ >
Frogs	Southern African Frog Atlas Project (SAFAP)	24 800	110	Minter et al. (2004) Atlas and red data book of the frogs of SA, Lesotho & Swaziland
Butterflies	Southern African Butterfly Conservation Assessment (SABCA)	326 000	657	Mecenero et al. 2013

¹ Only terrestrial bird species considered; aquatic bird species (sensu Crowe 1990) removed on the basis of habitat usage taken from Hockey et al. (2005).

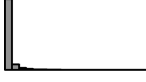
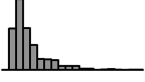

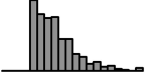

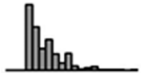
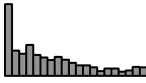
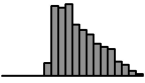
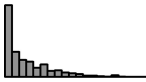
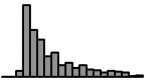
South Africa is fortunate to have well-surveyed distributional datasets generated from national atlas projects for a range of taxa, notably plants, birds, reptiles, frogs, and butterflies (Table 4.1). It is therefore feasible to interrogate regional biogeographic patterns across taxa. The progression of biogeographic techniques used for South African taxa has evolved from purely descriptive accounts based on intuition and expert knowledge (e.g. Weimarck 1941; Goldblatt and Manning 2000), through to high spatial resolution empirical analyses using point locality data and environmental themes (Gess 1992; Kuhlmann 2009; Prendini 2005), with the utilization of multivariate statistics and advanced algorithms for calculations of resemblance matrices and clustering based on species-by-site matrices (Crowe 1990; Born et al. 2007; De Klerk et al. 2002; van Rensburg et al. 2004). These comprehensive species datasets and more robust quantitative analyses enabled us to undertake a comparative biogeographic study of different South African taxa, and assess their biogeographic patterns.

Point locality data from collection-based records and recently collated national atlas projects were used to delineate biogeographic divisions based on a uniform, repeatable, and modern analytical approach that clusters grid cells hierarchically according to the shared presence of species. In order to investigate the hypothesis of a Cape Biochorion, we analysed national species datasets in order to retrieve the major biogeographical patterns within South Africa. This allowed us to determine whether the taxa analysed suggest a

Cape Biochorion, and where this is situated. Since the analysed datasets are national, our results are unfortunately restricted to South Africa, but this is problematic only in the northernmost part of our area of interest, namely the arid winter rainfall zone of southwestern Namibia.

Except for frogs, data were analysed at the quarter degree square (QDS) level of resolution (Edwards and Leistner 1971) as historically these grid cells have been most widely employed for capturing biological distribution data in South Africa. Frogs were analysed at the half degree square level (HDS) of resolution due to the relatively low numbers of species found in South Africa, which translates into low species richness per grid cell, therefore diminishing the discrimination ability of clustering techniques. QDS and HDS are limited by their coarseness of resolution (a *c.* 25 × 25 km block for QDS, and a *c.* 50 × 50 km block for HDS), which renders them insufficiently sensitive to retrieve finer-scale biogeographical patterns, or features with low taxon representation (Moline and Linder 2006; Bradshaw et al. submitted). In addition, sampling effort (number of records per grid cell) varies dramatically between QDS or HDS, which may mislead biogeographic analyses where the sampling effort for a given cell lies well below its potential species richness (i.e. species are omitted due to a lack of sampling). To minimize this bias, we used conservative sampling effort thresholds to rid the datasets of poorly collected grid cells (Table 4.2). Unfortunately, this resulted in several grid cells not being assigned to biochoria, with the result

Table 4.2 Species richness and grid cell numbers per taxonomic group for each of the original and modified distributional datasets analysed, and the richness-per-grid sampling cut-off used to discard grid cells (deemed to be under-sampled; see text for details) for biogeographic analysis. While the sampling cut-off could result in a dramatic reduction in the area analysed (reptiles by 82%), species' representation in the datasets dropped much less markedly (reptiles by 4%), if at all.

	Original dataset		Min. cut-off	Modified dataset			Maximum richness	richness per grid cell ¹
	No. spp.	No. grid cells		No. spp.	No. grid cells	Grid cells per taxon ¹		
Plants	20 657	2009 (99%)	200	20 314	997 (49%)		2499	
Reptiles	409	1469 (72%)	15	393	361 (18%)		73	
Frogs	110	508 (94%)	6	110	318 (59%)		46	
Birds	627	2009 (99%)	120	626	1361 (67%)		355	
Butterflies	656	1410 (69%)	40	650	394 (19%)		278	

¹ Histograms were produced using the modified datasets. In the 'grid cells per taxon' histograms, species distribution sizes were separated into 20 bins, with the proportion of species of the given distribution sizes displayed for each bin. In the richness-per-grid histograms, grid cell species richness was divided into 20 bins, with the proportion of species richness displayed for each bin.

that the mapped results of cluster analyses typically contain gaps (e.g. Linder et al. 2005). In order to set thresholds, the number of records for each grid cell was plotted against its species richness. For under-sampled grid cells, the species richness is usually equal or near equal to the number of records (i.e. a strong linear relationship between the two). We determined the threshold minimum number of records as the point at which this linear relationship started to break down (i.e. where the number of records is no longer a strong predictor of species richness in a given grid cell). This threshold varies across datasets due to differences in overall species richness.

