

UNDERSTANDING THE EVOLUTIONARY RADIATION OF THE
MEGADIVERSE MONKEY BEETLE FAUNA (SCARABAEIDAE: HOPLIINI)
OF SOUTH AFRICA

by

JONATHAN F. COLVILLE

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Hoplocnemis crassipes (Olivier); male (left) and female (right) (Photo: Mike Picker).

*Two roads diverged in a yellow wood,
And sorry I could not travel both
And be one traveller, long I stood
And looked down one as far as I could
To where it bent in the undergrowth;*

*Then took the other, as just as fair,
And having perhaps the better claim,
Because it was grassy and wanted wear;
Though as for that the passing there
Had worn them really about the same,*

*And both that morning equally lay
In leaves no step had trodden black.
Oh, I kept the first for another day!
Yet knowing how way leads on to way,
I doubted if I should ever come back*

*I shall be telling this with a sigh
Somewhere ages and ages hence:
Two roads diverged in a wood, and I—
I took the one less travelled by,
And that has made all the difference.*
[The Road Not Taken, by Robert Frost]

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DECLARATION

PhD THESIS TITLE: Understanding the Evolutionary Radiation of the Megadiverse Monkey Beetle Fauna (Scarabaeidae: Hopliini) of South Africa.

I, Jonathan F. Colville

Hereby

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Beta diversity data was run by Simon Ferrier and Glenn Manion in their generalised dissimilarity software. Python programming script was written by Kevin Colville. GIS maps were drawn by Peter Bradshaw. Richard Cowling compiled plant species similarity matrix for bioregions.

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ABSTRACT

AIMS

South Africa is the global centre of diversification for monkey beetles (Scarabaeidae: Hopliini), with 98% of the 1040 South African species and 80% of the genera endemic to this country. This thesis is the first analysis of the regional distribution patterns, and the processes underlying the generation of the megadiverse monkey beetle fauna of South Africa. Specifically, the aims of the thesis are to:

1. Identify hotspots of richness and endemism, and to explore the relationship between area and richness.
2. Compare centres of endemism of monkey beetles with those of other faunal and floral taxa, and to investigate patterns of biogeographic congruence.
3. Explore the role of local environmental factors (rainfall, temperature, habitat heterogeneity, host plant diversity) as explanatory variables of regional richness patterns of monkey beetles.
4. Model spatial turnover (beta diversity) in beetle community composition as a function of environmental (rainfall, temperature, altitude, soil fertility) and plant (host species, vegetation types, and bioregions) variables.
5. Describe and quantify patterns of sexual dimorphism and putative sexually selected traits and investigate the role of sexual selection in the generation of species richness.

METHODS

A geo-referenced presence-only dataset, comprising 6959 unique point locality records for the 1040 monkey beetles species currently recognised in South Africa, was compiled from field observations and museum collections and analysed with a geographical information system (GIS), to portray spatial variations in richness and endemism. Centres of endemism were delimited using an Integrated Weighting technique in conjunction with GIS interrogation and then spatially matched to other faunal and floral biogeographic centres to search for congruence.

Localised regression techniques were used to relate regional beetle richness patterns and beta diversity measures of monkey beetles and associated host plants to smaller scale environmental explanatory variables (rainfall, temperature, habitat heterogeneity, host plant diversity).

Generalised dissimilarity models (GDM) were used to explore compositional dissimilarity (beta diversity) as a function of environmental (rainfall, temperature, altitude, soil fertility) and plant (host species, vegetation types, and bioregions) variables, at regional (quarter degree grid cells; presence-only data) and field survey (presence/absence data from winter rainfall field survey sites) scales.

Leg and colour dimorphism was measured across two beetle feeding guilds, Embedders (relatively sessile beetles feeding embedded in the capitulum of disk-shaped flowers) and Non-embedders (highly mobile beetles feeding on a wider range of flower shapes), in order to explore the possible evolutionary role of sexual selection influencing rates of speciation.

RESULTS

1) Hotspots of richness and endemism for South African monkey beetles were concentrated within the winter rainfall biomes (Fynbos and Succulent Karoo). The Fynbos Biome showed the highest beetle richness, accumulated species significantly faster and showed higher richness per unit habitat area. Habitat heterogeneity was indicated as more important than area *per se* in explaining species richness.

2) 18 centres of endemism were delimited, the largest were located in the winter rainfall western regions and these recorded the highest levels of endemism and species richness. Within these regions, fairly good spatial congruence with plant and other insect biogeographic centres was seen, highlighting the presence of shared centres of diversification across taxonomic groups.

3) Plant richness was an important predictor of regional beetle richness, but the predictive power of explanatory variables (rainfall, temperature, habitat heterogeneity, host plant diversity) varied geographically (strong spatial non-stationarity), and is fundamentally different between the winter rainfall and summer rainfall areas.

4) Spatial turnover (beta diversity) at field site and regional scales was most strongly correlated with environmental factors (rainfall, temperature, altitude, soil fertility), though plant variables related to habitat heterogeneity of vegetation types and bioregions were also important. Interestingly, geographic distance between sites only explained minimal amounts of species turnover at both data scales.

5) Striking and highly divergent secondary sexual traits (hind leg and colour) were features of a high percentage of species. Dimorphism patterns were strongly linked to feeding guild (Embedders and Non-embedders) and mating system (aggressive male-male combat with prolonged mate guarding in the former vs. non-aggressive combat, with limited mate guarding in the latter). Leg dimorphism was almost exclusively associated with Embedders. In contrast, colour dimorphism occurred in equally high frequencies across both guilds.

MAIN CONCLUSIONS

The winter rainfall biomes (Fynbos and Succulent Karoo) are global centres of monkey beetle endemism and richness. Endemism was found to be strongly associated with monkey beetle species richness. Moreover, congruence was observed between centres of monkey beetle endemism and those of other taxa, including plants. This pattern suggests a coevolved response to, and with the plant radiation in the winter rainfall biomes of South Africa. Furthermore, the diverse and species rich

invertebrate fauna of these biomes, which includes strong representation of relictual taxa, probably owes its persistence to the absence of extreme climatic conditions during the Pleistocene. Despite this congruence, spatial variation was noted in the association of plant richness as a predictor of beetle richness, highlighting the importance of using a modelling approach that can relate regional richness patterns with smaller scale variations in host plant diversity, rainfall, temperature, and habitat heterogeneity.

With regards to turnover, at both regional and field site scales, beetle beta diversity was strongly correlated with environmental and plant variables, but the former appears to be a slightly stronger predictor of beetle turnover. Interestingly, and in contrast to other species-rich regions, geographic distance between sites explained minimal amounts of species turnover. Furthermore, within the beetle-rich winter rainfall biomes, high beetle alpha diversity was matched by high beta diversity indicating that locally co-existing species do not represent a large proportion of the regional species pool.

Ecological models incorporating environmental and plant variables, unsurprisingly, do not fully account for variation in beetle species diversity. The prevalence of pronounced sexual dimorphism suggests that strong sexual selection pressures may be an important driving force of speciation and thus an additional explanatory factor in species diversity.

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“...after plentiful rains had fallen, the whole country was a vast carpet of marigolds tenanted by numberless Hopliini” – L. Péringuey (1902).

INTRODUCTION

Biogeographers and ecologists seek to understand patterns of species distribution and diversity and the processes that produce them (Rosenzweig 1995, Gaston 2000). As David Currie (2007) succinctly asked “*Why are there more organisms ... here than there?*” This question is particularly pertinent to the megadiverse taxon Insecta - perhaps the most evolutionary successful group ever (Grimaldi and Engel 2005). Over 400 million years of evolution has resulted in a bewildering number of species, and functional ‘grades of evolution’. Moreover, their pivotal role and dominance in terrestrial ecosystems is undisputed (Wilson 1992).

PATTERNS OF INSECT DIVERSITY AND DISTRIBUTION IN SOUTH AFRICA

Southern Africa has a rich and diverse insect fauna (Scholtz and Holm 1985, Scholtz and Chown 1995), characterised by high levels of endemism, often of phylogenetically ‘deep’ lineages (Picker and Samways 1996, Wishart and Day 2002, Klass et al. 2003). Moreover, the fauna has various unusual components, including a very well-represented palaeoendemic element (Stuckenberg 1962, Endrödy-Younga 1988, Stuckenberg 2000, Day 2005), and novel adaptive radiations of various pollinator groups (Goldblatt and Manning 1998, Goldblatt and Manning 2000, Whitehead and Steiner 2001). The magnitude of this rich faunal diversity is still not totally explored (Hesse 1969, Bowden 1978, Kuhlmann 2005) with remarkable recent discoveries of new taxa, such as a new insect order (Picker et al. 2002, Colville 2006).

The rich monkey beetle (Scarabaeoidea: Melolonthinae: Hopliini) fauna of South Africa was recognized at the turn of the previous century by Péringuey (1902) who remarked: “*The number of genera and species of Hopliini occurring in South Africa is the most striking feature of the Coleopterous fauna of this part of the world*”. Thus, monkey beetles are an ideal group for insect biogeographical studies in South Africa because of their exceptional diversity and high levels of endemism (Table 1). South Africa is the global centre of diversification for monkey beetles (Scarabaeidae: Hopliini), with 98% of the 1040 species and 80% of the genera endemic to this country (Table 1).

Table 1. Number of Hopliini species and genera found within South Africa in comparison to other African countries and World regional areas. Number of endemic species and genera are given for each country and region where adequate data were available. Grey shading represent the three most speciose and endemic rich regions.

Country/Continental Region	Total Species (% of World total)	Number endemic (% of total species for that region)	Total number of genera (% of World total)	Number of endemic genera (% of total genera)	Mean number of species/genus
South Africa	1040 (63.07)	1032 (98.9)	51 (38.35)	41 (80.4)	20.5
Namibia	17 (1.03)	10 (58.8)	7 (5.26)	2 (28.6)	2.4
Angola	12 (0.73)	6 (50.0)	4 (0)	0	3.0
Botswana	1 (0.06)	1 (100.0)	1 (0.75)	1 (100)	1.0
Tanzania	7 (0.42)	3 (42.9)	6 (4.51)	0	1.2
Zimbabwe	4 (0.24)	3 (75.0)	4 (3.01)	0	1.0
Mozambique	3 (0.18)	2 (66.7)	2 (0)	0	1.5
Ruanda	2 (0.12)	1 (50.0)	2 (1.50)	0	1.0
Burundi	1 (0.06)	0 (0.0)	1 (0.75)	0	1.0
Malawi	1 (0.06)	0 (0.0)	1 (0.75)	0	1.0
Zaire	11 (0.67)	7 (63.6)	6 (4.51)	1 (16.7)	1.8
Other African countries ^{SS}	7 (0.42)	7 (100.0)	1 (0.75)	0	7.0
North Africa ^{NS}	5 (0.3)	3 (60.0)	1 (0.75)	0	5.0
Madagascar	302 (18.31)	302 (100.0)	40 (30.08)	39 (97.5)	7.6
Asia	185 ^{HH} (11.22)	40 ^H (21.6 ^H)	13 (9.77)	12 (92.3)	3.3
Europe	34 (2.06)	?	1 (0.75)	0	34.0
North America	30 (1.82)	?	1 (0.75)	0	30.0
South America	2 (0.12)	2 (100.0)	1 (0.75)	0	2.0
Total:	∑ = 1649^A	1417	133	96	Average = 6.7 (±10.3)

Taxonomic references used in compilation of table: General - (Burmeister 1844, von-Dalla-Torre 1913); southern Africa - (Péringuey 1888, 1902, von-Dalla-Torre 1913, Schein 1950-1951, Schein 1958, Schein 1959a, Schein 1959b, Kulzer 1960, Andreae 1965, Dombrow 1997, 1997a, 1997b, 1997c, 1997e, 1998a, 1998b, 2000a, 2000b, 2001a, 2001b, 2001c, 2002a, 2002b, 2002c, 2002d, 2002e, 2002f, 2003); Angola - (Moser 1918, 1919); North Africa - (Reitter 1890, Baraud 1981); Madagascar - (Lacroix 1997, 1998); Nearctic - (Arnett 1963, Hardy 1977); Palearctic - (Reitter 1902, Medvedev 1949, Tesar 1969, 1971, Sabatinelli 1983); Europe - (Baraud 1977, 1992).

^AThe total number of World species is an approximation from literature sources, undescribed species, and personal communication with Holger Dombrow (Hopliini taxonomist).

^{SS}South of the Sahara; ^{NS}North of the Sahara.

^{HH}Including the genus *Hoplia* Illiger 1803, ^HExcluding the genus *Hoplia*, as species endemic to this genus within the Asian region could not be determined. Approximately 144 species of this genus are known from the Asian region.

Plant biogeographic studies have revealed high concentrations of species and local endemics in the winter-rainfall regions of South Africa (Goldblatt and Manning 2002, Born et al. 2007). Two global floristic biodiversity hotspots are recognised within these regions – the Cape Floristic Region and Succulent Karoo (Myers et al. 2000). Péringuey (1902) noted the abundance of monkey beetle species and genera that were restricted to this floristically diverse and unique area. Furthermore, several other insect groups (Dirsh 1965, Tjeder 1967, Klass et al. 2003), particularly pollinators (Eardley 1989,

Whitehead and Steiner 2001, Barraclough 2006), have their highest global levels of diversity and endemism and their greatest adaptive radiation within the winter-rainfall region.

