RESEARCH ARTICLE

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Delimiting zoogeographic centres for South African Orthoptera

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Abstract

Biogeography attempts to find explanations for the distributions of species, based on their past histories and present environmental conditions. Historically, biogeographic studies were modelled on intuitive and expert knowledge, whereas recent studies have advanced with the aid of digitised natural history collections, computational power and repeatable methods. In South Africa, biogeographical studies on insects are greatly lacking and very little is known about the zoogeographic patterns for many insect groups in the region. South Africa has a high level of diversity and endemism of orthopterans (> 800 species), making them an ideal group to investigate zoogeographic patterns. The aim of this study was to identify and describe the zoogeographical patterns of South Africa's orthopteran species, based on the distributions and levels of diversity of all major families. Point locality data was used to conduct a hierarchical cluster analysis based on the shared presence of species to delimit zoogeographical centres. In addition, delimited centres were compared to plant-based biomes and phytogeographic regions. Results showed that orthopteran species richness was evenly distributed across the region and clustered into six zoogeographical centres. There was a primary split, separating species into a western winter-rainfall and an eastern summer-rainfall group. The western and eastern regions contained three centres each, with the east being less diverse and taxonomically distinctive than the west. Strong consensus was seen between orthopterans and the Greater Cape Floristic Region, and between orthopterans and the Cape zoogeographic region for butterflies, reinforcing the notion that this region is representative of a biochorion. In addition, this region had the greatest numbers of orthopteran families, highlighting its importance for orthopteran diversification.

Highlights

- This study identified zoogeographic centres for orthopteran species of South Africa by using computational analyses.
- Analyses identified a primary split between species, showing western winter-rainfall and eastern summer-rainfall groups.
- Six centres were recognized, and the Greater Cape Floristic Region was identified as an area with the highest orthopteran diversity and richness.
- Results show that there is a large portion of South Africa that is under sampled for many orthopteran species.
- Identifying biogeographic centres for species groups allows for the discovery of links between taxa and their environment, and aids in conservation management strategies.

Keywords: Biochorion, biogeography, Cape Floristic Region, grasshopper, hierarchical cluster analysis, Southern Africa, species richness.

Introduction

Biogeographical studies can provide possible explanations for species' geographical distributions based on their evolutionary histories, present ecological processes, and future predicted dispersals (Sanmartín 2012). Earlier studies of biogeography did not incorporate the ecology of species' distributional patterns and confined their approaches to historical zoogeography. Although many important biogeographic patterns were retrieved, the major disadvantage of this approach is that the authors made use of their intuitive and often subjective knowledge to model species distributions, making it a non-repeatable approach (Linder 2001). Nevertheless, over the intervening years, biogeography has evolved in its emergent understanding of historical processes (e.g., continental drift) and much attention has been devoted to the integration of disciplines, such as biology, geography, and ecology (Wien and Donoghue 2004, Ricklefs and Jenkins 2011, Sanmartín 2012). In addition, the modelling of species' spatial distribution patterns has greatly advanced with the emergence of geographic information systems (GIS) and remote sensing technologies (Sanmartín 2012).

It has been suggested that when searching for shared historical and evolutionary patterns across taxa, 'units of area' is a useful standardized method for mapping and delineating species distributions (Hausdorf 2002). This allows for the clustering of predefined operational geographic units (OGU) that are based on the shared presence-absence of species (Crovello 1981). Historically, distributions of species were surveyed according to grid cells, e.g., quarter degree square (QDS) levels of resolution (Edwards and Leistner 1971). However, more recently, the use of precise GPS coordinates (locality point data) has become more commonplace. Therefore, with the use of point locality data from digitized collection records together with OGU, studies have been able to delineate biogeographic divisions based on a modern analytical approach (e.g., Seymour et al. 2001, Colville 2009, Linder et al. 2012, Gonzalez-Orozco et al. 2013, Colville et al. 2014, Bradshaw et al. 2015, Rodrigues et al. 2015, Lenormand et al. 2019). This shift towards a more quantitative approach within biogeographic studies, with the use of numerical methods and increased computational power, now permits the analysis of larger datasets, and more objectively defines biogeographic patterns (Kreft and Jetz 2010, Bradshaw et al. 2015). The delineating of species distributional regions assists in identifying areas for conservation importance and subsequently aids in conservation management strategies (Kreft and Jetz 2010, Olivero et al. 2012). In addition, the discovery of links between insect distribution patterns and phytogeographic regions or plant biomes is of significant interest (Procheş and Cowling 2007) towards understanding their ecological and evolutionary interactions (Bernays 1992).

South Africa has a rich and diverse orthopteran fauna, with approximately 323 genera and 809 species (Bazelet 2014). There are approximately 366 genera native to southern Africa, of which an estimated 88% occur in South Africa (Lomer et al. 2001, Eades et al. 2013), making this an ideal taxonomic group for regional biogeographical studies. Orthopteran species occur globally in a wide variety of habitats, apart from the polar regions, and are the most diverse of the polyneopteran insect lineages (Grimaldi and Engel 2005, Eades et al. 2014, Song et al. 2015). With the ability to inhabit various environments, orthopterans are known to be associated with certain plant species, by being host plant specific (e.g., *Eremidium*; Armstrong and Brand 2012, Brijlal et al. 2021). In addition, several orthopterans can camouflage well with their surroundings to avoid predation. For example, members from the families Pamphagidae, Lathiceridae and Lentulidae, are known to camouflage themselves with their host plants and with soils/ rocks for ground-dwelling species (Brown 1962, Scholtz et al. 2021). Therefore, plants, geology and soil type would be expected to potentially correlate with grasshopper biogeographic patterns.