Using a species presence matrix, a dissimilarity matrix of the relationships between cells was calculated using Kulczynski's second (K2) similarity equation (see Jurasinski 2012), an equation commonly employed in biogeographic studies (Shi 1993; Moline and Linder 2006; Born et al. 2007). Importantly, K2 does not take shared absences into account (Shi 1993; Linder 2001), and is not unduly influenced by differences in richness between cells (Born et al. 2007). The unweighted pair group method with arithmetic means (UPGMA; Sokal and Michener 1958) agglomerative clustering

technique was used to cluster grid cells using the function `hclust` in the R statistical environment (R Development Core Team 2012). UPGMA has generally been found to outperform most other available hierarchical agglomerative clustering methods (Shi 1993; Linder 2001; Kreft and Jetz 2010).

Instead of applying the commonly used, and arguably arbitrary, phenon line (Rosen 1988; Rueda et al. 2010), we employed a branch ranking technique derived from Strahler stream order assignment (Strahler 1957; Borchert and Slade 1981), which focusses to a greater extent on dendrogram structure than a visually determined similarity cut-off (Bradshaw et al. submitted). The premise is that branches are scored from tip to root and upon merging, the 'new branch' receives a higher branch order number when two or more branches of equal score intersect (e.g. $1 + 1 = 2$; $2 + 2 = 3$; $3 + 3 = 4$). Where branches are unequally scored, however, the highest branch order is retained (e.g. $2 + 1 = 2$; $3 + 2 = 3$ and $3 + 1 = 3$; $4 + 3 = 4$ and $4 + 2 = 4$ and $4 + 1 = 4$). Branch order numbers were assigned to all branches in the dendrogram using the `pytools` library for R (Revell 2012). Using this branch order assignment, we were able to identify hierarchical

biogeographical units (comprising grid cells) based on species similarity. Being intrinsically hierarchical, the resultant dendrograms allowed us to determine the relationships between biogeographical areas, thus allowing us to test the hypotheses outlined above. Since we were dealing with highly disparate taxonomic groups, biogeographic patterns retrieved at different hierarchical levels were interpreted against regional climate zones and gradients (e.g. whether biogeographic intervals are coincident with rainfall seasonality boundaries, or recognized mesic/semi-arid intervals (Fig 4.1, Rutherford and Westfall 1986)). Also, given the comparative nature of this study and the disparate taxa analysed, we restricted our investigation to the broad patterns reflected in the highest levels of the dendrogram (i.e. primary and secondary breaks; Fig 4.2).

We defined our regional climate zones in terms of their rainfall regimes, distinguishing winter and aseasonal (rain falling throughout the year, but predominantly between autumn and spring) rainfall areas from those receiving most of their rainfall in summer. Within the winter/aseasonal rainfall zone (Fig 4.1), and concomitant with our stated hypotheses, we identify mesic ('winter mesic'; total annual precipitation: 275–900 mm; >65% rainfall in winter) and arid winter ('winter arid'; total annual precipitation: 100–275 mm; >65% rainfall in winter) rainfall zones, and mesic ('aseasonal mesic'; total annual precipitation: 275–900 mm; 35–65% rainfall in winter) and arid aseasonal ('aseasonal arid'; total annual precipitation: 100–275 mm; 35–65% rainfall in winter) rainfall zones.