This biotic uniqueness is generally attributed to the Mediterranean climatic system, which is restricted to the extreme south western parts of Africa, and a strong presence of southern Gondwanan elements which have persisted in, and are endemic to, temperate, montane refugia (Stuckenberg 1962, Endrödy-Younga 1988, Day 2005). Palaeo-elements may be both localised relics e.g. stag beetles (Endrödy-Younga 1988) and vermilionid flies (Stuckenberg 1996), and common occurring, wide-spread taxa, e.g. the occurrence within the Cape fauna of world-wide, speciose, and abundant Bombyliid fly taxa that are of at least Gondwana or Laurasian origin (Bowden 1978). This complex biotic assemblage allows for interesting floristic – faunal comparisons of diversity and endemism in a biodiversity hotspot, and the exploration of the potential causes for the profuse evolutionary radiations that this region has witnessed.

Early zoogeographic studies generally did not relate insect distributional patterns in terms of ecology and history (see references in Werger 1978), but confined their approaches to historical zoogeography. These early studies were, however, invaluable in subdividing Africa into a number of clearly defined zoogeographical zones (Carcasson 1964; and see references in Werger 1978), but they were based on a largely intuitive approach to examining species distribution maps, and the studies were essentially unrepeatable because of the lack of empirical techniques (Linder 2001).

Detailed, modern biogeographical studies on South African insects are to date conspicuously lacking. Modern analytical techniques have enabled the objective analysis of large taxonomic and distributional datasets and identification of biogeographic patterns, such as centres of endemism (e.g. parsimony analysis of endemism – PAE (Rosen 1988). Recently, modern clustering techniques have been undertaken for a number plant groups within southern Africa (Linder et al. 2005, Born et al. 2007), but these techniques have by and large not been utilized for faunal studies. Geographic information systems (GIS) have further revolutionized the analysis of spatial data allowing more detailed ecological zoogeographic studies (Minter et al. 2004, Foody 2007). Progression of techniques have evolved from descriptive accounts based on expert knowledge of a group, e.g. Masarine wasps (Gess 1992) through to GIS based empirical analyses using point locality data in conjunction with GIS environmental themes, e.g. for scorpions (Prendini 2005). Another modern spatial techniques used on southern African insect group is phylogeography, although few such studies exist for the region e.g. that for flightless *Scarabaeus* dung beetles (Sole et al. 2005).

Some of the above techniques are employed in the current study to explore biogeographic patterns in South African monkey beetles. The rich monkey beetle fauna of South Africa makes them an ideal group for insect biogeographical studies in South Africa because of their diversity and high levels of endemism. In addition, the co-occurrence of faunal and floristic diversity within the winter rainfall biomes allows for interesting floristic – faunal comparisons of diversity and endemism in two biodiversity hotspots.

Beyond their role in testing biogeographic hypotheses, knowledge of monkey beetle distribution and diversity patterns has important conservation implications, particularly within the winter rainfall areas. The very rich insect fauna of this region has been all but ignored in conservation profiles (Hamer and Slotow 2002, Cowling et al. 2004, Colville 2006) and conservation decisions have been based largely on plant data, with the occasional inclusion of vertebrate data where this is available. However, vertebrate groups show low levels of endemism and adaptive radiation in comparison to that of the insects (Vernon 1999). Insects are generally underrepresented in conservation planning because of the large number of species involved, the poor taxonomic state of many of the groups and the difficulty of identifying the taxa from general collections. Nonetheless, conservation planning in the absence of such data is unlikely to protect the biggest component of biodiversity.

EXPLAINING PATTERNS – HISTORICAL, ECOLOGICAL, AND EVOLUTIONARY PROCESSES

CENTRES OF ENDEMISM

Establishing patterns of areas over-represented in range restricted taxa is one of the fundamental steps in historical biogeography (Nelson and Platnick 1981). Such areas of unique evolutionary history are commonly referred to as “centres of endemism”. These areas are generally accepted to represent centres of diversification and clade origin (Croizat et al. 1974, Ricklefs and Schuller 1993), and are therefore good indicators of zoogeographic regions.

In addition, delimiting centres of endemism provides ‘units of area’ (Hausdorf 2002) to work with in searching for congruent biogeographical patterns across taxa (“biogeographic homology” – Morrone 2001) in terms of their respective putative centres of diversification (Rosen 1978, Calsbeek et al. 2003). Patterns of centres of endemism can also be placed within their historical context of landscape evolution (e.g. geomorphic changes – Cowling et al. 2008). Thus, centres of endemism provide insights into the evolutionary history of an area and its associated biota and help explain contemporary patterns of species distributions.

Clustering techniques used in the delimitation of centres of endemism have been progressively refined to account for both wide-spread and narrow range restricted taxa (Williams 1992, Linder 2001). Such statistical approaches include the use of various weighting techniques which maximize the valuable information obtained from range restricted taxa, while reducing the noise created by less informative, wide-spread taxa (Nelson and Platnick 1981, Linder 2001, Bradshaw and Linder 2009). Recently, Bradshaw and Linder (2009) have developed an integrated weighting technique that uses a range of modern weighting techniques to seek spatial congruence in the results obtained from multiple clustering analyses. Furthermore, they refine delimited centres based on the best results from each technique by investigating results within GIS, which allows areas of congruence and conflict to be highlighted, and subsequently interrogated and resolved (see also Huang et al. 2008). Thus, this approach effectively delimits centres in terms of their physical size and numbers of endemics captured.

Within South Africa, advanced clustering techniques for delimiting centres of endemism have been undertaken for a number of plant groups (Linder et al. 2005, Born et al. 2007). However, the work presented in this thesis represents the first study to utilize these recently developed techniques in a faunal study. Ironically, the only previous study delimiting centres of endemism for a South African insect group (Morrone 1994) did not place any biogeographical or ecological context to its findings, but rather used the insect group of choice purely to highlight a methodological approach (parsimony analysis) used in delimiting areas of endemism.

Centres of endemism are representative of areas of high conservation importance (Lamoreux et al. 2006) and are weighted heavily in conservation assessments when assigning global “hotspot” status (cf. Cape Floristic Region (Myers et al. 2001)). Moreover, their underlying character of reflecting historical evolutionary processes highlights their importance in conservation strategies that seek spatial surrogates which capture key processes, for example geographic speciation and local adaptation (Rouget et al. 2003).

ENVIRONMENTAL AND FLORAL CORRELATES OF INSECT DIVERSITY

SPECIES RICHNESS

The ecological literature is replete with studies focusing on the explanatory variables associated with regional richness gradients (Currie et al. 1999, Gaston 2000). Regional richness of plants and animals appears to be strongly influenced primarily by climate, especially energy and water (Pianka 1967, Currie 1991, Wright et al. 1993, Hawkins et al. 2003, Rodríguez et al. 2005) and habitat heterogeneity (topography, vegetation types) (Rosenzweig 1995, Kerr 2001). The most important variables in

explaining regional richness patterns are captured in five, well-known hypotheses: three associated with energy (ambient energy, water-energy balances, and for animals, plant productivity), one with habitat heterogeneity, and one associated with climatic stability (Wright et al. 1993, Gaston 2000, Rodríguez et al. 2005). However, the spatial scale at which these abiotic and biotic variables are investigated often determines their explanatory power (Foody 2004). Furthermore, the geographic range of the species under study can influence observed species richness patterns (Jetz et al. 2007).

To date, studies focusing on ecological determinants explaining insect species richness, mostly seek explanatory variables from the close association many insect groups have with plants and plant communities (Murdoch et al. 1972, Strong et al. 1984, Miller 1987, Gaston 1992, Hawkins and Porter 2003, Novotny et al. 2006, Condon et al. 2008). Plants are hypothesized to be strongly influential in insect diversification and almost half of all insects appear to have co-radiated with angiosperms (Grimaldi and Engel 2005). A host of studies have shown that various plant variables, including taxonomic diversity (Barraclough et al. 1998, Hawkins and Porter 2003, Novotny et al. 2006); phylogenetic diversity (Symons and Beccaloni 1999, Proches et al. 2009); architectural (fractal) complexity (Strong et al. 1984); host specificity (Ehrlich and Raven 1964, Schoonhoven et al. 1998, Dyer et al. 2007); host geographic range (Southwood 1961, Cornell 1985); and the evolutionary arms race between insects and plants (Mitter and Farrell 1991, Mello and Silva-Filho 2002) are able to explain insect richness patterns with varying degrees of success.

However, there are many insect groups that are not directly associated with plants and even amongst phytophagous insect groups, plant explanatory variables have not always correlated with insect richness patterns (Hawkins and Porter 2003, Hunt et al. 2007, Condon et al. 2008). Moreover, convincing evidence of reciprocal diversifying co-evolutionary relationships between plants and insects has as yet not been established (Schoonhoven et al., Miller, 1987; Hawkins and Porter, 2003), suggesting that environmental and climatic factors maybe important drivers of insect diversification.

Energy, habitat heterogeneity and climatic stability are broad scale ecological processes that are good explanatory variables for insect richness patterns (Turner et al. 1987, Wright et al. 1993, Kerr et al. 2001, Gotelli and Ellison 2002). In addition, topography and edaphic requirements are also important (Irish 1990, Gess and Gess 1998, Gervais and Shapiro 1999, Prendini 2001b, Sole et al. 2005, Colville 2006, Botes et al. 2007). Thus, as for other faunal and floral groups, insect richness patterns appear to be determined by a complex, and often interacting suite of ecological factors.

As mentioned above, South Africa supports a remarkably speciose and endemic-rich insect fauna. Within the political boundaries of the country there are two main centres of insect diversity: a western winter rainfall centre; and an eastern summer rainfall tropical and subtropical centre (Hesse 1969, Usher 1972, Endrödy-Younga 1978, Mansell 1985, Kuhlmann 2005). The Fynbos and Succulent Karoo Biomes in the west are predominantly winter-rainfall biomes, comprised of temperate, mesic, and semi-arid to arid habitats (Cowling et al. 1999, Mucina and Rutherford 2006). They make up approximately only 14% of the relative biome area of South Africa, whereas the eastern biomes make up roughly 60%; the rest being the arid biomes of the central part of the region (Mucina and Rutherford 2006). Furthermore, in terms of standard climatic variables related to high energy and favourable environments conducive to high species richness, the Fynbos and Succulent Karoo biomes show noticeably lower values, with a clear east-west gradient in the severity of summer drought conditions extending across South Africa (O'Brien 1993, Cowling et al. 1997, Schulze 1997).

In comparison to eastern biomes of South Africa, the Fynbos and Succulent Karoo biomes in the west are overrepresented in term of species richness for a number of insect groups (Tjeder 1967, Mansell 1985, Gess 1992, Kuhlmann 2005, Colville 2006). They also show remarkably high levels of plant richness and endemism (Cowling et al. 1989, Cowling et al. 1998, Cowling et al. 1999). This pattern of high richness in relatively water and energy poor biomes contrasts with several ecological axioms that associate areas of high energy and abundant water (e.g. tropical rain forests) predicatively contain higher species richness (Currie 1991, Hawkins et al. 2003). Furthermore, the importance of area size and associated habitat heterogeneity in determining species richness would also predict greater richness associated with the larger sized and habitat diverse eastern Savanna and Grassland biomes (Rosenzweig 1995, Cowling et al. 1997).

The winter-rainfall biomes provide interesting global and local contrasts for recognised explanatory variables determining insect richness patterns. Fynbos and Succulent Karoo are highly heterogeneous habitats with characteristically steep environmental and floristic gradients (Cowling et al. 1997, Goldblatt and Manning 2002, Latimer et al. 2005). Furthermore, these two biomes appear to be reasonably climatically stable (Cowling et al. 1997, Cowling et al. 1998, Cowling et al. 1999), with western fynbos areas showing climatic stability extending over evolutionary time (Cowling and Lombard 2002, Linder 2003). To date, however, only a handful of studies have focussed their attentions on explaining insect richness patterns within the Fynbos and Succulent Karoo biomes. Of particular interest is the relationship between the very diverse flora and insect diversity within the Cape Floristic Region (CFR) (Picker and Samways 1996, Wright and Samways 1998, Giliomee 2003, Proches and Cowling 2006, Proches et al. 2009). Findings to date suggest that overall plant species richness (Wright and Samways 1998, Proches

and Cowling 2006), plant phylogenetic diversity (Proches et al. 2009), host plant diversity (Gess 1992, Wright and Samways 2000), parasitoid host diversity (Gess and Gess 1998), soil type (Gess and Gess 1998) and temperature (Stuckenberg 1969, Botes et al. 2006, Botes et al. 2007) are all important ecological factors explaining insect richness. High species turnover, or beta diversity, a potentially strong influential component of regional diversity (Whittaker 1972), further appears to be a significant explanatory variable (Colville et al. 2002).

Almost all of these studies, however, have focussed on sub-sets of insect distributions and richness patterns within South Africa, using correlations between local insect richness calculated from field study site data and associated localised ecological variables, thus limiting the spatial context of their findings (Currie et al. 1999). Moreover, the single study incorporating a full distributional data set (Gess 1992) did not statistically relate richness patterns with ecological variables, but instead used expert natural history knowledge and matching broad based plant patterns in explaining Masarine wasp richness patterns across South Africa.

This study uses recently developed local regression techniques (Fotheringham et al. 2002, Foody 2004) to model regional monkey beetle richness and investigates the power of environmental and plant variables in explaining species richness.

BETA DIVERSITY

The change in species composition (beta diversity, species turnover or compositional dissimilarity) along ecological and geographic gradients has fascinated ecologists for many decades. Robert H. Whittaker in two seminal papers (Whittaker 1960, Whittaker 1972) first introduced the concept of beta diversity and studied the changes in species composition between communities and their ecological and spatial determinants. Subsequently, a plethora of beta diversity measurements and approaches have been developed (Wilson and Mohler 1983, Lennon et al. 2001, Koleff et al. 2003, Kiflawi and Spencer 2004, Legendre et al. 2005, Harborne et al. 2006, Tuomisto and Ruokolainen 2006, Ferrier et al. 2007) with some confusion developing within the ecological literature (Laiberte 2008, Legendre et al. 2008, Pelissier et al. 2008, Tuomisto and Ruokolainen 2008). Further, the statistical appropriateness of the mostly linear approaches used when measuring species similarities across sites has been questioned (Faith and Ferrier 2002, Ferrier 2002, Ferrier et al. 2007). Nonetheless, the ecological importance of beta diversity in understanding regional diversity patterns (Whittaker 1972, Cody 1986, Cowling et al. 1989, Cowling 1990, Kerr et al. 2001, Veech et al. 2002, Kiflawi and Spencer 2004, Beck and van Khen 2007, McKnight et al. 2007) and its important role in biodiversity assessment and conservation planning (Ferrier et al.