Orthopterans also serve as bioindicators for ecological and conservation processes in a variety of environments, both globally and locally (Sauberer et al. 2004, Steck et al. 2007, Bazelet and Samways 2011, Matenaar et al. 2015). However, insects are generally underrepresented in the planning and assessments of conservation strategies, largely due to the lack of available data (Cowling et al. 2004) as well as the poor taxonomic state of many groups (Melin and Colville 2019). Recent studies have also observed that there has been a massive global decline in insects (Hallmann et al. 2017, Lister and Garcia 2018, Cardosao et al. 2020). The results of an orthopteran biogeographic study should therefore further improve our knowledge in identifying areas of richness and endemism for conservation importance.

The aim of this study was to identify and describe the zoogeographical patterns of South African orthopteran species based on their distribution and diversity. This was achieved using a South African orthopteran database and conducting a hierarchical cluster analysis based on the shared presence of species to delimit zoogeographical centres. In addition, this study aimed to test whether orthopteran species match or show spatial consensus with plant-based biomes and phytogeographic regions, and to compare this information with what is known for other insect groups (e.g., butterflies (Carcasson 1964)).

Materials & Methods

Compilation of orthopteran distribution dataset

Point locality georeferenced data for orthopteran species records from South Africa were acquired from the following institutes: National Museum of Bloemfontein, Iziko South African Museum, Albany Museum, Durban Natural Science Museum, Ditsong National Museum of Natural History, the Karoo BioGaps Project (South African National Biodiversity Institute, SANBI), Stellenbosch University and the University of the Western Cape (Table 1). Locality points for species were plotted in QGIS 3.10.1 (QGIS Development Team 2019) and verified.

Table 1. Institutions from which data records were received and used in this study.

No.	Institution	Contact	Date Accessed	Source
1	National Museum of Bloemfontein	B. Muller	July 2018	Unpublished
2	Iziko South African Museum	A. Mayekiso	July 2018	Specify6
3	Albany Museum	T. Bellingan	May 2018	Unpublished
4	Durban Natural Science Museum	N. Govender	October 2018	Unpublished
5	Ditsong National Museum of Natural History	T. Perregil	September 2018	Unpublished
6	Karoo BioGaps Project	C. Bazelet	August 2018	Published online
7	Stellenbosch University	C. Bazelet	June 2018	Unpublished
8	The University of the Western Cape	V. Couldridge	October 2018	Unpublished

Points that fell outside of South African borders, were removed. In total, 19 of the 20 South African orthopteran families, 700 species (~86% of species) and 4774 unique locality records were used in the analysis.

Operational Geographic Unit (OGU)

Quarter Degree Grid cells (QDS) were used as the operational geographical unit (OGU) for biogeographical analysis (Moline and Linder 2006, Bradshaw et al. 2015). Orthopteran point distribution maps were overlaid onto a QDS vector file (Edwards and Leistner 1971) and a list of species by QDS was generated. Following Bradshaw et al. (2015), all QDS cells that contained less than five records, were removed.

Statistical and biogeographical analyses

The approach of Colville et al. (2014) and the detailed methodological steps given in Bradshaw et al. (2015) were followed in this study. A brief synopsis of these steps is given here. All analyses were calculated using the statistical programme R within the R-studio environment (R Development Core Team 2012). Firstly, a presence-absence matrix of species by OGU was created and then used to generate a dissimilarity matrix using Kulczinski's second (K2) similarity equation within the similarity index matrix package 'simba' (Juransinski 2012). This matrix displays each row as representing a grid cell and each column a species. The Kulczinski's equation was used as it has been frequently utilised in several previous biogeographic studies (Shi 1993, Moline and Linder 2006, Born et al. 2007). Once the similarity matrix was generated, it was then used to run the cluster analysis with unweighted pair group method with arithmetic means (UPGMA; Sokal and Michener 1958). This analysis grouped grid cells using the hierarchical clustering function 'hclust' found in the 'stats' package within the R statistical environment (R Core Team 2020).

Following Bradshaw et al. (2014), a branch order cut-off method (BOC; Bradshaw et al. 2015) was used to generate a dendrogram consisting of branch order numbers. Each of these numbers were then assigned to all branches within the dendrogram using the 'phytools' package in R (Revell 2012). The dendrogram was converted into a phylogram for better visualization of the branches using the 'ape' package (Paradis and Schliep 2019). The hierarchical biogeographical units (clustered QDS grid cells) were identified based on species similarities, which resulted in determining the relationships between biogeographical areas. Branch orders were then plotted in QGIS 3.10.1 and the number (level) of centres were selected showing the most realistic biogeographical areas.

These clustered areas were carefully examined, and disjunct grid cells were removed after further investigation, which entailed several steps. Firstly, if the disjunct cell contained < 5 records, it was removed. However, if disjunct cells had > 5 records, the species within the cell were inspected and based on known information regarding the species' biology and distribution, they were either retained or removed. Species within their respective known habitats and regions were investigated post analyses, using platforms such as the IUCN Red List of Threatened Species (www.iucnredlist.org) and Orthoptera Species File (http://orthoptera.speciesfile.org). Disjunct occurrences may be the result of misidentifications of species or erroneous locality information. Once the final biogeographic centres were identified, attribute tables for each of these centres were exported and descriptive statistics calculated. These calculations included the number of records and species found in each centre, as well as the number of families identified.

Production of biogeographic maps

The final map representing the biogeographical centres was created and used as a template for creating additional maps. A species richness map was created with a colour gradient to indicate the abundance of species found within each QDS cell. This species richness map, as well as the resulting biogeographical centres, were then overlaid with South African biomes (Mucina and Rutherford 2006). Finally, the biogeographic centres were additionally overlaid with Carcasson's (1964) southern African faunistic butterfly divisions for regional comparisons.