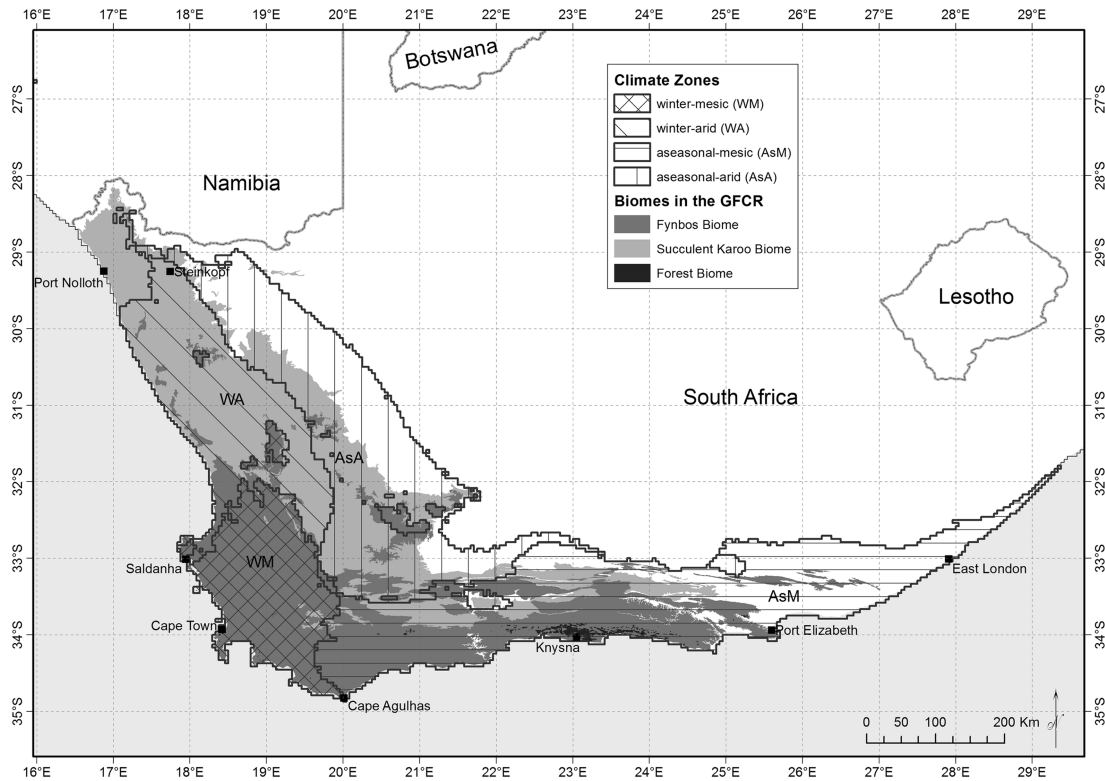


Figure 4.1 Climatic zones used to describe biogeographic patterns for plant and animal groups within the aseasonal/winter rainfall zone. Seasonal rainfall zonation is as defined by Chase and Meadows (2007) and Ackerly et al. (Chapter 16). The winter rainfall zone is divided into winter-mesic (total annual precipitation: 275–900 mm; >65% rainfall in winter) and winter-arid (total annual precipitation: 100–275 mm; >65% rainfall in winter) zones, as is the aseasonal rainfall zone (mesic: total annual precipitation: 275–900 mm; 35–65% rainfall in winter; arid: total annual precipitation: 100–275 mm; 35–65% rainfall in winter). With the exception of the extreme northwestern corner of South Africa, which receives predominantly (>65%; but <100 mm) winter rainfall, the areas lying outside the rainfall zones indicated receive predominantly summer rainfall.

4.4 Floristic and faunal biogeographic patterns

4.4.1 Flora

Analysis of the plant dataset revealed a clear primary split between the summer rainfall area and the rest of the country, with the winter and aseasonal rainfall areas forming a single biogeographical unit, indicative of a GCFR (Fig 4.2a, upper and lower panels). Nested within the GCFR, as retrieved here, were three subregions (Fig 4.2a, middle and lower panels), comprising: (a) the winter-mesic zone; (b) the aseasonal-mesic zone; and (c) the winter-arid zone. The winter-mesic subregion essentially incorporates Goldblatt and Manning's (2000) Northwest and Southwest phytogeographic centres and generally coincides with the mediterranean-type climate portion of the broadly winter rainfall zone (Chapter 2). The aseasonal-mesic subregion incorporates Goldblatt and Manning's (2000) Karoo Mountain, Langeberg, and Southeast phytogeographic centres. The winter-arid subregion is essentially coincident with the western succulent karoo region (Chapter 1, see also Born et al. 2007; Snijman 2013).

The winter-mesic subregion clusters most closely with the aseasonal-mesic subregion, forming an entity essentially equivalent to the CFR (*sensu* Manning and Goldblatt 2012). These two subregions share a similar geology, namely the Cape Supergroup rocks (Chapter 2). The eastern limit of the aseasonal-mesic subregion, however, extends well beyond the eastern boundary of the CFR, stretching as far as East London (see also Weimarck 1941 and Bradshaw 2009). While extensive tracts of fynbos and renosterveld vegetation in this area are restricted to the Cape Supergroup substrata of the Zuurberg range east of Port Elizabeth, Cape floristic elements are commonly found in coastal grassland and thicket mosaics, especially on calcareous substrata, well beyond the Fish River (Cowling 1983). In contrast to the winter-mesic and aseasonal-mesic subregions, the winter-arid subregion is associated largely with shales of the Karoo Supergroup and gneiss and granite of the Namaqua–Natal Metamorphic Belt (Chapter 2). The southwestern extent of this subregion penetrated further south along the west coast than the Olifants River, the boundary employed by Goldblatt and Manning (2000) to delineate the CFR. This pattern is consistent with Marloth's (1908) West Littoral area and Acocks' (1953) vegetation map. Succulent karoo components, therefore, reach further south into the CFR than originally thought (Chapter 1, Bradshaw et al. submitted).

4.4.2 Fauna

Regional patterns

The animal groups showed considerable variation in the number of primary breaks (regional clusters) obtained, ranging from two for reptiles and butterflies, four for birds, and six for frogs (Fig 4.2b–e, upper and lower panels). Although there were some similarities in biogeographic boundaries across groups, none of the clustering patterns were identical. For reptiles, the primary division suggested a broad split between temperate and afrotropical reptiles, as retrieved by Crowe's (1990) biogeographic zones for snakes and lizards. The precise location of the boundary between these two major groups is somewhat obscured by the low level of sampling in central South Africa, but appears to cut directly through the Highveld region, from the Kei River towards the northwest, with the western division incorporating the CFR, succulent karoo, thicket, Nama karoo, and the drier grassland and savanna regions. Similarly for birds, a western division, encompassing the CFR, succulent karoo, and Nama karoo, was retrieved, but its eastern border shows more limited eastward and northward extension into savanna and grassland. Both Chapin (1932) and De Klerk et al. (2002) retrieved southwestern divisions for birds comparable to our western division, but with deeper intrusion into savanna and grassland. The southeastern coastal extent of our western division for birds is essentially limited to the CFR. Chapin (1932) retrieved a very similar pattern with southern intrusions of afrotropical bird fauna along coastal areas reaching well into the aseasonal-mesic zone.