1999, Lombard et al. 1999, Condit et al. 2002, Ferrier 2002, Steinitz et al. 2005, Ferrier et al. 2007) is widely appreciated. A further important, and perhaps more appealing role of beta diversity, has been its use in estimates of terrestrial global species richness (Erwin 1982, Gaston 1991), especially for the megadiverse tropical rainforests (Lewinsohn and Roslin 2008).

Hypotheses focussing on explaining beta diversity have most often explored determinants of the dimensions of ecological niches and dispersal abilities. Of recent interest within the beta diversity literature is the partitioning of explained percentage variance for species compositional similarity into its component parts of geographic distance only, environmental variables only, and distance and environmental variables combined (Borcard et al. 1992, Ferrier et al. 1999, Duivenvoorden et al. 2002, Faith and Ferrier 2002, Tuomisto et al. 2003, Steinitz et al. 2005, Chust et al. 2006, Ferrier et al. 2007). Typically, an unexplained component remains, which indicates missing unmeasured environmental variables (Faith and Ferrier 2002). A recently developed statistical model – generalised dissimilarity models (GDM) (Ferrier et al. 2002, 2007) – is effective in modelling spatial turnover in species composition across sites in relation to geographic distance and the environmental variation between sites, in that explained variance can be easily partitioned into component parts, and the influence on turnover patterns of individual environmental variables can be assessed. GDM models have the further advantage that they use a more ecologically realistic non-linear approach to matrix regression (Ferrier 2002, Ferrier et al. 2007). To date, most commonly used linear distance matrix approaches (Legendre and Legendre 1998, Legendre et al. 2005) to modelling compositional dissimilarities have been limited by two violations of non-linearity (De'ath 1999, Ferrier 2002): (i) the relationship between species compositional dissimilarity and geographic distance is in fact asymptotic (Gauch 1973, Faith et al. 1987, Cody 1993, Faith and Ferrier 2002); and (ii) the rate of change of species composition across environmental gradients is most often not constant (i.e. shows non-stationarity), but fluctuates along respective gradients (see e.g. Simmons and Cowling 1996). Furthermore, GDM models offer several advantages for biodiversity assessment and planning relative to other dissimilarity techniques (Faith and Ferrier 2002, Ferrier et al. 2002, 2007).

Within South Africa, patterns and determinants of beta diversity have been poorly studied, particularly across regional scales, and are less well understood than patterns in species richness or within habitat (alpha) diversity (Cowling et al. 1989, Cowling 1990). Those studies that have explored beta diversity have focussed almost exclusively on the role of environmental gradients (Sigfried and Crowe 1983, Cody 1986, Cowling et al. 1989, Samways 1989, Cowling 1990, Palmer and Cowling 1994, Simmons and Cowling 1996, Davis et al. 1999, van Rensburg et al. 1999, Bond et al. 2001, Gaston et al. 2001, Colville et al. 2002, van Rensburg et al. 2004, Botes et al. 2006, Botes et al. 2007). In addition, Latimer et al.

(2005), focussed on the plant rich Cape Floristic Region, which shows high beta diversity. The study highlighted weak migration (dispersal) rates associated with fynbos plant communities (Linder 1985).

The role of biotic factors such as competition, predation etc. has, however, not been established.

Moreover, the influence of geographic distance on species turnover has been essentially studied in the context of gamma diversity (Cody 1986, Cowling et al. 1989, Cowling et al. 1992). However, the largest and perhaps most important gap in our knowledge on beta diversity patterns within South Africa, is the possible sharing of similar spatial beta diversity patterns across disparate taxa (see Mcknight et al. 2007). This study models the spatial turnover in beetle community composition (beta diversity) between pairs of sites as a function of geographic distance, and environmental (rainfall, temperature, altitude, soil fertility) and plant (host species, vegetation types, and bioregions) differences.

EVOLUTIONARY RADIATIONS

SEXUAL DIMORPHISM AND SEXUAL SELECTION

The exaggerated morphology of many male insects (Emlen and Nijhout 2000) suggests that climatic and environmental factors are not the only processes that drive speciation. Sexual dimorphism was explained originally by Darwin (1871) through his theory of sexual selection as a result of competition for mates involving male-male combat or female choice. Fisher (1930) in his seminal study built on Darwin's theory of sexual selection and through his "runaway process" was able to explain the evolution of secondary sexual traits through mate choice. Lande (1981) used genetic models to show that male secondary sexual traits and female preferences can evolve in a Fisherian runaway process. He was able to show that sexual selection could promote speciation through reproductive isolation through diversification of secondary sexual traits. Sexual selection and related processes (e.g. sexual conflict) can generate rapid evolutionary divergence of traits involved in reproduction (Arnqvist et al. 2000, Panhuis et al. 2001, Ritchie 2007), thus resulting in differential mating success among individuals within a population (Andersson 1994, Andersson and Simmons 2006). This divergence can be independent of ecological differences and is considered a strong possible driver of sympatric speciation in that sexual selection can cause divergence in a uniform mating system of a population, effectively reproductively isolating part of a population causing sympatric speciation (Higashi et al. 1999, Seehausen and Alphen 1999, Gavrilets and Waxman 2002).

Subsequently, empirical and theoretical studies have shown sexual selection to be a strong driving force in speciation (West-Eberhard 1983, Barraclough et al. 1995, Møller and Cuervo 1998, Higashi et al. 1999,

Gray and Cade 2000, Panhuis et al. 2001, Gage et al. 2002). In addition, strong correlative support for a role of sexual selection in promoting rates of speciation comes from studies relating species richness between sister taxa possessing various surrogates of sexual selection (Barraclough et al. 1995, Møller and Cuervo 1998). However, some debate exists about the direct role on speciation by sexual selection, with arguments suggesting that it rather occurs either in conjunction with ecological divergence in sympatry or that natural selection is the overriding force (Gage et al. 2002, Ritchie 2007).

A related process of sexual selection, sexual conflict or “differing evolutionary interests of the two sexes” (Parker and Partridge 1998) has recently been recognised as being widespread amongst animals (Chapman et al. 2003, Parker 2006). Furthermore, it is recognised as a strong evolutionary force inducing antagonistic co-evolution between males and females, which in turn has the ability to generate rapid divergence in traits involved in reproduction, with subsequent speciation through reproductive isolation (Holland and Rice 1998, Parker and Partridge 1998, Arnqvist et al. 2000, Gavrillets 2000, Arnqvist and Rowe 2002, Gavrillets and Waxman 2002, Martin and Hosken 2003). Sexual conflict in insects is particularly well developed with conflict seen pre- and post-copulation (Thornhill and Alcock 1983). The influence of inter-specific sexual conflict has also been shown to be a strong driving force causing trait divergence, e.g. colour polymorphism (Johnson 1975).

Most studies focussing on speciation through sexual selection have concentrated on female choice (Fisher 1930, Andersson 1994, Arnqvist et al. 2000, Andersson and Simmons 2006, Emlen 2008). However, the role of male-male combat in competition over females and resources required for procuring females (e.g. feeding and oviposition sites), is seen as a powerful selective force in explaining the huge diversification recorded in the array of weaponry used in male contests (Darwin 1871, Andersson 1994, Moczek 2005, Emlen 2008). Beetles, bugs, bees, wasps, ants, flies, and earwigs all have representatives showing exaggerated and often highly diverse weaponry (reviewed in Emlen 2008). Scarab (Scarabaeoidea) beetles, due to their well-known and bizarre array of horn development have attracted the most interest and are a particularly well studied group (Emlen et al. 2005, Hosoya and Araya 2005, Moczek 2005).

The South African monkey beetles appear to be highly unusual amongst the world’s Hopliini in that they display high levels of sexual dimorphism (colour and hind legs) (von-Dalla-Torre 1913, Lacroix 1997, 1998). In addition, the occurrence of dimorphism in hind leg traits for monkey beetles appears to be a highly unusual occurrence within the super-family Scarabaeoidea (see Emlen 2008 for list of exaggerated secondary sexual traits in the Coleoptera).

Male-male combat is a common feature of many species of monkey beetle (Louw 1987, Midgley 1992, Picker and Midgley 1994). Males, using their enlarged hind legs as weapons, will aggressively fight rival males over females, and have also been observed to guard females post-copulation for extended periods of time (Midgley 1992, Lewis 2007). Females are polyandrous, mating with multiple males (Lewis 2007). Furthermore, the ratio of males to females within populations appears to be strongly male biased (Louw 1987, Midgley 1992). Thus, the competition between males appears to be high. Moreover, due to the lengthy periods of male guarding and the relatively sessile nature of the females there exists extended opportunities for male-male combat (Thornhill and Alcock 1983, Saeki et al. 2005), and the possibility of antagonistic sexual conflict (Gosden and Svensson 2007, Svensson et al. 2007).

In South Africa, mating and feeding for most species of monkey beetle takes place on disc-shaped flowers (Asteraceae, Aizoaceae) and bowl-shaped geophytic flowers, which are large, and offer an ideal platform for feeding, mating and male-male combat (Picker and Midgley 1996, Steiner 1998). Several geophytic plant families pollinated by monkey beetles show strong convergent evolution towards bowl shaped flowers (Goldblatt and Manning 1998). Flowers are thus focal points of monkey beetle activity (Péringuey 1902). Furthermore, within their centre of adaptive radiation, host flowers emerge in mass spring flowering displays (Cowling et al. 1999). Monkey beetle emergence is timed to coincide with this huge but ephemeral floristic resource during the spring months. Péringuey (1902) describing one of his (successful) spring collecting trips wrote: “...*so plentiful indeed that they [monkey beetles] had to be scooped by the hand from the flower into the killing bottle...*” The beetles only live for approximately 5-7 days (this study), so the temporal pressures for reproduction are seemingly also high. Thus, reproductive stresses are most likely high, generating elevated competition between males for securing females in a limited period of time.

Within this environment, three broad monkey beetle feeding guilds occur: two flower feeding guilds, the Embedding and Non-Embedding guilds (Picker and Midgley 1996), and a poorly known and studied assemblage of non-anthophilic species. Female Embedders feed partially, or wholly embedded inside the capitulum of the flower, with the pygidium being the only body part exposed. During this period they are inactive, remaining embedded in the same flower for up to a few days (Lewis 2007). Although sluggish fliers, male Embedders are more active, searching for females. Non-Embedding species are fast-flying, active pollinators (Picker and Midgley 1996, Steiner 1998, van Kleunen et al. 2007), visiting many flowers and feeding more superficially on pollen and nectar.

This study focuses on species found in the two feeding guilds of Embedders and Non-embedders. The two feeding guilds appear to differ in species richness, diversity of secondary sexual traits and degree of

sexual dimorphism. They thus provide a framework for testing the intensity of sexual selection (as measured by sexual dimorphism and degree of development of secondary sexual traits) against guild species richness. Strong sexual selection pressures have the potential to promote speciation and thus species richness, and may provide additional insights into species richness patterns over and above models utilizing purely ecological explanatory variables.

AIMS AND FORMAT OF THESIS

The central aim of this thesis was to explore the distribution and richness patterns of a unique and megadiverse group of pollinating beetles, the Hopliini (monkey beetles). Globally, the centre of diversification for monkey beetles is clearly South Africa with *ca.* 63% of the world's species located here, and with almost all these species (98%) and over three quarters (80%) of the genera being endemic to this country.

The thesis is presented as chapters that investigate and explain different aspects of monkey beetle diversity and distribution in South Africa. The chapters can be read as “stand alone” documents that will subsequently be adapted for publication. The chapters describe the patterns of richness and endemism of the South African Hopliini, and then attempt to explain these patterns through modelling of species richness and turnover (beta diversity), and investigating the evolutionary role of sexual selection as an explanatory factor in species diversity. The thesis as a whole develops around a logical progression of ideas, and compares the relative importance of these factors in explaining beetle biogeography. The overarching structure of the thesis therefore means that the whole is much greater than the parts.

The central theme of the thesis is a comprehensive analysis of the factors that explain the described patterns of monkey beetle distribution and diversity. Specifically, the following aims are addressed:

1. To locate hotspots of richness and endemism, and to explore the relationship between area and richness.
2. To compare monkey beetle centres of endemism with centres of endemism of other faunal and floral taxonomic groups, and to investigate patterns of biogeographic congruence.
3. To explore the role of local environmental factors (rainfall, temperature, habitat heterogeneity, host plant diversity) as explanatory variables of regional beetle richness patterns.
4. To model spatial turnover (beta diversity) in monkey beetle community composition as a function of environmental (rainfall, temperature, altitude, soil fertility) and plant (host species, vegetation types, and bioregions) variables.

5. To describe and quantify patterns of sexual dimorphism and putative sexually selected traits and investigate the evolutionary role of sexual selection as an explanatory factor in species diversity.

PART ONE - DIVERSITY, DISTRIBUTION PATTERNS AND ENDEMISM

In Chapter 1, a geo-referenced presence-only dataset, comprising 6959 unique point locality records for the 1040 monkey beetles species currently recognised in South Africa, is compiled and spatially analysed in a geographic information system (GIS). Patterns of hotspots for richness and endemism are highlighted as is the relationship between area and richness.