Results

Biogeographic centres

Results from the BOC technique showed a primary split at branch order cut-off level 6, producing a clear east and west zone (Fig. 1). Roughly, these zones indicate differences in orthopteran species between the winter and all-season (west) and summer (east) rainfall regions. A total of six centres at level 5 were retrieved (Fig. 2 and Table 2), with three of the six centres falling within each of the two primary zones. Within the western zone, three distinct centres could be observed: the Cape Fynbos, the Central Nama-Karoo, and the Succulent-Karoo centre.

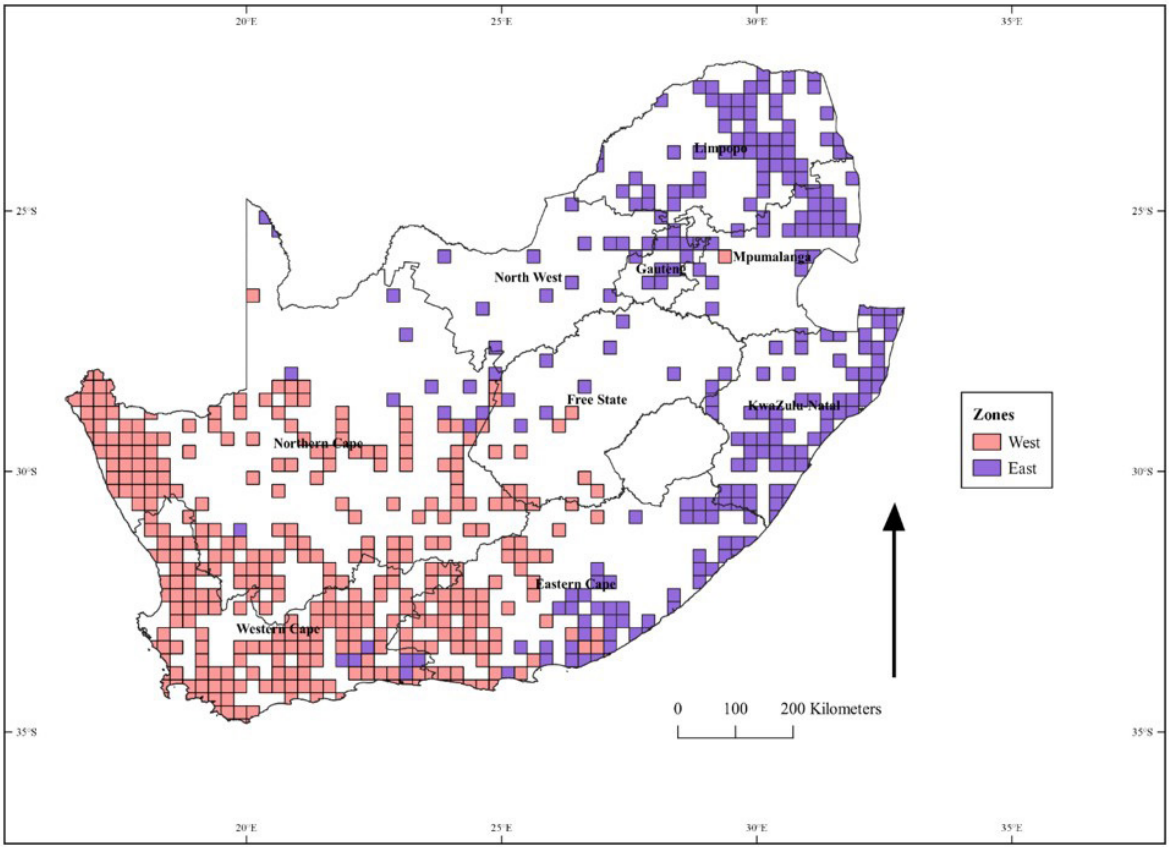

Figure 1. The primary split for South African orthopteran species, showing clear western (predominantly winter-rainfall) and eastern (predominantly summer-rainfall) biogeographical zones.