Butterflies showed a similar primary biogeographic division to plants, centred on the boundary of the summer rainfall zone; however, this division was less distinctive than for plants with some summer rainfall grid cells included within the winter/aseasonal rainfall zone. The primary division retrieved here for butterflies does not match either Carcasson's (1964) zoochorological divisions for butterflies nor Endrödy-Younga's (1978) for beetles. Carcasson's (1964) western 'Cape Subregion' division included the CFR, the succulent karoo, and large areas of Nama karoo and grassland. The southeastern coastal extent of our western division for butterflies, however, matched that of Carcasson (1964), who retrieved a strong afrotropical forest element which extends deep into the aseasonal-mesic CFR, having possibly displaced or limited the northeastern reaches of fynbos species. By contrast, Endrödy-Younga's (1978) southeastern coastal extent of Cape faunal elements extended northwards along

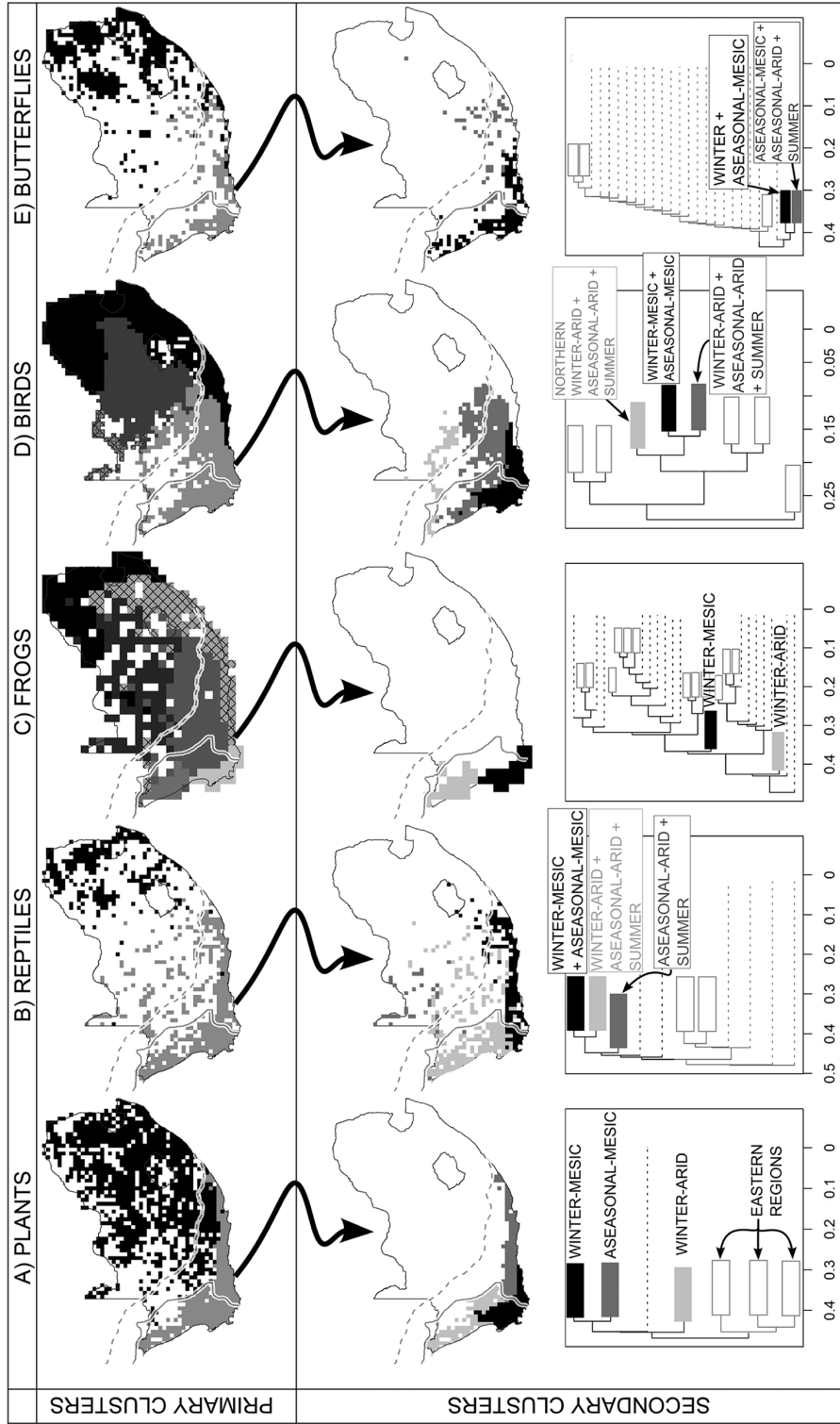


Figure 4.2 Top panel: Geographical extent of the primary (regional) biogeographic clusters resolved by the plant and animal groups included in this study. The eastern boundaries of the aseASONAL (dashed lines) and winter (solid lines) rainfall zones are indicated. Middle panel: Geographical extent of the secondary (subregional) clusters identified within the westernmost primary clusters (regions). For frogs, the secondary decomposition is provided for the two westernmost regions, whereas for all other groups the decomposition is provided for the single westernmost region. Lower panel: Simplified dendrograms showing the relationships of secondary clusters falling within the western regions; clusters representing the areas falling outside the western primary cluster(s) are indicated by open boxes. Grid cells not assigned to any clusters are shown as dashed lines, these being a common feature of this type of analysis (e.g. Linder 2001). These grid cells probably lack the taxa linking them to other clusters, instead having only ubiquitous species.

the east coast into subtropical savanna. Endrödy-Younga (1978) explained these southeastern extensions through the presence of Cape relictual taxa found in the temperate coastal forests and Drakensberg Mountains and the radiation of these (Gondwanan) elements into younger more adaptive groups.