Chapter 2 delimits centres of endemism using modern analytical techniques (Linder 2001, Bradshaw and Linder 2009) and then examines the relationship between richness and endemism within centres.

Congruence with the beetle centres is identified amongst plant and insect groups, highlighting areas of biotic interest and shared evolutionary history. The diversity patterns observed in Chapter 1 and 2 of high concentrations of beetle richness within the winter rainfall, floristically rich and habitat heterogeneous biomes determines the analytical framework and techniques used in Chapter 3 and 4.

PART TWO – MODELLING SPECIES RICHNESS AND TURNOVER

In Chapter 3, localised regression techniques (Fotheringham et al. 2002, Foody 2004) are used to relate regional beetle richness patterns to smaller scale environmental (rainfall, temperature, habitat heterogeneity, host plant diversity) explanatory variables and diversity measures (beta diversity of monkey beetles and associated host plants). Chapter 4 examines compositional dissimilarity (beta diversity) as a function of environmental (rainfall, temperature, altitude, soil fertility) and plant (host species, vegetation types, and bioregions) gradients, at regional (quarter degree grid cells; presence-only data) and field survey (presence/absence data from winter rainfall field survey sites) scales.

PART THREE – SEXUAL DIMORPHISM AND SEXUAL SELECTION

Chapter 5 shifts focus from ecological explanations towards an evolutionary approach in order to explore sources of unaccounted variation in species diversity recorded in chapters three and four. This chapter describes and quantifies patterns of sexual dimorphism and putative sexually selected traits in monkey beetles and investigates the evolutionary role of sexual selection as an explanatory factor in species diversity. Finally, the thesis conclusions summarize the main findings and highlight their biogeographic and conservation significance.

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PART 1

DIVERSITY, DISTRIBUTION PATTERNS AND ENDEMISM

1 PATTERNS OF MONKEY BEETLE DIVERSITY AND DISTRIBUTION IN SOUTH AFRICA – ZOOGEOGRAPHIC ZONES AND AREA RELATIONSHIPS

ABSTRACT

Biogeographical patterns of regional insect distribution and diversity within South Africa are sorely lacking. This affects the basic understanding of areas of evolutionary interest (centres of speciation) and is of conservation importance. Early zoogeographical studies, using largely intuitive approaches, delimited several broad zoogeographical zones, with the western, climatically-distinct Cape Faunal Zone segregating from the Afrotropical fauna in the east. The western zone shows strong congruence with floristic global hotspots – the Cape Floristic Region and Succulent Karoo, highlighting its biotic importance. However, the insect components of these unique areas have been poorly studied. Here, I compile a distributional data set for South African monkey beetles, a speciose group of pollinating beetles, to further our understanding of regional patterns of diversity (hotspots of richness and endemism) and distribution (range restricted taxa and local habitat endemics) of South African insects. Observed richness patterns were investigated using species-area relationships as a primary measure of ecological pattern at several different ecological scales (biome, bioregion, and vegetation type). Spatial analysis of beetle distributions and hierarchical clustering analyses revealed two distinct zones: a high diversity, western, winter rainfall Cape Zone; and a lower diversity, eastern, summer rainfall Afrotropical zone. The beetles of the western zone appeared to have developed in isolation, with high numbers of range restricted taxa, local habitat endemics, and diversifications mostly confined to within and between its two component biomes. At the biome scale, species-area relationships showed area as a poor explanatory variable of richness, with the Fynbos and Succulent Karoo biomes showing disproportionately high beetle richness in relation to their areas. The western Fynbos and Succulent Karoo biomes showed the highest overall beetle richness; 541 and 364, respectively. In contrast, the Savanna Biome, which showed the highest beetle richness for eastern biomes, only recorded 82 species. At the finer bioregional scale, a third-order (cubic) polynomial regression better explained the relationship between area and beetle richness. However, at both the biome and bioregional scale, habitat heterogeneity (number of vegetation type habitats) appeared to be of greater importance than area in explaining beetle richness patterns. Focusing on habitat patch sizes within biomes, a significant but weak relationship between beetle richness and habitat patch size was recorded across biomes. A similar, but stronger relationship was seen across biomes when using more habitat heterogeneous bioregional patches. Focusing within specific biomes, for both vegetation and bioregional habitat patch sizes, the Fynbos Biome accumulated species faster than other biomes, and had higher richness per unit habitat area.

INTRODUCTION

“Patterns and processes” – a much favoured ecological expression and avenue of biological investigation. Of course, the first step needed in such investigations is seeking and describing patterns, be they spatial and/or temporal. Myers and Giller (1988) state: “The determination of species distribution patterns is a starting point for all biogeographic analysis” Thus, once biogeographic patterns of distribution and diversity have been found and described, they then can be placed within ecological processes and/or historical context. Furthermore, dominant processes change depending on the scale of analysis, and it is therefore important to link pattern, process and scale in biogeographic analysis (Girvetz and Greco 2007).

Detailed, modern biogeographical studies on South African insects are lacking. Early zoogeographic studies generally did not interpret insect distributional patterns in terms of ecology and history (see references in Werger 1978) and confined their approaches to historical zoogeography. A secondary shortcoming of these early studies was the largely intuitive approach to examining species distribution maps, with the lack of empirical techniques essentially making these studies unrepeatably (see Linder 2001). Modern analytical techniques have made it possible to analyse large taxonomic and distributional datasets and more objectively to identify biogeographic patterns, such as centres of endemism (e.g. parsimony analysis of endemism – PAE (Rosen 1988)). Nonetheless, these early studies were invaluable in subdividing Africa into a number of clearly defined zoogeographical zones (Carcasson 1964; and see references in Werger 1978).

Within southern Africa, the two most detailed maps for butterflies (Carcasson 1964) and beetles (Endrödy-Younga 1978) show broad zoogeographical congruence in their delimitation of zones. A strongly congruent pattern is the uniqueness of the Cape fauna, demonstrated by repeated retrieval in disparate faunal groups (Ponyton 1961, Dirsch 1965, Tjeder 1967, Hesse 1969, Usher 1972, Mansell 1985, Crowe 1990, Gess 1992, Stuckenberg 1998, 2000, Greathead and Evenhuis 2001, Wishart and Day 2002, Klass et al. 2003, Alexander et al. 2004, Kulhmann 2005, Prendini 2005, Sole et al. 2005, Barraclough 2006, Dippenaar-Schoeman and Gonzalez 2006, Ribera and Balke 2007). The uniqueness of the Cape as a biotic zone is strongly supported by phytogeographical studies (Goldblatt and Manning 2002, Born et al. 2007). This is exemplified by the high levels of diversity and endemism recorded for the Cape region, often at high taxonomic levels, for floral (Goldblatt and Manning 2002, Helme and Trinder-Smith 2006) and invertebrate faunal elements (Picker and Samways 1996, Sharrat et al. 2000). This biotic uniqueness is generally attributed to its Mediterranean climatic system and a strong presence of southern Gondwanan elements which have persisted in, and are endemic to, temperate, montane refugia (Stuckenberg 1962, Endrödy-Younga 1988, Day 2005). Palaeo-elements include relictual taxa, for

example Cape stag beetles (Endrödy-Younga 1988) and vermilionid flies (Stuckenberg 1996) and common-occurring, globally wide-spread taxa; for example the occurrence within the Cape fauna of world-wide, speciose, and abundant Bombyliid fly taxa that are of at least Gondwana or Laurasian in origin (Bowden, 1978; and see also Stuckenberg 1962 and Eardley 1996). Thus, the Cape Faunal Zone has ancient lineages of insects, showing long persistence within this region. However, as Bowden (1978) emphasises “Other localized [Cape] taxa represent not the regression of relics but active speciation...”

In contrast, the eastern and north eastern areas of southern Africa are essentially made up of tropical and sub-tropical elements of Afrotropical origin (Lawrence 1952, Ponyton 1961, Carcasson 1964, Endrödy-Younga 1978, Dijkstra 2007). On the eastern coast of southern Africa, a narrow coastal band of sub-tropical and tropical fauna has been retrieved, with several invertebrate and insect groups showing concentrations of species here (Lawrence 1952, Usher 1972, Oelofse 1996, Herbert 1997, Potgieter and Edwards 2005), and sharing many of their taxa with tropical east and central Africa (Mansell 1985, Tjeder and Hansson 1992). As one moves inland from the east coast, and altitude increases, grassland habitats begin to dominate the landscape, interspersed by patches of Afromontane forests. In the far north-eastern areas of South Africa savanna habitats dominate. The main faunal characteristic of these inland areas is their transitional nature with a complex assortment of faunal elements of different origins (Endrödy-Younga 1978). Elements of Ethiopian and southern African origin occur here, with influxes of tropical, sub-tropical and arid taxa from bordering biogeographical zones. An important zoogeographic zone in the “fauna-evolution” of this area is the cross continental link between Namibia, Angola, Zimbabwe, South Africa and arid areas of East Africa (Balinsky 1962, Carcasson 1964, Endrödy-Younga 1978, Irish 1990, Prendini 2001a).

The rich monkey beetle fauna of South Africa was recognized at the turn of the previous century by Péringuey (1902) who remarked, “The number of genera and species of Hopliini occurring in South Africa is the most striking feature of the Coleopterous fauna of this part of the world”. Thus, monkey beetles are an ideal group for insect biogeographical studies in South Africa because of their diversity and high levels of endemism. Péringuey (1902) further noted the abundance of monkey beetle species and genera restricted to the floristically diverse winter rainfall areas of South Africa. Furthermore, several other groups of insect pollinators have their highest levels of species richness, endemism and adaptive radiation within the winter rainfall region (Eardley 1989, Gess 1992, Whitehead and Steiner 2001, Barraclough 2006). This co-occurrence of faunal and floristic diversity allows for interesting floristic – faunal comparisons of diversity and endemism in a biodiversity hotspot (Myers et al. 2000) and the exploration of the potential causes for high biotic diversity. Of additional biogeographical interest are

faunal comparisons (richness and endemism) of the western, central and eastern regions of southern Africa; with distinct faunal centres in the west and east, and a depauperate central zone.

Beyond their role in testing biogeographic hypotheses, knowledge of monkey beetle distribution and diversity patterns has important conservation implications, particularly within the winter rainfall areas. The biologically important insect fauna of the winter rainfall area has all but been ignored in conservation assessments (Cowling and Pressey 2003, Cowling et al. 2003, Colville 2006), which use mainly plant data, with the occasional inclusion of vertebrate data where these are available (Kerley et al. 2003). However, vertebrate groups show low levels of endemism and adaptive radiation in comparison to that of the insects (Vernon 1999). The lack of inclusion of insect data into conservation assessments and planning is not out of lack of concern, but rather due to the lack of available data (Cowling et al. 2004). Insects are generally underrepresented in conservation planning because of the large number of species involved, the poor taxonomic state of many of the groups and the difficulty of identifying the taxa from general collections. Thus, the results of this biogeographical study of monkey beetles should further enhance our knowledge in identifying areas of richness and endemism that are of conservation importance for consideration in conservation and land use planning.

Furthermore, ecological factors explaining drivers of regional insect diversity are important to consider, especially in light of the lack of fossil and phylogenetic evidence available. Studies focusing on ecological drivers of regional insect speciation within, and across South Africa's biomes are few and far between. Since the nature and composition of biota result from a combination of historical (evolutionary) and past and present ecological factors (Ricklefs 2004), explanatory variables can be sought from current ecological patterns. In this context, monkey beetle richness patterns are investigated by using one of the most basic and fundamental of ecological measures, that of area and its relationship with numbers of species.

The aim of this chapter is to explore and describe the biogeographic patterns of monkey beetle distribution and diversity within South Africa. In order to achieve this, I first compile a comprehensive distributional dataset for the South African monkey beetles. Second, using this distributional dataset, I explore (1) spatial patterns of species richness and endemism at the level of climatic zone, biome, bioregion and vegetation type; (2) the relationship between levels of endemism and species richness within and between biomes (3) diversifications of genera, as measured as the percentage occurrence of species from respective genera within each of South Africa's biomes; (4) clusters of quarter degree grid cells - ranked together by hierarchical cluster analyses according to their shared presence of genera - to

search for primary biogeographic zones; and (5) the relationship between area - at various ecological scales (biome size, bioregion size, and habitat patch size) - and species richness.

METHODS

COMPILATION OF DISTRIBUTIONAL DATA SET

A point locality distributional data set was collated from several sources. Early taxonomic revisions (Péringuey 1902, von Dalla-Torre 1913, Schein 1951, 1959a,b, Kulzer 1960), together with a number of more recent revisions and descriptions of new species (Dombrow 1997a, 1997b, 1997c, 1997d, 1997e, 1998a, 1998b, 2000a, 2000b, 2001a, 2001b, 2001c, 2002a, 2002b, 2002c, 2002d, 2002e, 2002f, 2003), provided point locality records for a large number of species. Further monkey beetle distributional data was obtained from an extensive pinned collection housed at the Iziko Museum (formerly South African Museum), Cape Town. Additional locality data was supplemented by material collected during the spring flowering seasons (1999-2007).

Each point locality was geo-referenced using 1: 50 000 and 1:250 000 topo-cadastral maps of South Africa sourced from Chief Directorate: Surveys and mapping (CDSM), Mowbray, Cape Town (www.w3sli.wcape.gov.za), and the GeoNet Names Server gazetteer (http://164.214.2.59/gns/htm/cntry_files.html). Only collection records of sufficient accuracy were used. Obscure and/or vague locality records, such as “Cape of Good Hope” were excluded. Highly disjunct records, suggesting misidentification of a species, or incorrect locality label information were further excluded from the data set. In total, 1040 species and 6959 unique locality records were compiled for use in GIS mapping. Distributional datasets collated from museum natural history collections are highly useful in biogeographic studies, although limitations of such presence-only data sets are recognised (Graham et al. 2004).