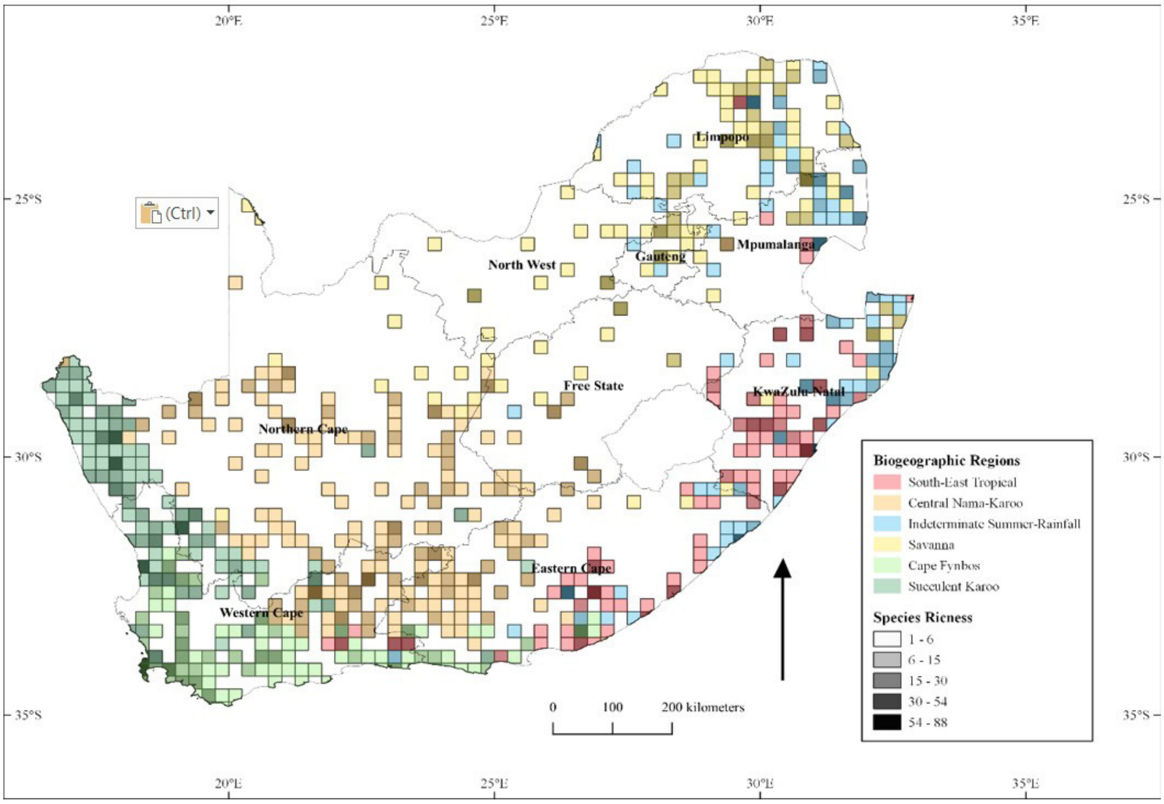

Figure 2. Species richness and clustered QDS cells showing the six identified centres of South African orthopteran species.

The Succulent-Karoo and the Cape Fynbos centres, together align strongly with the Greater Cape Floristic Region (GCFR) and are comprised of similar orthopteran families. The eastern zone had less distinctive centres, showing three centres: Indeterminate Summer-Rainfall, South-East Tropical and Savanna centre.

The species richness map shows orthopteran species appear to be evenly distributed across South Africa's biomes (Fig. 3) with grid cells displaying very high species richness (>50 species) seen scattered across all main biomes. The western zone contained a slightly larger number of orthopteran families in comparison to the eastern summer-rainfall region (Table 2).

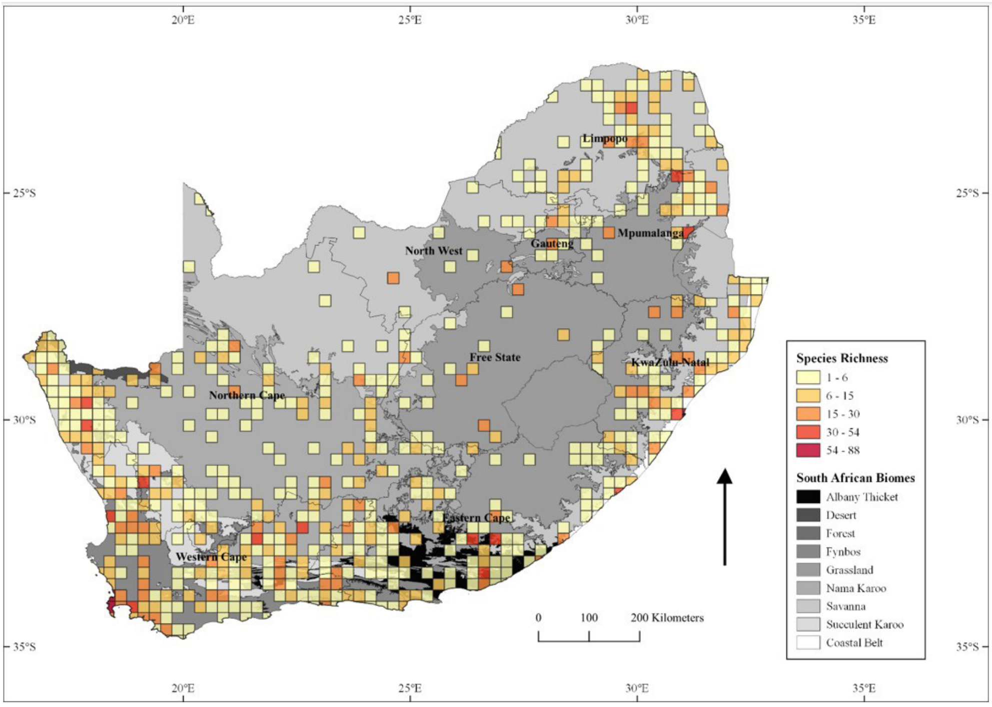

Figure 3. Distributional map of orthopteran species showing species richness based on the number of species found in each QDS overlaid with South African biomes (Mucina and Rutherford, 2006).

Table 2. The number of species records and the total number of species and families found in each centre

No.	Family Names	Cape Fynbos	Succulent-Karoo	Central Nama-Karoo	Savanna	Indeterminate Summer-Rainfall	South-East Tropical
1	Acrididae	219	188	398	77	152	247
2	Anostostomatidae	37	3	7	13	15	16
3	Euschmidtiidae	7	5	2	11	3	
4	Gryllacrididae	15	2		1	2	2
5	Gryllidae	17	5	14	9	16	10
6	Gryllotalpidae	8	1	1	1	1	1
7	Lentulidae	103	48	106	36	23	71
8	Lithidiidae	1	38	20	1		
9	Pamphagidae	87	229	362	72	26	20
10	Pamphagodidae				12		
11	Pneumoridae	119	96	9	4	25	73
12	Pyrgomorphidae	70	37	85	101	62	89
13	Rhaphidophoridae	1					
14	Schizodactylidae		3	2			
15	Stenopelmatidae	8	2		1	5	3
16	Tetrigidae	3			2	6	7
17	Tettigoniidae	220	131	108	210	317	85
18	Thericleidae	19	10	17	56	13	7
19	Tridactylidae	3	3			1	
No. of families per centre		**17**	**16**	**13**	**16**	**15**	**13**
No. of species per centre		**268**	**218**	**244**	**211**	**263**	**266**
No. of records per centre		**937**	**801**	**1131**	**607**	**667**	**631**