Overall, the primary divisions revealed by our analysis for reptiles, birds, and butterflies indicated broadly similar divisions between western temperate and eastern afrotropical faunas. Frogs, however, showed a distinct pattern from the rest of the animal groups, with six regional biogeographic divisions at the primary break. These were not aligned into western and eastern areas, as retrieved by (Crowe 1990; see also Seymour et al. 2001; Alexander et al. 2004). Only two of the six regional clusters, the winter-mesic and possibly the winter-arid, can be considered to constitute a Cape faunal division (Seymour et al. 2001; Alexander et al. 2004; Linder et al. 2012) which is distinct from the rest of South Africa, the latter being essentially defined by afrotropical elements. Similar to birds and insects, these eastern tropical elements penetrate deep into fynbos along the coast, reaching as far south as the winter-mesic's southeastern border.

Subregional patterns within the western cool-season rainfall zone

Focussing within the western divisions for animals (Fig 4.2b–e, middle and lower panels), some similarities were apparent in the delimitation of subregional clusters, but, as for the primary regional divisions, none of the biogeographic patterns were identical.

Analysis of the reptile data retrieved three subregions, comprising: (a) the southern winter-mesic and aseasonal-mesic zones; (b) the winter-arid and aseasonal-arid zones; and (c) the aseasonal-arid zone plus the northern extent of the summer rainfall zone (this northern subregion weakly defined). Crowe (1990) grouped areas falling within our northern subregion with winter-arid areas. Our northern subregion is, however, considered too obscure to describe in detail, likely extending beyond the northern study boundaries, and, for this reason, is not discussed further.

Subregion (a) for reptiles incorporates mostly the southern and southeastern parts of the CFR (its northwestern extent did not reach beyond the Cederberg) and incorporated areas of southern Nama karoo, thicket, and grassland. This subregion shows exceptional reptile richness and endemism, and is also an area of high zoogeographical complexity. Since the southeastern sector of this subregion, in the vicinity of Port Elizabeth, represents a meeting point of several

biomes (Chapter 1, Cowling 1983) and two rainfall zones (Fig 4.1), it supports a diversity of reptile species drawn from each of these areas, resulting in an unusual assemblage of overlapping faunas (see also Chapter 7). Subregion (b) incorporates succulent karoo, the northwestern portion of the CFR, Nama karoo, and desert. It offers a wide array of habitats and has many endemic habitat specialist species (e.g. several limbless skink and specialists along the west coastal dune areas and rupicolous (rock-dwelling) species found on exposed Table Mountain Group sandstone in the Cederberg (Vernon 1999; Edwards et al. 2012)). The northeastern portion of this subregion extends along the Orange River to the east, including areas on both sides of the Orange River. The reptile fauna is dominated by rupicolous species, but also has a high proportion of sand species, since there are large deposits of alluvial sand in this arid area. The continuity of sand along the Orange River acts as a corridor for many species into this area which are otherwise associated with rather different habitats (e.g. *Varanus niloticus*). Subregions (a) and (b) cluster together, linking the CFR, succulent karoo, and Nama karoo.

For birds, the western division also comprised three subregions (Fig 4.2d, middle and lower panels), comprising: (a) the winter-mesic and aseasonal-mesic zones; (b) the winter-arid and aseasonal-arid zones; and (c) the strongly winter-arid, aseasonal-arid, and northern extent of the summer rainfall zones. Subregion (a) falls predominantly within the CFR. The southeastern coastal border of subregion (a), however, does not reach the CFR's southeastern limit, reaching just east of Knysna. Terrestrial bird studies by Crowe (1990) and De Klerk et al. (2002) both retrieved CFR-coincident clusters (see also Werger 1978). Crowe's (1990) southeastern coastal (see also Chapin 1932) and northwestern borders were similar to ours. In contrast, the southeastern coastal border of De Klerk et al.'s (2002) 'Fynbos District' extended beyond the CFR, including thicket, but their northwestern border was similar to ours. Although subregion (a) has a relatively depauperate bird fauna, with only seven Fynbos Biome-endemic species, several of these represent some of the most ancient African bird lineages, highlighting the unique evolutionary affinities of this winter-mesic and aseasonal-mesic subregion. Subregion (b) for birds incorporates large areas of succulent karoo and the lower and upper parts of the Nama-Karoo Biome. In the north west it reaches the southern boundary of the Richtersveld. Both Crowe (1990) and De Klerk et al. (2002) retrieved similar, but far broader, arid subregions, linking the succulent karoo with

Nama karoo, savanna and grassland areas. They did not, however, separate out the Bushmanland, Richtersveld and other desert areas which correspond to subregion (c). The Succulent Karoo and Nama-Karoo Biomes share many bird species, including eight species restricted to these two biomes (Vernon 1999). Additionally, at least 30 grassland bird species extend into the Nama karoo across the extensive contact area between the borders of the Nama-Karoo and Grassland Biomes (essentially equivalent to the eastern border of subregion (b)). Many of these grassland species also extend westwards into succulent karoo. Subregion (c), which is somewhat similar to the Gariiep centre of endemism of van Wyk and Smith (2001), has a handful of arid-adapted bird species, and which extend into succulent karoo and Nama karoo (e.g. Sclater's lark (*Spizocorys sclateri*), which is found on the gravel plains of the Richtersveld). There are also savanna bird species (e.g. fawn-coloured lark (*Calendulauda africanoides*) and sociable weaver (*Philetairus socius*)) that extend across the savanna–Nama karoo interface, into the northern areas of the Nama-Karoo and Succulent Karoo Biomes. These arid-adapted and savanna elements separate subregion (c) from subregion (b). As for reptiles, the bird data cluster subregions (a) and (b) together, linking fynbos with core areas of succulent karoo and with the central and lower areas of Nama karoo.