Environmental themes of altitude (Jarvis et al. 2006), rainfall seasonality (Schulze 1997), and Mucina and Rutherford's (2006) vegetation categories (biomes, vegetation types, and bioregions) were spatially joined in Arcmap 9.2 (ESRI 2006) to the compiled beetle point locality data set, allowing the calculation of taxonomic diversity and endemism for selected ecological/vegetation themes. For the Fynbos Biome, an intermediate category (‘vegetation group’) exists between vegetation type and bioregion, based on edaphic criteria (see Mucina and Rutherford 2006). This information was used to create a combined vegetation group + bioregions theme. This theme uses the South African bioregions of Mucina and Rutherford (2006) to place the edaphic units in a phytogeographical context, as the edaphic units may

extend disjunctly across the entire Fynbos Biome, e.g. Sandstone Fynbos, which extends across the Fynbos Biome, is thus classed into five distinct geographical variants (differing in species composition) of Sandstone Fynbos based on which bioregion it falls in (see Appendix 1). Faunal justification for using the vegetation group + bioregions theme was seen in monkey beetle biotic elements in the Kamiesberg Uplands, which showed strong congruence with the bioregion level mapping category (Colville 2006). For all other biomes, the bioregion and ‘vegetation group’ category are the same, as presented by Mucina and Rutherford (2006). Goldblatt and Manning’s (2002) phytogeographical centres adds floristic justification to this further subdivision.

HOTSPOTS OF RICHNESS AND ENDEMISM

Monkey beetle point distribution maps were created using Arcmap 9.2 (ESRI 2006) and overlaid onto a Quarter Degree Square (QDS) grid (Edwards and Leistner 1971) of South Africa (including Lesotho and Swaziland). Taxonomic richness and endemism were calculated for each QDS, highlighting “hotspots” of high species richness and endemism (Reid 1998).

RANGE DISTRIBUTIONS OF SPECIES

Species fidelity ($\geq 50\%$ and $\geq 75\%$ of a species records occurring within a defined geographical unit) were calculated for biomes, bioregions, and vegetation types. These measures were crude indications of diversity patterns (e.g. range restricted species or habitat specialists – Cody 1996) and the alpha and beta components of regional (gamma) diversity (Whittaker 1972).

SPECIES ENDEMIC TO BIOMES, BIOREGIONS, AND VEGETATION TYPES

In order to assess whether endemic species occurred widely across biomes, or were locally restricted, the percentage of biome, bioregional, and vegetation type endemics were calculated for each biome. First, a list of all species endemic to a biome was compiled, from which the number of biome endemics (i.e. widespread within that biome), bioregion endemics (i.e. confined to a bioregion) and, vegetation type (local) endemics were calculated. These values were expressed as a percentage value of the total number of endemic species occurring within a biome, e.g. biome X contains 10 biome endemics, of these 2 are confined to a bioregion, 5 confined to a vegetation type, while the remaining 3 are found across bioregions and vegetation types within biome X. Thus, the percentage breakdown of regional and local endemics for biome X would be 30% biome endemics, 20% bioregional endemics, and 50% vegetation type local endemics.

ENDEMISM AND RICHNESS CORRELATIONS

Levels of endemism as defined above were correlated with species richness values for QDS grid cells, biomes, bioregions, and vegetation types. Richness (number of non-endemic species) was measured as the number of species found within a QDS/vegetation category minus the number of endemic species (species only found in respective QDS/ vegetation category). This approach supported the assumption of independence between variables used in correlations (Quinn and Keough 2003). Spearman's rank correlation tests were used for QDS grid cells, vegetation types, and bioregions; which all displayed non-normal distributions. At the biome scale, diversity and endemism were related using OLS regression after log transforming the two variables to normalize the data.

BEETLE DIVERSIFICATIONS WITHIN AND ACROSS BIOMES

Diversifications of genera were measured as the percentage occurrence of species from respective genera within each of South Africa's biomes. Only genera with ≥ 3 species were used. Such a measure should indicate which genera are centered within specific biomes and the extent of their diversifications across biomes.

BIOGEOGRAPHIC ZONES

Within South Africa, distinct western and eastern biogeographic zones have been identified for a number of faunal groups (Ponyton 1964, Werger 1978, Crowe 1990, Alexander et al. 2004). Here, similar broad zones ("sub-regions" cf. Alexander et al. 2004) were investigated using quantitative cluster analyses (hierarchical cluster analysis; procedures followed as outlined in the multivariate statistical package PRIMER (Clarke and Gorley 2006). Clustering was performed using presence-only data (i.e. no confirmed absences) of genera in each QDS grid cell ($n = 569$ QDS grid cells). The hierarchical cluster was produced from a resemblance matrix created using the Bray-Curtis similarity measure. A dendrogram plot was drawn showing relationships between clusters of grid cells. Groups of clusters at the primary split on the dendrogram were mapped in Arcmap 9.2 (ESRI 2006) to show broad-scale biogeographic patterns.

DIVERSITY AND AREA RELATIONSHIPS

Regional Scale Patterns - Biomes and Bioregions

Firstly, general patterns of diversity in relation to area were plotted for biomes and bioregions to ascertain whether regional diversity patterns were reflected by regional area sizes. For bioregions, sufficiently large

numbers of data points were available to test which model provided a better fit for the data. As Scheiner (2003) argues, it is theoretically possible for larger area sizes (regions) to contain less species than smaller area sizes. Furthermore, the Fynbos and Succulent Karoo biomes have been shown to contain disproportionately high plant species richness in comparison to their physical sizes (Cowling et al. 1989, Cowling et al. 1998, Goldblatt and Manning 2002). Partial *F*-tests (Quinn and Keough 2003) were used to test the fit of higher-order polynomial models to the bioregional species – area data.

Area and habitat heterogeneity have been argued to be strongly correlated, with increases in habitat heterogeneity linked to increases in habitat area (Rosenzweig 1995). In addition, many studies have shown positive correlations between habitat heterogeneity and diversity (e.g. Tews et al. 2004). In order to help explain patterns seen in species–area plots, beetle richness patterns were correlated with a simple measure of habitat heterogeneity (number of vegetation types). For biomes, OLS regression was used, whereas, for bioregions, variables were not normally distributed and Spearman’s rank correlation was used. In turn, to test whether habitat heterogeneity was related to area, number of vegetation types found within biomes and bioregions were correlated to the respective area sizes of biomes (OLS regression) and bioregions (Spearman’s rank correlation). The area size of each vegetation type within a biome or bioregion was not taken into account, and only the occurrences of vegetation types were recorded.

Local Scale Patterns - Habitat Patches

The double logarithmic (Type IV curve - (Scheiner 2003) form of the species-area curve (Connor and McCoy 1979, Rosenzweig 1995, Cowling et al. 1998, Cowling and Lombard 2002) was plotted for different species – area datasets. Species – area plots were generated at two habitat scales: vegetation type patches (homogenous habitat) and bioregion patches (more heterogeneous habitat) for comparison of slopes (accumulation of species with unit area) and intercepts (regional richness across a unit area) between and across biomes. To generate these curves, naturally occurring patches of vegetation types and bioregions were used as sampling units (Scheiner 2003), each with their own unique area. Beetle species data were collated from point locality records found within these patches, while area (km²) was the area for that habitat patch calculated in a GIS for the respective biome or bioregion. Analysis of covariance (area as covariate) was used to test the homogeneity of slope (preliminary step) and *Y* intercept between those biomes (treatment groups) showing significant linear relationships between area and number of species (Sokal and Rohlf 1995). Where the null hypothesis of equal slopes and intercepts across groups could not be rejected, unplanned multiple comparisons for regression coefficients were tested for significance (Sokal and Rohlf 1995). For biomes showing homogenous slopes and significantly different

Y intercepts (adjusted means), intercept ratios were compared, providing a comparison of regional richness when log Area = 0 (Gould 1979, Cowling et al. 1998, Cowling and Lombard 2002).

RESULTS

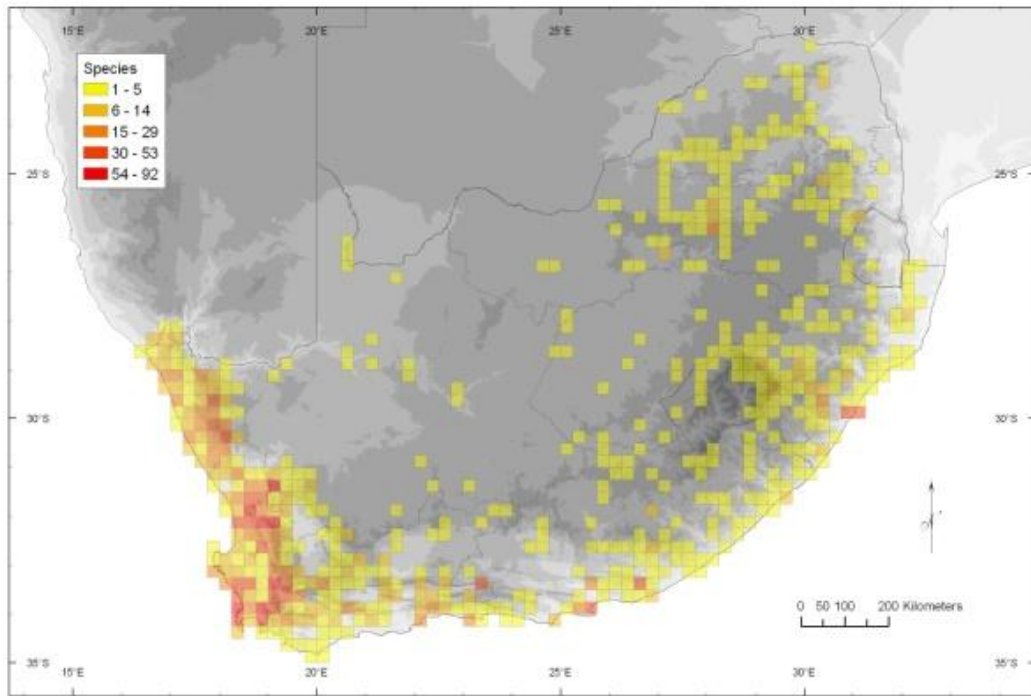
GENERAL CHARACTERISTICS OF THE FAUNA

Currently, approximately 1040 described and undescribed species within 51 genera of monkey beetle are known from South Africa (Dombrow pers. comm.). The centre of adaptive radiation for the world's Hopliini is clearly South Africa, with roughly 63% of the world's known species, and 38% of the world's genera, concentrated here (see Introductory Chapter). Remarkably, almost one half of the world's species are concentrated within the reasonably small (*ca.* 135 700 km²) winter rainfall region of South Africa. Two dominant genera; *Heterochelus* Castelnau 1840 and *Peritrichia* Burmeister 1844, make up approximately 35% of the South African fauna. Nine dominant genera, each with > 30 species make up approximately 70% of the South African fauna. A remarkably high percentage (98%) of species and genera (80%) recorded from South Africa are endemic to this country. Although less diverse, Madagascar has similarly impressive levels of endemism (100% species endemic, 97% genera endemic; see Introductory Chapter).

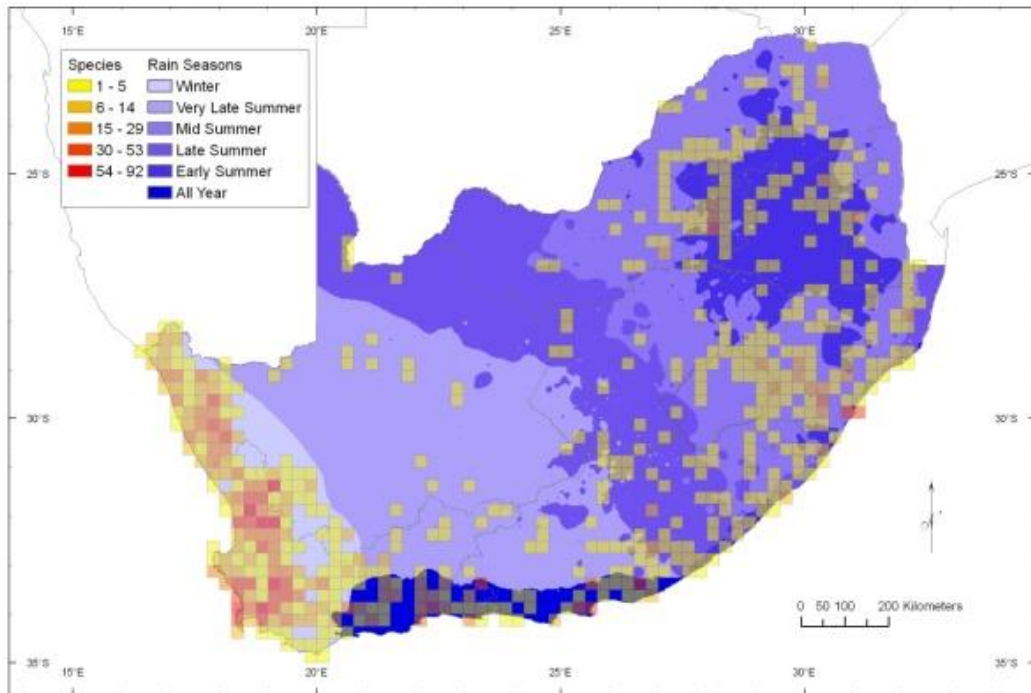
PATTERNS OF SPECIES DISTRIBUTION AND HOTSPOTS OF RICHNESS AND ENDEMISM

Spatial analysis of the distributions of South African monkey beetles revealed concentrations of species in the west and east. As can be seen from the QDS hotspot analysis (Figs. 1a, d), the majority of hotspots