The centre containing the highest family richness was the Cape Fynbos, with Tettigoniidae and Acrididae having the largest number of species found within this centre. Generally, these two families were the most frequently represented families across all centres, whereas Rhaphidophoridae and Schizodactylidae were the least. The Pamphagidae were most abundant within the Central Nama-Karoo and the Succulent-Karoo centres, and Pneumoridae were largely found in the Cape Fynbos centre. Lentulidae were mostly found in the Central Nama-Karoo and the Cape Fynbos centres.

Spatial congruence with plant biomes and Carcasson's butterfly divisions

In general, there was a broad spatial overlap between centres and vegetation biomes (Fig. 4 and 5). More specifically, the Cape Fynbos and Succulent-Karoo centres matched well with the GCFR. The Central Nama-Karoo centre also broadly related to the Nama Karoo vegetation type. However, the South-East Tropical Rainfall, the Indeterminate Summer-Rainfall and the Savanna centres are spread across several different biomes and extend into the Cape Fynbos and the Central Nama-Karoo centres.

In Figure 6, the identified centres from this study were overlaid with butterfly divisions retrieved from Carcasson (1964). The Cape Fynbos centre largely coincided with Carcasson's Cape butterfly division. The Central Nama-Karoo orthopteran centre also showed good consensus with Carcasson's Karoo division. Orthopterans from the Succulent-Karoo centre overlapped with two of Carcasson's faunistic divisions, the Namib, and the Karoo divisions. The Savanna centre largely forms part of Carcasson's Kalahari division, but also has species present within his Cape Grasslands, Eastern Karoo, Coastal and South African Highlands Forest divisions. Most of the South-East Tropical centre fell within Carcasson's Coastal and Eastern divisions; however, there were some outliers. The Indeterminate Summer-Rainfall centre fell across several of Carcasson's butterfly divisions, whereas Carcasson's Cape division was comprised of the Nama Karoo and the GCFR.

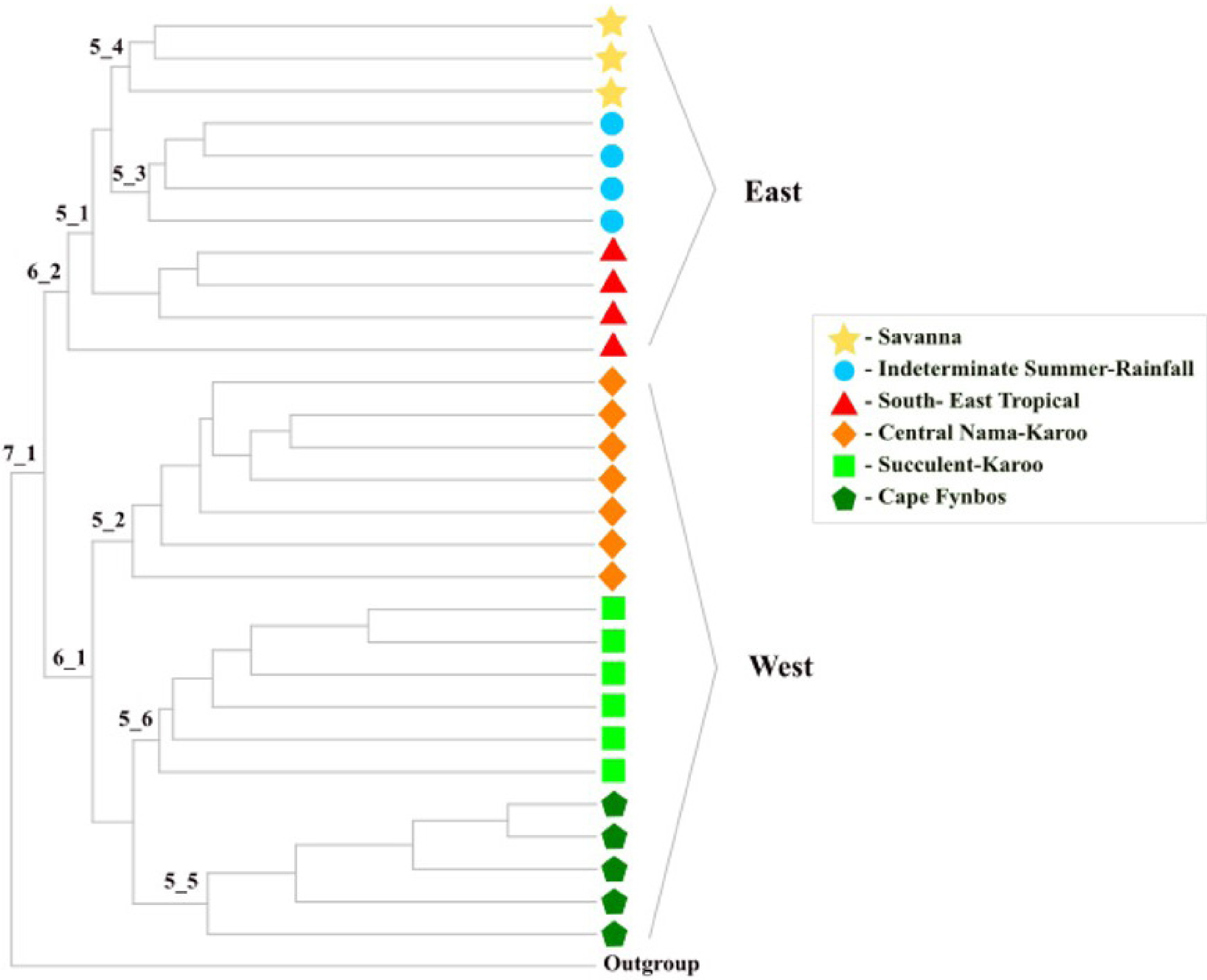

Figure 4. Phylogram showing the relationships between centres based on similarity of occurrence for South African orthopteran species (levels 7_1 to 5_6).