Butterflies revealed two subregions within their western division (Fig 4.2e, middle and lower panels), comprising: (a) the winter-mesic, winter-arid, and aseasonal-mesic zones; and (b) the southeastern extents of the aseasonal-mesic, aseasonal-arid, and summer rainfall zones (this southeastern subregion poorly defined). Neither the earlier studies on butterflies (Carcasson 1964) nor those on beetles (Endrödy-Younga 1978), the two most detailed insect biogeographic studies for South Africa to date, clustered the CFR and succulent karoo together in their zoochorological divisions. Carcasson (1964) considered the winter-mesic Cape as a separate subregion, whereas Endrödy-Younga (1978), while recognizing that winter-mesic Cape elements extended into winter-arid areas, nonetheless considered the northwestern parts of the succulent karoo to be part of a coastal Namib division. Both of these early biogeographers delineated the northwestern winter-arid areas of South Africa as part of an independent zoogeographic region that extended along a narrow band along the coast into northern Angola. A recent conservation assessment of South African butterflies using comprehensive and detailed distribution maps highlights the winter rainfall zone as a hotspot

of butterfly endemism (Mecenero et al. 2013). Many of the winter rainfall endemic species show distributions spanning the CFR and succulent karoo. For example, within the genus *Chrysothrix* (Lycaenidae) roughly 18 taxa with restricted winter-mesic ranges occur in both the CFR and succulent karoo. The clustering together of the CFR and succulent karoo for butterflies matches the pattern retrieved for plants. Congruence between these two groups was, however, expected, as almost all species of butterfly are phytophagous and associate strongly with plants. It remains to be established whether this pattern will hold for other insect and invertebrate groups that are less dependent on plants. Subregion (b) for butterflies is difficult to place biogeographically. It resembles Endrödy-Younga's (1978) southeastern part of his 'Cape-bilateral extension' dispersal pattern of Cape beetle taxa, which extends into thicket and grassland. He considered these extensions to represent relic areas of Cape taxa. Subregion (b) clustered with subregion (a) indicating its strong links with Cape elements. A number of putative Cape insect groups (richness and endemism concentrated in the winter rainfall zone) extend into aseasonal-mesic and aseasonal-arid areas (e.g. grasshoppers: Dirsch 1965; flies: Hesse 1969; Usher 1972; Bowden 1978; Stuckenberg 1997; Stuckenberg 2000; wasps: Gess 1992; beetles: Holm 1978; Colville 2009). However, the area falling within subregion (b) is also known to include a strong representation of East African elements which extend their ranges southwestwards along the coast, intruding into the CFR. Carcasson (1964) considered thicket to be characterized more by forest butterfly elements (e.g. *Charaxes* (Nymphalidae) and *Neptis* (Nymphalidae)). The zoogeographical links between Nama karoo, thicket, and surrounding winter rainfall clusters highlights the interesting and complex faunal composition of subregion (b) with the occurrence of CFR, succulent karoo, Nama karoo, grassland, and savanna insect elements being represented.

4.5 Cape biochoria: consensus and differences across taxa

Broad congruence across the butterfly, reptile, and bird datasets supports the recognition of western and eastern faunal divisions within South Africa (Table 4.3). Plants and butterflies showed the greatest similarity, with their western divisions being mostly restricted to winter and aseasonal rainfall areas. Birds and reptiles, on the other hand, retrieved a western division incorporating both the winter rainfall and large components

Table 4.3 Assessment of consensus of hierarchical clustering of biogeographical patterns across taxon groups to evaluate the hypothesis of a Cape Biochorion or Greater Cape Biochorion. Hierarchical clustering proceeds from primary breaks, subdividing South Africa into western and eastern regional divisions, through to lower level subregional delimitation.

Nested levels	Biogeographic consensus		Biotic group					
			plants	reptiles	frogs	birds	butterflies	
Primary division and chorology	I	Primary split between broad western versus eastern divisions		✓	✓	✗	✓ ¹	✓
	II	Winter-mesic (Core Cape Biochorion)		✓	✗	✓	✓	✗
	II	Winter-mesic + aseasonal-mesic (Cape Biochorion)		✓	✗	✗	✓ ²	✗
	II	Winter-mesic + aseasonal-mesic + southeastern extensions (Cape Biochorion <i>with extensions</i>)		✓	✓ ³	✗	✗	✗
	III	Winter-mesic + winter-arid + aseasonal-mesic + aseasonal-arid + southeastern extensions (Greater Cape Biochorion)		✓	✗	✗	✗	✓ ⁴
	III	Winter-mesic + winter-arid + aseasonal-mesic + aseasonal-arid + southeastern summer + northern summer (Greater Cape Biochorion <i>with extensions</i>)		✗	✓	✗	✓	✗

¹ There is a strong single primary division in the west, but multiple eastern divisions (see Fig 4.2d).