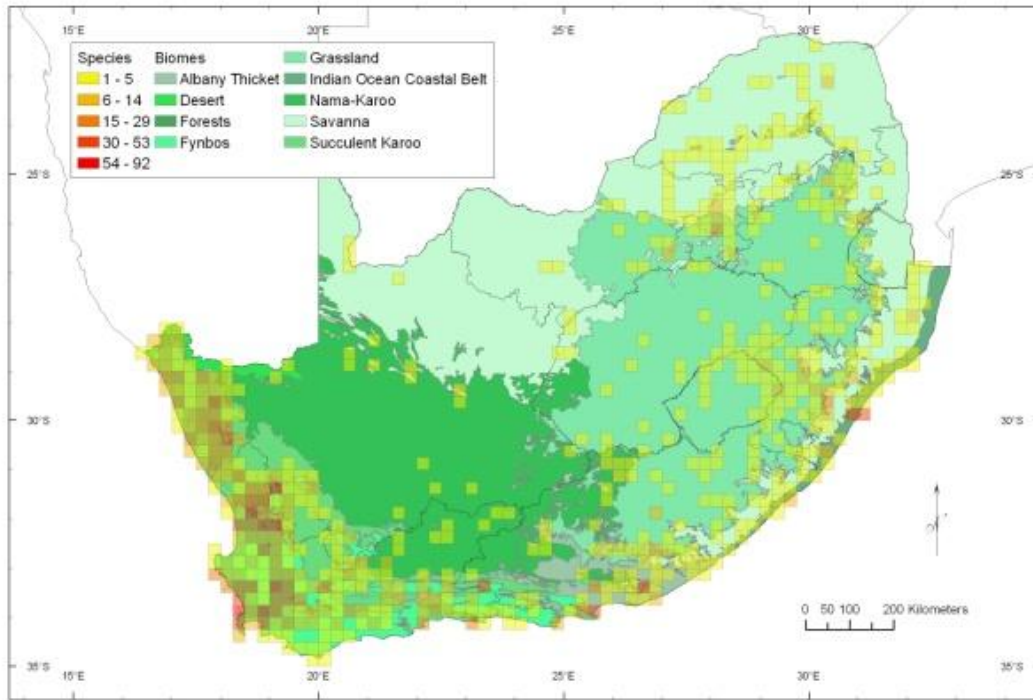
occurred in the west with far fewer in the east.



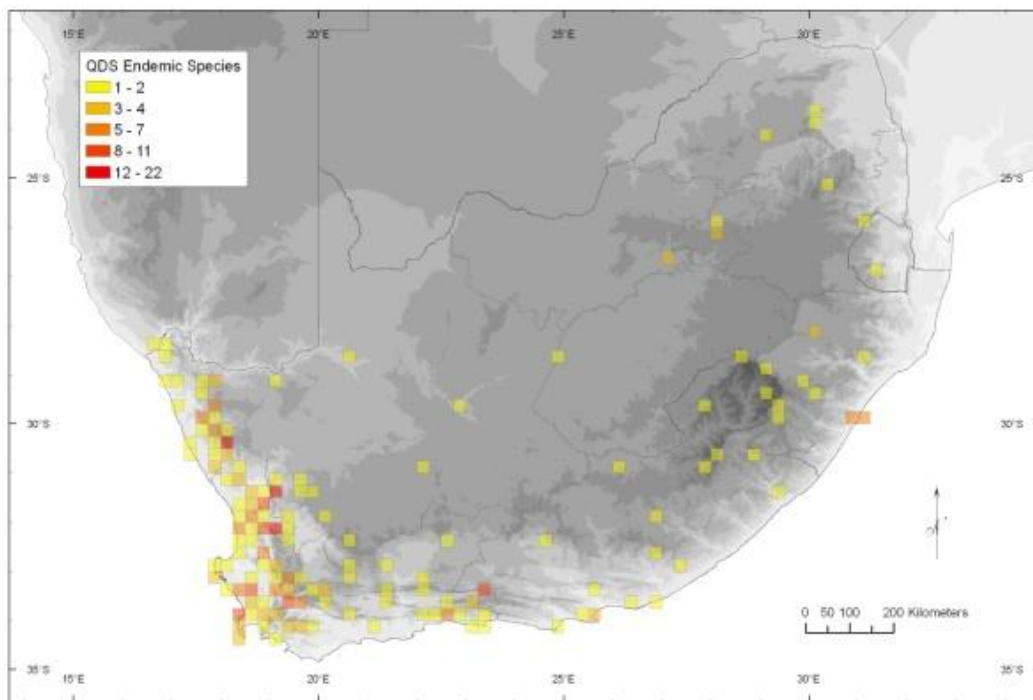
(a)



(b)



(c)



(d)

Figure 1a-d. Quarter Degree Grid Square (QDS) species richness and distribution patterns for South African monkey beetles overlaid (a) onto a 90 m digital elevation model (Jarvis et al. 2006), (b) South African rainfall seasons (Schulze 1997), and (c) South African biomes (Mucina and Rutherford 2006). Map (d) shows hotspots of species endemism, expressed as the number of endemic species per QDS grid cell.

BIOGEOGRAPHIC ZONES

Results of the cluster analysis using presence-only data for genera showed a primary split (at the < 5 % similarity level) producing two main clusters (Fig. 2a). These clusters are made up of grid cells falling within clear western and eastern zones within South Africa (Fig. 2b).

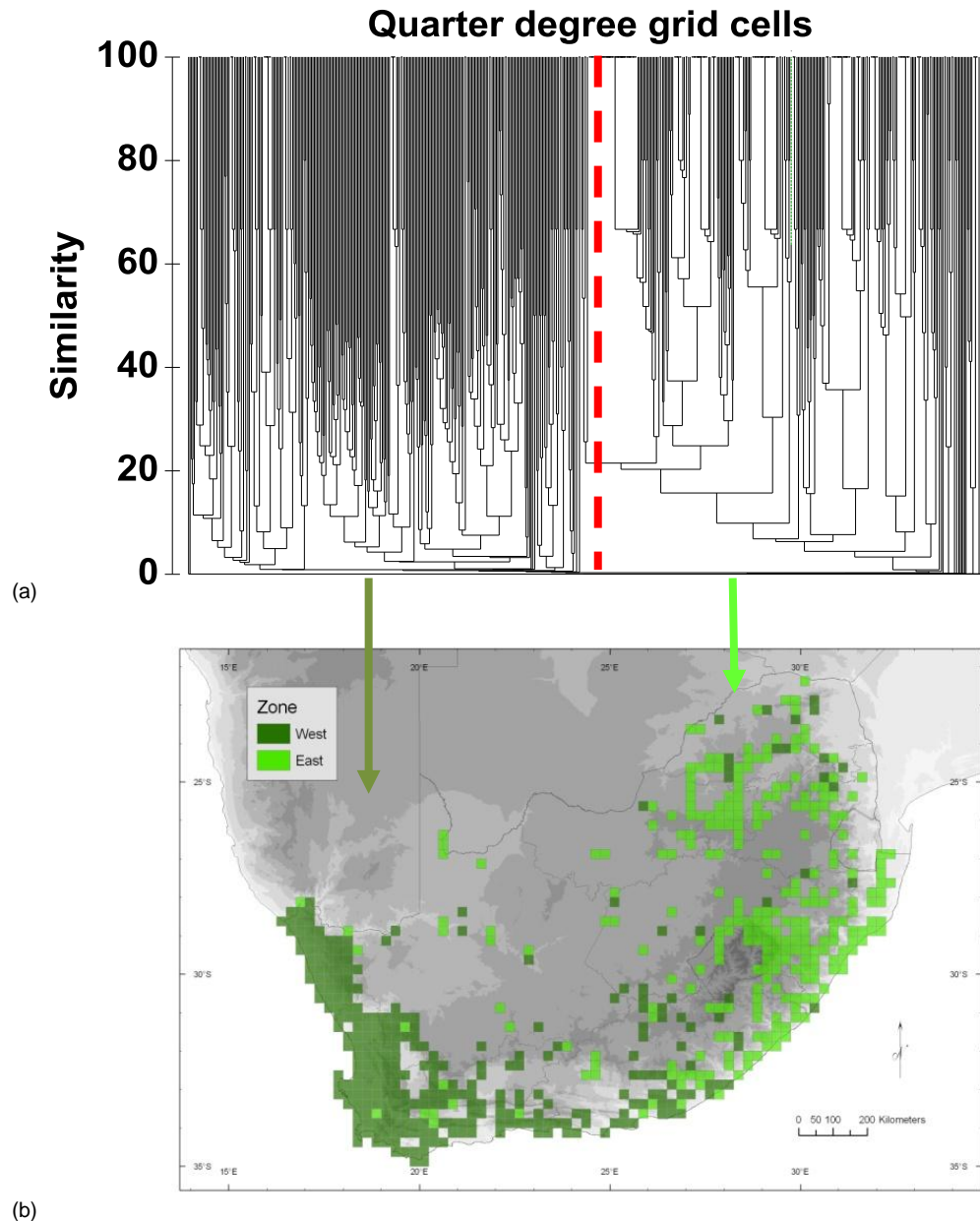


Figure 2. (a) Dendrogram showing relationships between clusters of QDS grid cells based on similarity of occurrence of genera. The primary split at the < 5% similarity (dashed red line) produces two main clusters, which are mapped (b), showing clear western and eastern biogeographic zones.

Western Zone

The western (Fig. 2b), predominantly winter rainfall zone (Fig. 1b), is comprised of high numbers of species (Table 1). Areas of highest richness and endemism were clearly focused within the south-western and north-western sections of the winter rainfall region of South Africa (Figs. 1a, d). This western zone is found within a reasonably narrow band matching the boundaries of the Fynbos and Succulent Karoo biomes (Fig. 1c) and extending from the south coast around longitude 23° E, northward westwards along the west coast, into and across the Olifantsrivierberge and Cederberg Mountains, further extending into Namaqualand, but with limited eastward extensions into the arid, summer-rainfall Bushmanland and Nama-Karoo.

Table 1. Selected descriptive statistics for South African biomes.

Biome	Size of biome (Km ²)	No. of bioregions	No. of vegetation types in biome	No. of beetle species (genera)	No. of vegetation types with beetle records (% of total)	Average no. of beetle spp. per vegetation type (± sd.)
Albany Thicket	29127.54	1	14	56 (18)	10 (71.43)	5.50 (4.01)
Desert	7165.66	2	15	17 (11)	6 (40.0)	3.00 (1.67)
Forests	4714.66	2	12	19 (11)	6 (50.0)	3.67 (2.50)
Fynbos	83943.86	51	119	541 (60)	90 (75.63)	18.48 (20.19)
Grassland	354593.56	4	72	72 (20)	51 (70.83)	4.86 (3.77)
Indian Ocean Coastal Belt	14281.97	1	5	47 (11)	4 (80.0)	15.25 (20.71)
Nama-Karoo	248279.94	3	14	36 (15)	8 (57.14)	5.13 (5.46)
Savanna	412544.60	6	87	82 (21)	41 (47.13)	5.22 (7.26)
Succulent Karoo	83284.00	6	63	364 (44)	50 (79.37)	17.08 (18.56)

Eastern Zone

The extensive eastern (predominantly summer rainfall – Fig. 1b) zone contains markedly fewer species and varieties (Table 1, Fig. 1a). Nonetheless, this zone retains a distinct fauna with separate zoogeographical affinities (Figs. 2a, b). Several small, isolated areas of richness and secondary hotspots of endemism (5-7 endemics) were seen. Most of these eastern areas of richness were centered on major cities (e.g. Port Elizabeth, Durban), indicating possible collector bias (see also Usher 1972). Notwithstanding the bias caused by undersampling, hotspots are general poorly represented across the eastern zone.

The eastern zone, extending eastwards in a narrow strip, mostly along the coastal and near inland areas, initially consists of a shared grouping of western zone (Cape) and more typical eastern zone, subtropical elements. Inland distributions of this shared grouping showed limited extensions across the Cape Fold

Mountain ranges. Proceeding from around longitude 25⁰ E, western elements fall away, being replaced by eastern subtropical forest and thicket, and savanna elements. The eastern fauna extends inland into the high altitude montane regions of the Drakensberg Mountains. A weakly diverse localized area of richness (grid cells with 5-9 species) was seen on the eastern side of the Drakensberg Mountains. The eastern zone further extends into the far northern regions of the Grassland and Savanna biomes (Fig. 2b).

Arid Central Zone

A further noticeable pattern was seen in the distinct paucity of monkey beetle species within the central interior, particularly the arid Nama-Karoo and north-western parts of the Savanna Biome (Fig. 1a). This observed pattern may, however, be a reflection of neglected collecting within this extensive and mostly isolated region of South Africa (see Gibbs Russel et al. 1984, Vernon 1999).

RANGE DISTRIBUTIONS OF SPECIES

Within, and between, the western and eastern zones, discrete distributional ranges were mostly seen for monkey beetle genera and species. The distributional ranges of closely related species appeared to be mostly allopatric or parapatric, although several genera recorded a number of species occurring in sympatry. Within the Fynbos and Succulent Karoo biomes, a high percentage of species had the majority of their ranges confined within these two biomes (Table 2, and see section below on endemism).

Considering the high number of bioregions (especially for the Fynbos Biome) and vegetation types found within these two biomes (Table 1), a relatively large number of Fynbos and Succulent Karoo species had the majority of their ranges confined to particular bioregions and vegetation types.

Table 2. Fidelity of species to biomes, bioregions, and vegetation types based on the proportions of locality records occurring within each vegetation category.