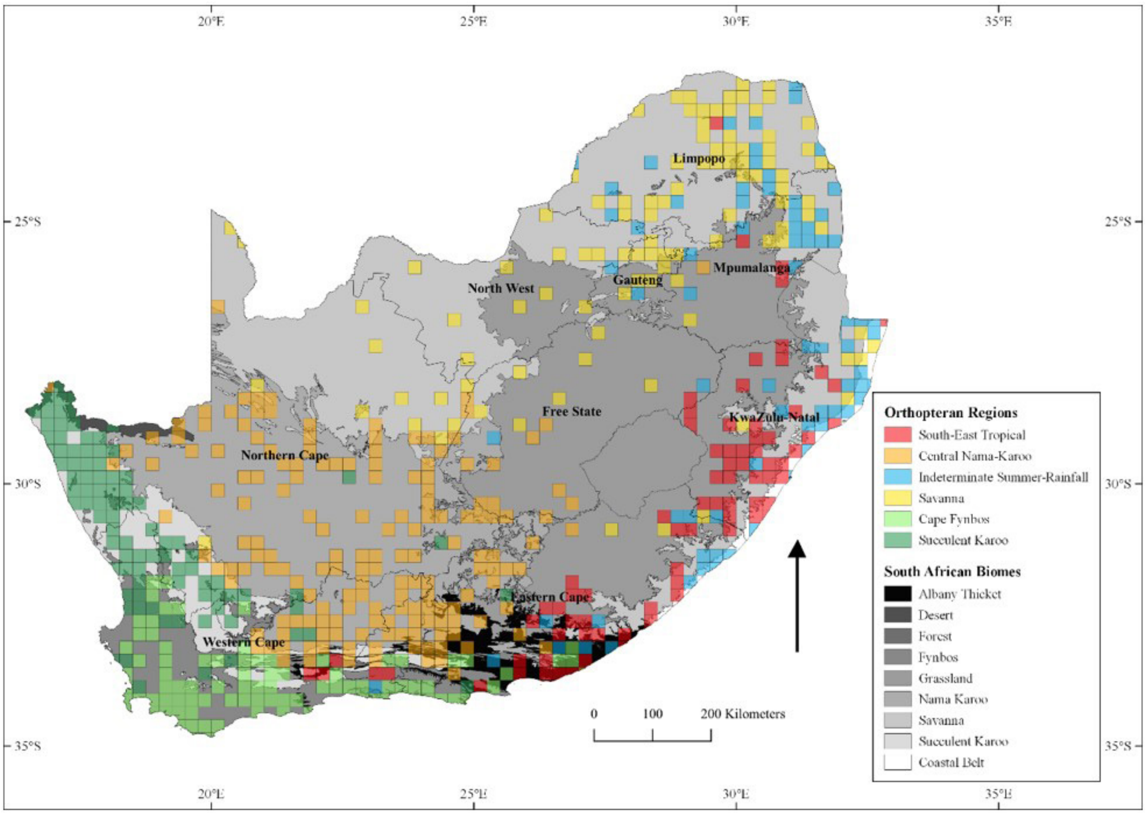

Figure 5. Clustered QDS centres of South African orthopteran species overlaid onto South African biomes (Mucina and Rutherford, 2006).