² Incomplete inclusion of aseasonal-mesic zone.

³ Truncated northwestern winter-mesic zone.

⁴ Some inclusions of aseasonal-arid and summer rainfall zone areas.

of the aseasonal-arid Nama karoo region and some summer rainfall regional areas (Table 4.3). In contrast to the other groups, frogs did not display a broad primary division, but rather revealed six clusters split at the primary level, with their western temperate faunal division essentially reduced to a narrow, winter rainfall area consisting of two separate regions.

Clear evidence of a Greater Cape Biochorion was only found in plants and butterflies, in which winter-mesic, winter-arid, and aseasonal-mesic zones grouped together into a nested biogeographic unit (Table 4.3). In contrast to plants and butterflies, the winter-arid areas for reptiles and birds appeared to show greater faunal affinity with aseasonal-arid Nama karoo areas to the east, rather than to winter-mesic areas to the south. For birds, the retrieval of two winter-arid subregions, linked to the southern and northern parts of Nama karoo, highlights a deeper biogeographic complexity between these two arid areas. Therefore, South African vertebrate groups appear not to conform to a Greater Cape Biochorion (Table 4.3, *sensu lato* Bayer 1984, Born et al. 2007). For reptiles and birds, the arid subregions (winter-arid plus aseasonal-arid) do, however, cluster with the winter-mesic and aseasonal-mesic subregions. The Greater Cape Biochorion, as retrieved for plants and butterflies, forms a core area of this grouping. We therefore consider a Greater Cape Biochorion *with extensions* (of eastern aseasonal-arid/summer rainfall areas) as an appropriate biogeographic unit for reptiles and birds (Table 4.3).

Within the plant- and animal-based Greater Cape Biochorion divisions, the winter-mesic and aseasonal-mesic rainfall areas retrieved differed substantially between groups in terms of both their bounds and extents (Table 4.3). Broad support for a Cape Biochorion was evident in three of the five groups (plants, frogs, and birds), each of which retrieved a core winter-mesic area, with a similar northwestern border. The extent of the aseasonal-mesic area incorporated by each of these groups was variable, however, as was the location of the coastal southeastern border. For plants, frogs, and birds, therefore, a Cape Biochorion is considered as an appropriate biogeographic unit, but with variable southeastern, aseasonal-mesic extensions (Table 4.3).

4.6 Interpretation of biogeographic similarities and differences

The regional biogeographic patterns retrieved here for plants and animals within the GCFR highlight several interesting and significant new findings. The retrieval of both contrasting and similar biogeographic patterns

between plants and animals is of importance when attempting to understand the development of the biota of both the CFR and the adjacent succulent karoo. The unequivocal support for the validity for a Greater Cape Floristic Region (Bayer 1984; Jürgens 1991; Born et al. 2007), using a comprehensive national species-level plant dataset, is a significant finding. Plants showed a clear primary split between the summer rainfall area and the remainder of the country. Floristically, this indicates that the floras of the CFR and succulent karoo are more similar to each than to any of the floras in the rest of South Africa. Plant biogeography therefore appears best considered within a GCFR concept (see Manning and Goldblatt 2012; Snijman 2013). Faunistically, however, patterns retrieved in this study suggest that efforts to understand the 'Cape' biogeography of animals will require a broader focus, extending beyond the confines of the CFR and succulent karoo, to incorporate areas of eastern neighbouring biomes. Additionally, the essentially floristically defined biomes of South Africa appear to show limited similarity with faunal biogeographic patterns (van Rensburg et al. 2004; Procheş and Cowling 2007).

The environmental factors limiting the distributions of plants and different animal groups, therefore, appear to be quite variable. Several faunally defined divisions, for example, reach beyond the confines of the rock types (Cape Supergroup) which are so critical in limiting the fynbos flora, as well as beyond the winter-dominant rainfall area, well into and sometimes beyond the aseasonal-arid zone. This can be seen in reptiles, with species shared between the succulent karoo and Nama karoo with areas of thicket (Chapter 7, Vernon 1999; Meyer et al. 2010). Likewise, the distributions of several bird species appear to be climatically defined, resulting in distributions that cut across vegetationally defined habitats which may be more closely linked to soil properties. Consequently, some bird species are shared between the Cape, succulent karoo, Nama karoo, and grassland regions (see also Allan et al. 1997).

Another pattern of biogeographic interest is the variable position of the southeastern coastal border of the aseasonal-mesic cluster across plants and animals. Plant data identify the southeastern border of the aseasonal-mesic cluster as extending further east than the current CFR border. This easterly extension may reflect the underlying eastern extent of Cape Supergroup rocks (Chapter 2), which may account for the presence of Cape floristic elements as far as the Great Fish River. This area receives some winter rainfall (Fig 4.1) and is thus capable of supporting a

flora that is adapted for winter growth. The crudeness of our grid cell units may, however, account for at least part of this pattern. Analysis of taxonomic datasets partitioned into biotic elements (high versus low altitude, mesic versus xeric, fynbos versus non-fynbos), or at finer spatial scales, would be required to assess more accurately the eastern extent of the GCFR. The aseasonal-mesic and southeastern aseasonal-arid areas are faunistically interesting in that they represent an area of transition or overlap between Cape clades and afrotropical elements. This limits the consensus for a Cape Biochorion, again emphasizing that chorological divisions depend heavily on the taxa examined.