Biome	Percentage (%) of spp. showing ≥50% and [≥75%] of their range confined to regional biomes	Average % of spp. showing ≥50% and [≥75%] of their range confined to regional bioregions	Average % of spp. showing ≥50% and [≥75%] of their range confined to local vegetation type habitats
Albany Thicket Biome *	28.9 [10.5]	-	25.2 [14.1]
Desert Biome	35.3 [23.5]	3.0 [22.5]	33.3 [23.8]
Forests	10.5 [5.3]	2.0 [5.3]	8.33 [2.8]
Fynbos	81.6 [66.0]	8.4 [12.6]	17.0 [11.7]
Grassland Biome	63.9 [41.7]	10.0 [25.6]	10.5 [7.7]
Indian Ocean Coastal Belt*	55.3 [40.4]	-	17.2 [9.8]
Nama-Karoo Biome	36.4 [21.2]	3.3 [13.7]	19.7 [8.6]
Savanna Biome	39.0 [18.3]	4.2 [10.2]	8.8 [3.0]
Succulent Karoo Biome	67.1 [46.2]	36.8 [20.8]	13.8 [7.0]

*Bio-regions not assigned (see Mucina and Rutherford, 2006).

Similar trends of limited range sizes were seen for, and within several other South African biomes. This was particularly evident for the Grassland Biome which supports the second largest number of vegetation types (Mucina and Rutherford, 2006). In contrast, the Savanna Biome, with an extensive area size and high number of vegetation types, showed low numbers of species with restricted ranges (Tables 1, 2).

SPECIES ENDEMIC TO BIOMES, BIOREGIONS, AND VEGETATION TYPES

Most biome endemic monkey beetle species showed strong local (vegetation type) endemism (Table 3). The Fynbos Biome showed the highest percentage of regional biome endemics (i.e. species endemic to this biome but occurring across bioregions and vegetation types within the biome), while several of the smaller biomes (Indian-Coastal Belt, Forest), and the large Grassland and Nama-Karoo biomes, recorded no regional biome endemic species (i.e. species endemic to these biomes were local endemics confined to bioregions or vegetation types). The Grassland Biome, did however, record high bioregional endemism. Five of the biomes, including the species rich Fynbos, and Succulent Karoo biomes, recorded almost a third of their respective biome endemic species as local vegetation type endemics.

Table 3. The percentage of regional and local endemic species found within each biome.

Biome	Percentage (%) of spp. endemic to regional biomes	Percentage (%) of spp. endemic to regional bioregions	Percentage (%) of spp. endemic to local vegetation type habitats
Albany Thicket Biome*	3.57	-	16.07
Desert Biome	11.76	11.76	29.41
Forests	0.00	0.00	5.26
Fynbos	17.19	1.48	35.86
Grassland Biome	0.00	6.94	33.33
Indian Ocean Coastal Belt*	0.00	-	34.04
Nama-Karoo Biome	0.00	8.33	16.67
Savanna Biome	3.66	2.44	12.20
Succulent Karoo Biome	5.22	2.47	29.95

*Bioregions undefined (see Mucina and Rutherford 2006).

ENDEMISM AND RICHNESS CORRELATIONS

Patterns of endemism hotspots (Fig. 1d) generally mirrored those of species richness hotspots with western biome QDS showing higher numbers of endemics. A moderately strong positive correlation was seen between the number of endemics and species richness of QDS grid cells (Spearman's rank correlation: $r_s = 0.516$, $n = 520$, $P < 0.0001$). At the QDS scale, several areas of high richness showed low numbers of endemic species in both the western and eastern diversity zones (Fig. 1a, d). This pattern was particularly evident in the species rich QDS of the south western Cape and northern Namaqualand, and for west coast grid cells. Stronger, positive correlations between endemism and richness were evident at

the three ecological scales of vegetation types ($r_s = 0.611$, $n = 282$, $P < 0.0001$); bioregions ($r_s = 0.872$, $n = 70$, $P < 0.0001$); and biomes (Fig. 3; OLS regression: $F_{(1,7)} = 31.29$, $r^2 = 0.817$, $P = 0.0008$).

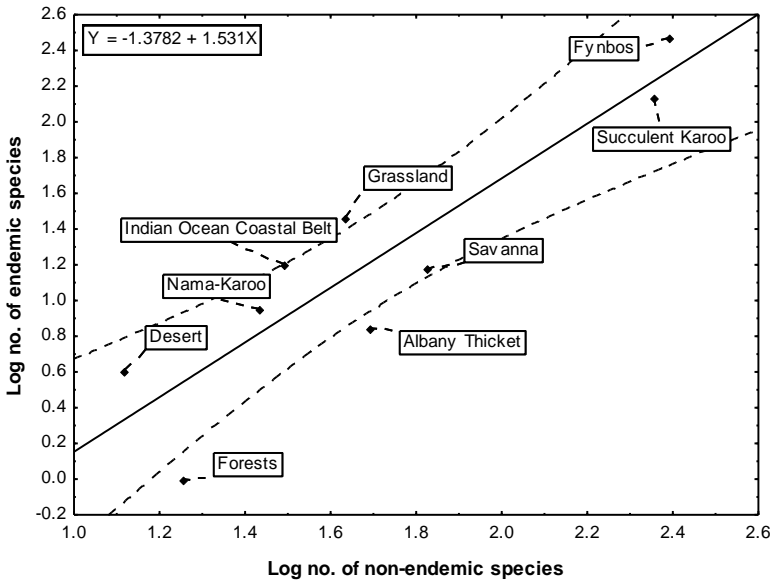


Figure 3. The relationship between species richness (number of non-endemic species) and number of endemic species for South African biomes. Dashed lines show 95% confidence intervals. Both variables log transformed to account for non-normality.

BEETLE DIVERSIFICATIONS WITHIN AND ACROSS BIOMES

Most genera (*ca.* 80%) had the majority of their species occurring within the Fynbos and Succulent Karoo biomes (Table 4). Generally, genera found within the Fynbos and Succulent Karoo biomes showed a high percentage of occurrences of their respective species within and across these two biomes. The Fynbos Biome had at least 11 genera with $> 70\%$ of their species found within this biome, with a number of these genera clearly centered here, e.g. *Dichelus*, *Anisonyx*, *Goniaspidius*, *Kubousa*, and *Dolichiomicroscelis*. Four genera appeared to be centered within the Succulent Karoo (*Denticnema*, *Pachycnema*, *Scelophysa*, and *Goniaspidius*). In contrast, other biomes showed mostly low species occurrences of genera found within their respective biomes. The Albany Thicket showed a reasonably high percentage (44.4%) of *Gymnoloma* species occurring within this biome. A single lineage (*Eriesthis*) was centered within the Grassland Biome (84.2% species occurrences); however, it also showed reasonably high (63.2%) species occurrences within the Savanna Biome. Species of *Monochelus* also showed quite high occurrences within these two biomes (43.3% in each, respectively).

Table 4. Representation of genera with ≥ 3 species in South African biomes. Values indicate percentage representation of species from respective genera. Blank spaces indicate absences.

Biome	Albany Thicket	Desert	Forests	Fynbos	Grassland	Indian Ocean Coastal Belt	Nama-Karoo	Savanna	Succulent Karoo
Genus									
<i>Anisochelus</i>	-	-	-	100.0	-	-	-	-	100.0
<i>Chasme</i>	-	33.3	-	66.7	-	-	-	-	100.0
<i>Dolichiomicroscelis</i>	-	-	-	100.0	-	-	-	-	-
<i>Knysna</i>	-	-	-	100.0	-	-	-	-	-
<i>Mauromecistoplia</i>	-	-	-	100.0	-	-	-	-	33.3
<i>Rectoscutaria</i>	-	-	-	66.7	-	-	33.3	-	66.7
<i>Khoina</i>	25.0	-	25.0	100.0	25.0	-	-	-	35.0
<i>Amblymelanoplia</i>	-	-	-	80.0	-	-	-	-	60.0
<i>Diaplochelus</i>	-	-	-	100.0	-	-	-	-	20.0
<i>Hoplia</i>	20.0	-	20.0	40.0	20.0	20.0	-	20.0	-
<i>Lepitrichula</i>	20.0	-	20.0	-	40.0	40.0	-	20.0	-
<i>Clania</i>	-	-	-	83.3	-	-	-	-	83.3
<i>Goniaspidius</i>	-	-	-	33.3	-	-	-	-	66.7
<i>Denticnema</i>	-	42.9	-	25	-	-	14.3	-	100.0
<i>Leptocnemis</i>	-	-	-	100.0	-	-	0.0	12.5	50.0
<i>Gymnoloma</i>	44.4	-	-	77.8	-	-	11.1	-	55.6
<i>Lepisia</i>	-	11.1	-	66.7	-	-	22.2	-	77.8
<i>Scelophysa</i>	-	10.0	-	30.0	-	-	20.0	-	90.0
<i>Kubousa</i>	-	-	-	86.7	-	-	-	-	46.7
<i>Dicranocnemus</i>	31.3	-	-	75.0	6.3	-	-	31.3	12.5
<i>Hoplocnemis</i>	11.8	5.9	-	70	5.9	-	11.8	-	52.9
<i>Eriesthis</i>	26.3	-	21.1	26.3	84.2	31.6	10.5	63.2	-
<i>Ischnochelus</i>	5.3	-	-	57.9	-	-	5.3	-	68.4
<i>Anisonyx</i>	-	-	3.6	85.7	28.6	-	3.6	17.9	28.6
<i>Monochelus</i>	10.0	-	13.3	30.0	43.3	46.7	-	43.3	20.0
<i>Omocrates</i>	3.3	3.3	-	63.3	-	3.3	10.0	-	23.3
<i>Dichelus</i>	2.9	-	2.9	88.2	2.9	5.9	-	5.9	8.8
<i>Pachycnema</i>	8.3	8.3	-	63.3	5.6	-	11.1	8.3	83.3
<i>Lepithrix</i>	-	-	5.4	78.4	2.7	-	-	-	73.0
<i>Platychelus</i>	3.0	3.0	-	54.5	4.5	-	1.5	9.1	54.5
<i>Peritrichia</i>	4.1	2.7	1.4	77.0	-	-	6.8	5.4	63.5
<i>Heterochelus</i>	2.1	0.5	1.0	71.3	5.6	7.2	3.1	7.7	40.5
Total No. of genera with ≥ 3 spp.	15	9	10	31	13	7	14	15	28
Average % spp. occurrence (\pm sd.)	6.8 (11.3)	3.8 (9.6)	3.6 (7.4)	72.9 (25.1)	8.6 (18.1)	4.8 (12.1)	5.1 (8.2)	8.9 (14.8)	49.1 (32.2)

BIOMES AND BIOREGIONS - REGIONAL SCALE PATTERNS OF RICHNESS AND AREA RELATIONSHIPS

For those datasets showing a significant relationship between area and beetle richness, area generally only explained a low proportion of the variance seen in beetle species richness. Biome area size showed a weakly positive, non-significant relationship ($F_{(1,7)} = 2.11$, $r^2 = 0.23$, $P = 0.19$) with beetle richness (Fig. 4a). The Succulent Karoo and the Fynbos biomes were the two most species rich biomes, accounting for 29.01% and 44.29% of total South African monkey beetle richness, respectively; however, both biomes only account for 6.50% and 6.60%, respectively, of the total biome area in South Africa (see Mucina and Rutherford (2006) for relative biome areas within South Africa). One of the largest biomes, the arid Nama-Karoo (19.50% relative area) only houses 2.71% of South Africa's monkey beetle richness. In

contrast, the Albany Thicket Biome (2.20% relative area), and approximately only 11.73% the size of the Nama-Karoo, houses 4.52% of South Africa’s monkey beetle richness.

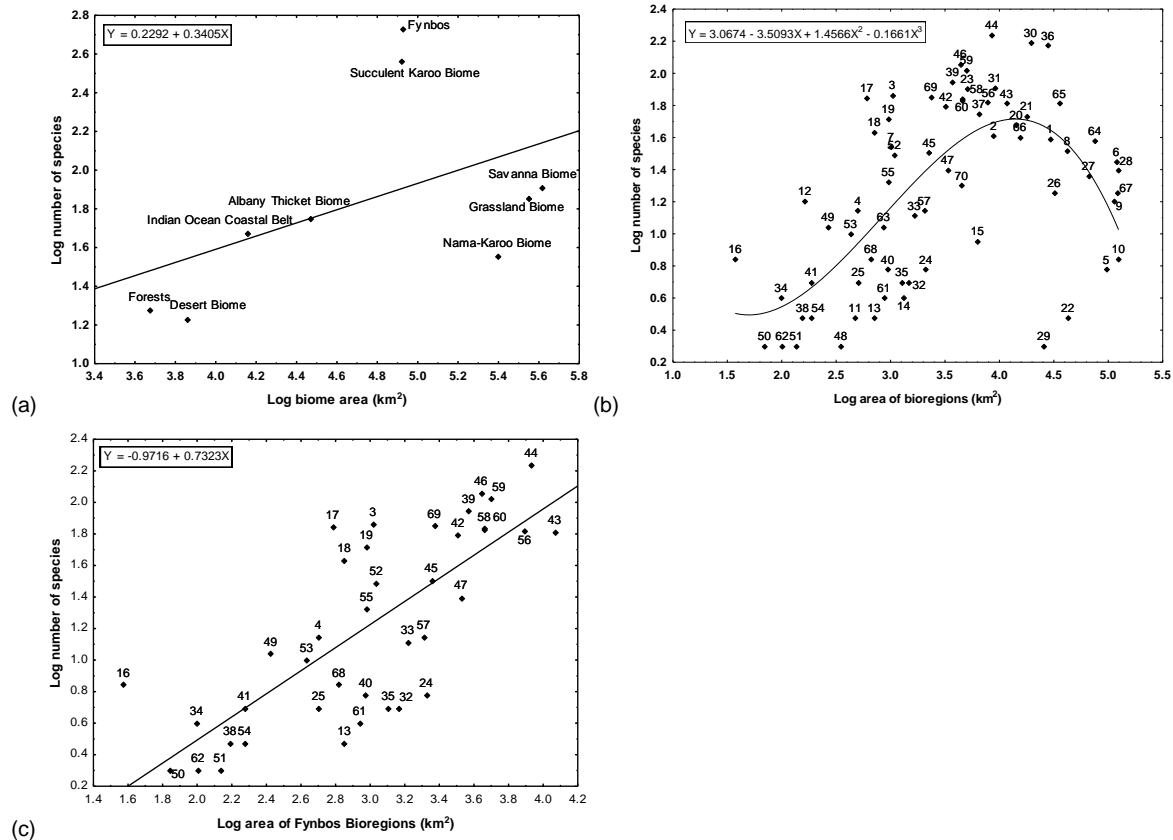


Figure 4. (a) Regional scale patterns of species–area relationships for South African biomes, (b) bioregions, and (c) for fynbos bioregions only. At the bioregional scale for fynbos, habitat heterogeneity was strongly correlated with area (Spearman rank correlation: $r_s = 0.76$; $N = 39$; $P < 0.001$). (See methods for bioregional definition and Appendix 1 for number labels).