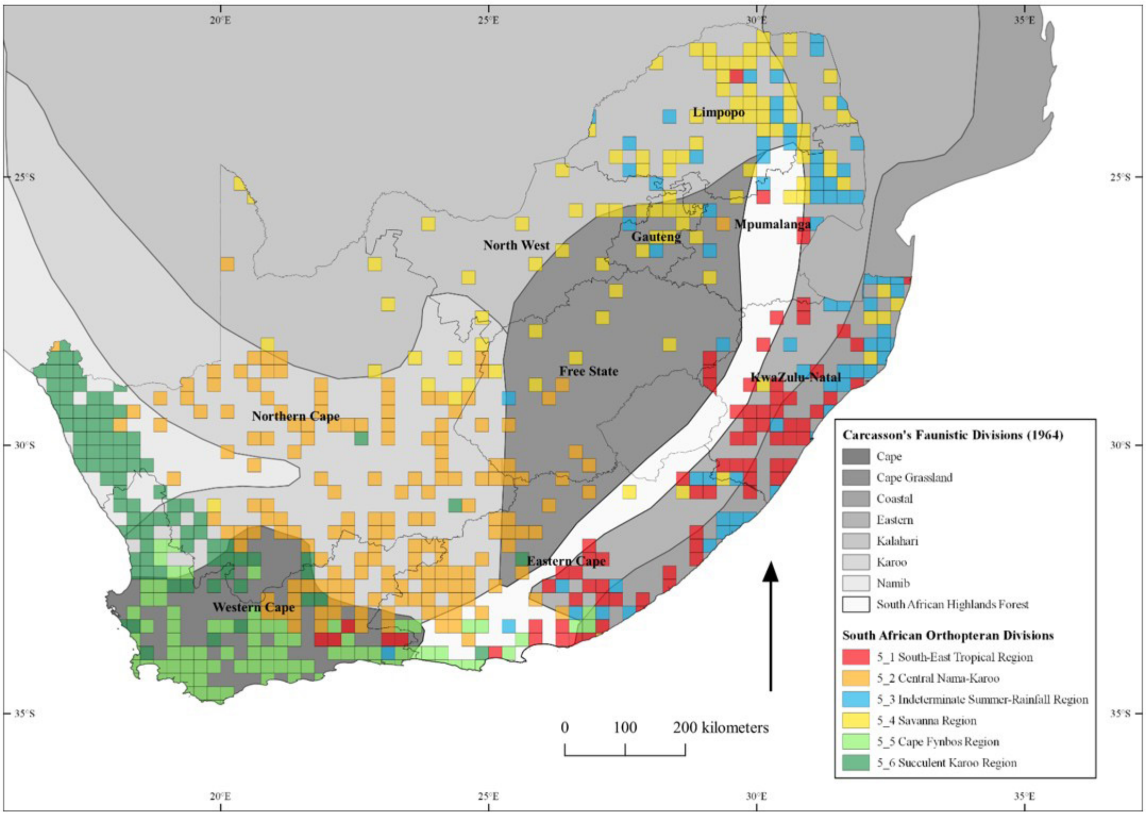

Figure 6. South African orthopteran centres overlaid with a map of the divisions from Carcasson's (1964) biogeographical analysis of African butterflies.

Discussion

Biogeographic centres and patterns of diversity

Two broad biogeographic regions were seen, with a clear primary break between the western winter-rainfall and the eastern summer-rainfall zones (Fig. 1). This is in broad congruence with Carcasson's (1964) butterflies, Endrödy-Younga's (1978) beetles, Colville's (2009) monkey beetles, Colville et al.'s (2014) plants and butterflies, and Crowe's (1990) reptiles. Each zone contained three biogeographic centres, in which the western zone showed distinct centres, whereas the eastern zone had less defined centres. Orthopteran species richness was generally evenly distributed across South Africa, but generally lower in the eastern zone in comparison to the western zone, particularly for family richness. Well-collected areas in the east, such as those close to major towns, showed comparable grid square diversity between the two zones suggesting that diversity is most likely underestimated for this zone (Fig. 3).

The eastern zone contained three summer-rainfall centres: the Savanna, the South-East Tropical and the Indeterminate Summer-Rainfall centres. The Savanna centre had several disjunct cells present within the Grassland biome, as well as within the tropical and summer-rainfall regions found along the east coast (Fig. 5). The South-East Tropical centre extended into the Cape Fynbos, a distributional pattern that has previously been observed for birds and beetles (Endrödy-Younga 1978, Colville et al. 2014). The Savanna centre had the most familial diversity within the eastern zone; however, the South-East Tropical centre had the highest species count. Two families Rhaphidophoridae and Schizodactylidae were not found in any of the summer-rainfall regions and are restricted to the western winter-rainfall regions. In contrast, the small family Pamphagodidae was not present in the western regions but rather confined to the eastern summer-rainfall region. The Indeterminate Summer-Rainfall centre was concentrated in the north-eastern and south-eastern regions of South Africa and extended along the coast into the winter-rainfall Cape (Fig. 5). This geographically large, but less distinctive region is most likely the result of data deficiencies and an increase in sampling efforts could potentially provide better biogeographic resolution. Alternatively, this region may share several faunal links with tropical and subtropical areas further north and therefore may remain unresolved (Carcasson 1964).

The western zone of the primary break also had three distinct centres: the Cape Fynbos, the Succulent-Karoo, and the Central Nama-Karoo centre. The distinctiveness of the centres retrieved is potentially the result of having higher orthopteran endemism, which has also been identified for several other insect groups in this zone, such as monkey beetles (Colville et al. 2014), lacewings (Sole et al. 2013), heelwalkers (Klass et al. 2003), weevils (Colville et al. 2014), bees (Kuhlmann 2009), butterflies (Mecenero et al. 2013), katydids (Naskrecki and Bazelet 2009), and bladder grasshoppers (Dirsh 1965, Gordon, 2022). The Central Nama-Karoo centre had the highest number of orthopteran records, which is attributed to the increase in our knowledge of the Karoo region, through a recent national survey project (the Karoo BioGaps Project conducted by SANBI in 2016). The Cape Fynbos region is known for being particularly rich in orthopteran species (Naskrecki and Bazelet 2009), many being endemic and flightless (Matenaar et al. 2014), suggesting habitat/host specialisation and limited dispersal abilities; both features can lead to more distinctive biogeographic centres (Liebherr 1994, Tuomisto et al. 2016, White et al. 2020). The Cape Fynbos and the Succulent-Karoo centres are interesting in that they represent an area of faunal transition or overlap. Additionally, results identified the Cape Fynbos centre as the area with the most familial taxa present and the highest species diversity (Table 2) providing further evidence that this area is an area of high insect diversification.