A lack of biogeographic congruence across groups is not unusual (see Rueda et al. 2010 for regionalization of European biota). One may expect that where primary producers show strong biogeographic pattern (i.e. the unique GCFR vegetation), this will have a direct influence on the patterns shown by consumers. However, animal groups often show minimal fidelity to vegetation types (Liversidge 1962; Allan et al. 1997; Cox 2001; Jenkins et al. 2013), being aligned instead with other habitat variables (e.g. soil structure for scorpions (Prendini 2001a), insects (Endrödy-Younga 1978; Irish 1990; Sole et al. 2004; Botes et al. 2007), and reptiles (Bauer 1999); aquatic habitats for frogs (Mokhatla et al. 2012) and insects (Samways and Niba 2010); and nesting and roosting sites for bats (Monadjem et al. 2010)). Modern phylogenetic studies of Cape faunal groups provide support for this idea, linking areas not necessarily along floristic lines, but rather along geographic or altitudinal gradients, such as mountain ranges and lowland areas (e.g. Chapter 7, Prendini 2001b; Measey and Channing 2003; Sole et al. 2004; Pitzalis and Bologna 2010; Tolley et al. 2010; Predel et al. 2012).

Several interrelated factors have undoubtedly been influential in generating the differences outlined above. The winter–summer rainfall regime interface is an important boundary, and therefore driver, of biogeographic pattern (Linder and Mann 1998; van Wyk and Smith 2001; Cowling and Ojeda 2005). In addition, the Greater Cape region is an area of discrete geological boundaries (Chapter 2, Cowling et al. 2009), contrasting fire regimes (Chapter 3), habitat heterogeneity (topography, climate, and soils; Chapter 2), and concomitant ecological specialization (Chapters 6, 10, 11). These factors, explored elsewhere in the book, have undoubtedly played a central role in structuring the unique biota of the GCFR. Given the strongly contrasting biologies and life-history requirements of plant and animal lineages, however, as well as their contrasting dispersal capabilities (Croteau 2010),

we should not expect these taxa to respond to these drivers in a uniform way. Frogs, for example, are ectothermic and mostly require water for survival and reproduction. They are also less vagile than birds and butterflies. These physiological and life-history traits most probably make frogs more susceptible to habitat idiosyncrasies which can lead to narrow ranges and more detailed regional patterns (Rueda et al. 2010). The greater vagility of birds, by contrast, enables them to track habitats (e.g. wooded river courses) and to follow pulses of resource availability related to seasonality, as seen between areas of succulent karoo (winter arid) and Nama karoo (aseasonal arid; Allan et al. 1997). In this context, it is unsurprising that the fauna and flora of the GCFR show different histories of assembly (Chapters 5, 7) and patterns of biogeographic association. Understanding biogeographic structure and the formation of Cape biochoria requires consideration of a complex array of historical and ecological factors, each of which will interact with a taxonomic group in an idiosyncratic manner.

4.7 Conclusion

Our analysis for plant and animal biogeographic patterns has the advantage of covering all of South Africa, thereby providing a rigorous test of the relationships between cool-season rainfall areas and summer rainfall areas. Only in plants and butterflies did the winter rainfall and aseasonal-mesic areas cluster to form a Greater Cape Biochorion in the traditional sense. For birds and reptiles, winter-arid areas showed greater affinity to the aseasonal-arid Nama karoo and arid summer rainfall areas, than the winter-mesic areas to the south. Frogs, on the other hand, retrieved the winter-mesic and winter-arid areas as distinct regions. Thus, limited consensus was found for a Greater Cape Biochorion using the distribution data of plant and different animal taxa. For birds and reptiles, however, the CFR clustered with succulent karoo and the aseasonal-arid parts of Nama karoo indicating that the faunal affinities of succulent karoo and Nama karoo appear closest with the Cape fauna. Therefore, we consider a Greater Cape Biochorion *with extensions* as a concept for investigating Cape faunal biogeography. The Nama-Karoo Biome has, however, been poorly surveyed for most taxonomic groups (Gibbs Russell et al. 1984; Vernon 1999). Increased collection and exploration of the Nama karoo may either strengthen its faunal relationship with the winter rainfall areas, or highlight its faunistic distinctness. A Cape Biochorion centred on the winter-mesic CFR is a core area for plants, frogs (regional) and

birds. However, the retrieval of a CFR-centred Cape Biochorion, incorporating both the winter-mesic and aseasonal-mesic zones, requires consideration of differing southeastern coastal borders between plants and animals related to the falling-off or extension of Cape clades. The floristic coherence of the GCFR and CFR are not, therefore, necessarily reflected in the biogeographic patterns of other taxonomic groups, as the ecological and evolutionary processes differed between the taxa on account of their divergent physiological, morphological, and life-history traits.

Our analysis reveals the complexity of reconciling biogeographic patterns across taxonomic groups. Future studies should concentrate on using data that are more spatially refined or using criteria of endemism (*sensu* Linder 2001) to delineate areas. This may yield more accurate biogeographic boundaries, and so provide further insights into the historical relationships between and within areas of the broader Cape Region, particularly when combined with palaeoclimatic and phylogenetic data.

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