There are several interesting Orthoptera in the Cape Fynbos region, such as the high diversity of relictual Pneumoridae (Dirsh 1965, Gordon 2022). A dated phylogeny indicated that the forest species are the most basal and split from the non-forest species at approximately ± 116.91 MYA (Gordon 2022). Therefore, it is suggested that these species may have been more widely distributed at one stage. A similar distribution pattern was identified for forest butterflies, and it was suggested that this was the result of forest vegetation being forced to break up and retreat to higher levels (mountainous areas or dispersal further north into Africa) during the hot and dry interpluvial stages (Carcasson 1964). Furthermore, the grasshopper family Lentulidae is highly concentrated in certain areas of the Cape Fynbos region and appears to be a Fynbos endemic clade (Matenaar et al. 2018). In contrast, species-rich families such as Acrididae and Tettigoniidae appear widespread throughout the country (Picker et al. 2004; Song et al. 2018). Overall, there are both similarities and differences between the defined western zone centres from this study and that of Carcasson's (1964) butterflies and Colville et al.'s (2014) plants.

Biogeographic consensus with other animals and plants

This study highlighted several significant findings for the biogeographic patterns of orthopteran species, as well as supporting the validity of a GCFR biochorion (*sensu* Colville et al. 2014). In the western zone, the Cape Fynbos and the Succulent-Karoo centres matched well with the 'Cape Sub-region' of Carcasson's (1964) butterflies, as well as the winter-mesic and aseasonal-mesic subregions of Colville et al. (2014) for plants. Similar to the Cape Fynbos centre presented here, these sub-regions extend eastwards across the aseasonal-rainfall regions into the summer-rainfall areas as far east as the city of East London. In these eastern areas, Carcasson (1964) retrieved a strong Afrotemperate forest element for butterflies, which has also been indicated for the grasshopper family Lentulidae, showing links between eastern areas of South Africa and forest mountainous regions of East Africa (Hemp et al. 2020).

There was also strong consensus for the Cape Fynbos centre of orthopterans and the Cape Floristic Region (*sensu* Manning and Goldblatt 2012). This suggests that orthopterans and plants may either share a common biogeographical history and/ or that orthopterans have evolved specializations towards Fynbos host plants (Naskrecki and Bazelet 2009). The Central Nama-Karoo centre seems to be closely related to the 'Karoo Sub-region' from Carcasson's (1964) map, in addition to the phytogeographical region for arid plants of Jürgens (1997). However, it is possible that if a better surveyed and more comprehensive dataset was used, there would likely be a split into a western winter-rainfall group more aligned with the Succulent-Karoo centre and an eastern summer-rainfall group, the Nama-Karoo centre. Studies have identified spatial congruence between plants and animals, such as strong arid links between areas of the Nama and Succulent Karoo for butterflies (Carcasson 1964) and birds (de Klerk et al. 2002). Whereas several different animal groups have shown strong connections between the cape Succulent Karoo areas (Endrögy-Younga 1978, Vernon 1999).

In the eastern zone, the South-East Tropical centre extended into the Cape Fynbos centre, which was also seen for beetles (Endrödy-Younga 1978). These extensions could be explained through the presence of Cape relictual taxa that had been previously found within the temperate coastal forests and Drakensberg Mountains, causing these radiations to be a younger and more adaptive group (Endrödy-Younga 1978). The Indeterminate Summer-Rainfall region roughly matches the 'South African Highland Forest' distribution pattern for beetles (Endrödy-Younga 1978) and the 'Coastal and Eastern' pattern for butterflies (Carcasson 1964). Carcasson (1964) suggested that the eastern South African butterfly region extends northwards into African tropical and subtropical areas, because of shared faunal links further north into Africa; this is most likely also true for Orthoptera (Otte and Armstrong 2017). The Savanna centre encompasses both Savanna and Grassland biomes and has potentially separated from the drier grassland areas around the Kalahari. A study on arthropod assemblages (Botha et al. 2016) discovered that there are high levels of species similarity in parasitoids and pollinators between the Savanna and Grassland biomes. With better sampling efforts for Orthoptera, these centres may become more defined and additional centres identified.

Conclusion

Biogeographic patterns are important for conservation because they identify areas of evolutionary distinctiveness and interest. From this study, South Africa is divided into two broad zoogeographical zones aligned with rainfall seasonality. The Cape Fynbos and the Succulent Karoo of the GCFR are areas of high taxonomic orthopteran distinctiveness and high species and familial richness. There was good spatial congruence found between orthopteran centres, other insect centres, and phytogeographic centres within the GCFR. This would suggest that the GCFR is a biochorion, or an area of distinct biogeographic patterns for a range of taxonomic groups. It must be stressed that due to the large number of unidentified species in natural history collections, and imprecise locality information, the final dataset was reduced significantly. There was also clear evidence of under sampling in certain regions, such as the Nama-Karoo. A large portion of the South African region has not been surveyed for orthopteran species, which is evident by the number of grid cells (69%) that did not contain any records, as seen for South African bees (Melin and Colville, 2019). As such, even though distributional datasets collated from natural history museums are useful for biogeographical studies, such as our orthopteran dataset, there are recognized limitations when using such data (Graham et al. 2004). Future biogeographic studies for orthopteran species would benefit from using a larger dataset to provide additional biogeographic insights and align less distinctive biogeographic patterns observed in the summer-rainfall zone; however, this would require extensive sampling throughout the South African region.

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Author Contributions

Dr M. L. Gordon (Lead author): Conceptualised the study, compiled, collected, and analysed all data as well as drafting the written material. Dr J. Colville (Second author): Conceptualised the study, assisted with analyses and data, and contributed to the writing process. Dr V. Couldridge and Dr A. Engelbrecht: Assisted with editing of the written material.

Data Availability Statement

Point locality data for South African orthopteran species used in this study is not publicly available. Data was obtained for use from the following institutions: National Museum of Bloemfontein, Iziko South African Museum, Albany Museum, Durban Natural Science Museum, Ditsong National Museum of Natural History,

the Karoo BioGaps Project (South African National Biodiversity Institute, SANBI), Stellenbosch University and the University of the Western Cape.

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