At the bioregional scale, area was a stronger explanatory variable than for biomes, although still only explaining low proportions of variance in species richness ($F_{(1,66)} = 17.16$, $r^2 = 0.438$, $P < 0.0001$). A third-order (cubic) polynomial regression (Fig. 4b) explained significantly more variance in bioregional richness compared with a simple linear model (Partial- F test: $F_{(1,67)} = 18.98$, $P < 0.001$). Focusing only on bioregions within the Fynbos Biome, a moderately strong relationship ($F_{(1,37)} = 52.32$, $r^2 = 0.586$, $P < 0.0001$) between bioregional area and richness was seen (Fig. 4c). The Sandstone Fynbos - Northwest Fynbos Bioregion (8524.23 km²) showed the highest richness (172 beetle species), while only a single species was recorded from the Shale Band Vegetation - Southern Fynbos Bioregion (68.67 km²).

Correlations between habitat heterogeneity (number of vegetation types) and beetle richness showed a significant positive relationship at the biome scale (Fig. 5a; $F_{(1,8)} = 11.39$, $r^2 = 0.586$, $P = 0.0162$), with habitat heterogeneity explaining 58.6% of variance seen in beetle richness. At this scale, habitat heterogeneity showed a weak relationship with area (Fig. 5b; $F_{(1,8)} = 5.76$, $r^2 = 0.450$, $P = 0.0478$). At the bioregion scale, habitat heterogeneity and beetle richness were strongly correlated (Spearman's rank correlation: $r_s = 0.682$, $n = 70$, $P < 0.0001$), and in contrast to the biome scale result, bioregion habitat heterogeneity was further strongly correlated to area ($r_s = 0.744$, $n = 70$, $P < 0.0001$).

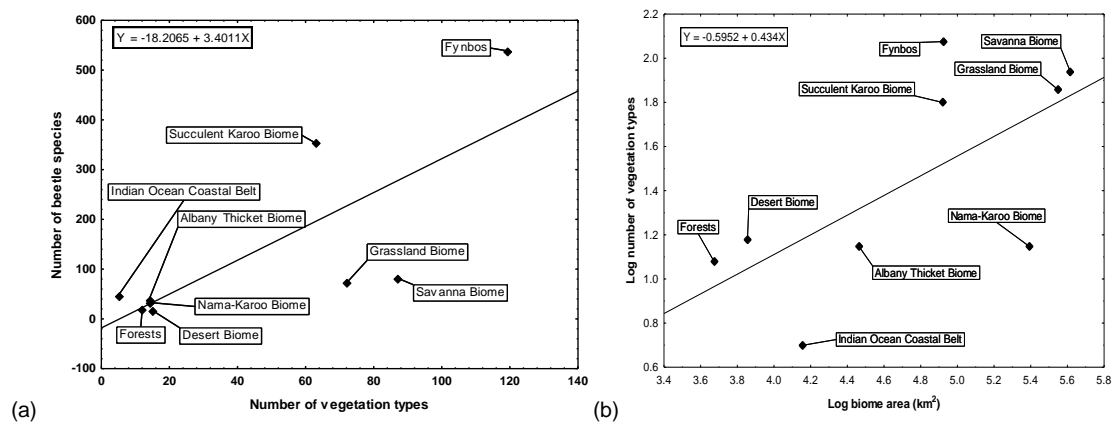


Figure 5. (a) Relationship between habitat heterogeneity and area and (b) relationship between habitat heterogeneity and monkey beetle species richness for South African biomes.

HABITAT PATCH SIZE - LOCAL SCALE PATTERNS OF RICHNESS AND AREA RELATIONSHIPS

Vegetation Type Habitat Patch

For the double logarithmic regression model of vegetation type patch size and beetle richness, area was a particularly weak explanatory variable when compared across all biomes (Fig. 6a; $F_{(1,488)} = 17.19$, $r^2 = 0.034$, $P < 0.0001$), accounting for only 3.4% of the variance in species richness patterns (see Fig. 6b for median patch size per biome). Separate regression models for selected biomes, showed a significant relationship between area and beetle richness for the Fynbos ($F_{(1,178)} = 70.08$, $r^2 = 0.283$, $P < 0.0001$), Succulent Karoo ($F_{(1,104)} = 17.93$, $r^2 = 0.147$, $P < 0.0001$), and Grassland biomes ($F_{(1,81)} = 12.57$, $r^2 = 0.134$, $P < 0.001$) (Fig. 7a, b). However, for these three biomes, area was still seen to explain low proportions of variance in species richness (< 30%). The Nama-Karoo ($F_{(1,9)} = 1.90$, $r^2 = 0.175$, $P = 0.21$), Savanna ($F_{(1,67)} = 1.03$, $r^2 = 0.015$, $P = 0.31$), Albany Thicket ($F_{(1,17)} = 1.72$, $r^2 = 0.039$, $P = 0.21$), Desert ($F_{(1,5)} = 0.06$, $r^2 = 0.012$, $P = 0.82$), Forests ($F_{(1,13)} = 0.012$, $r^2 = 0.034$, $P = 0.49$), and Indian Ocean Coastal Belt ($F_{(1,6)} = 0.32$, $r^2 = 0.051$, $P = 0.59$) biomes all showed non-significant relationships between

area and beetle richness. For the Forest Biome, a weak negative relationship was seen between richness and area.

The Succulent Karoo, Grassland, and Fynbos biomes showed heterogeneous slopes ($F_{(2,365)} = 4.96, P = 0.0075$). Unplanned multiple comparisons showed a significant difference in slopes only between the Fynbos and Grassland Biomes (Fig. 7b). The Fynbos Biome accumulated species faster with increasing area than the Succulent Karoo, although not significantly so.

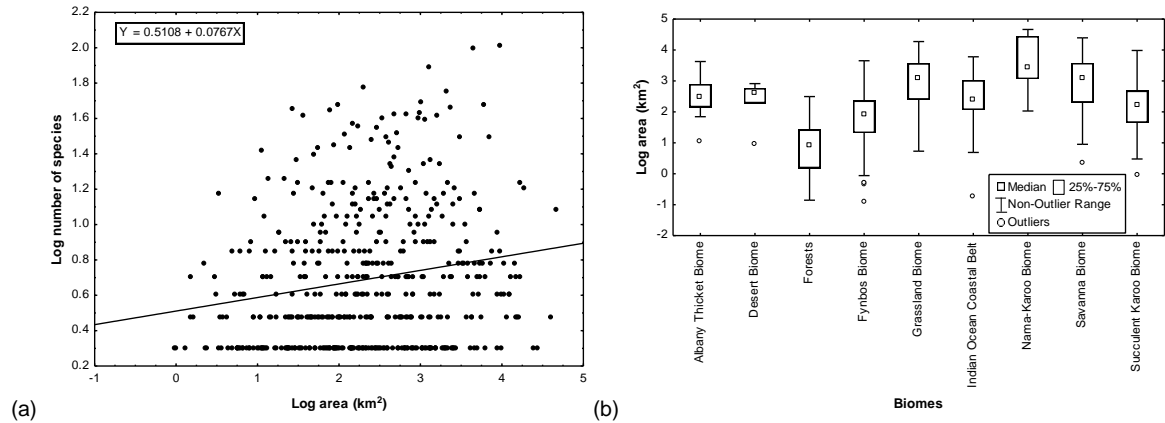


Figure 6. (a) Species-area relationship between monkey beetle species richness and vegetation type habitat patch size across all South African biomes and (b) median vegetation type habitat patch size used in species-area plots for biomes.

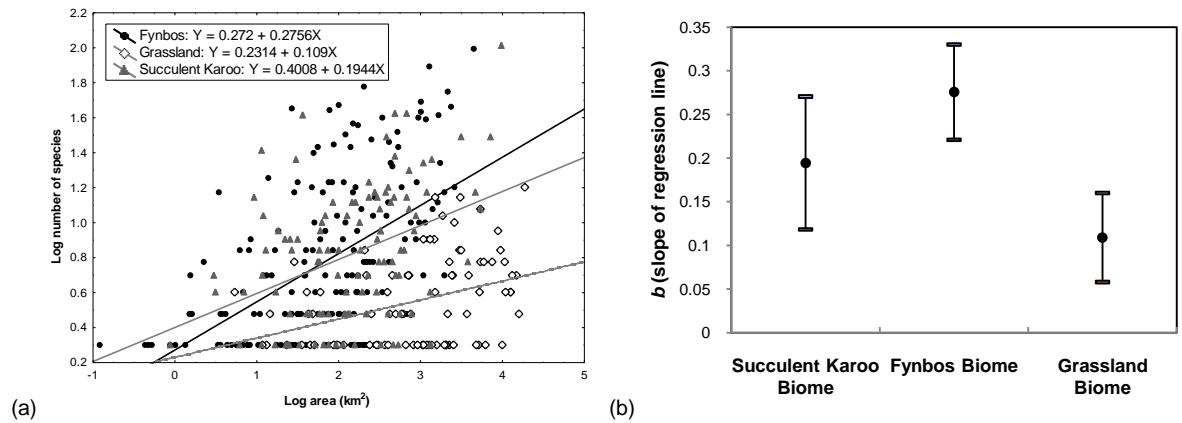


Figure 7. (a) Species-area relationship between monkey beetle species richness and vegetation type habitat patch size for the Fynbos, Succulent Karoo, and Grassland biomes. (b) Unplanned multiple comparisons between the three biomes showing unequal slopes (vertical bars denote 0.95 confidence intervals. Confidence intervals not overlapping indicate significant differences (Sokal and Rohlf 1995)).

Bioregion Type Habitat Patch

Species-area curves using bioregional patches as sampling units across all biomes also revealed area as a weak explanatory variable ($F_{(1, 250)} = 111.38, r^2 = 0.308, P < 0.0001$), accounting for only 30% of the

variance in species richness patterns (Fig. 8a, and see Fig. 8b for median bioregional patch size per biome). When species-area curves were plotted separately for selected biomes, the Fynbos ($F_{(1, 144)} = 78.94$, $r^2 = 0.354$, $P < 0.0001$), Succulent Karoo ($F_{(1, 37)} = 58.00$, $r^2 = 0.611$, $P < 0.0001$), and Grassland ($F_{(1, 16)} = 25.60$, $r^2 = 0.615$, $P = 0.0001$) biomes showed significant positive relationships between area and beetle richness (Fig. 9a). Species-area curves for the Desert and Nama-Karoo biomes, Indian Ocean Coastal Belt, and Albany Thicket biomes were not plotted due to low numbers of sampling units ($n < 6$). The Savanna Biome showed weak positive relationship between habitat area and beetle richness ($F_{(1, 13)} = 2.01$, $r^2 = 0.134$, $P = 0.179$).

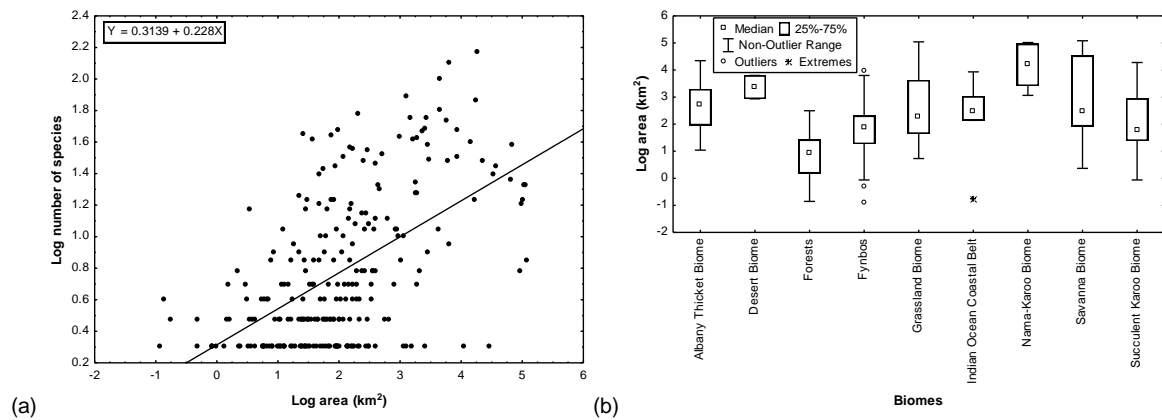


Figure 8. (a) Species-area relationship between monkey beetle species richness and bioregional habitat patch size across all South African biomes. (b) Median bioregional habitat patch size used in species-area plots for biomes.

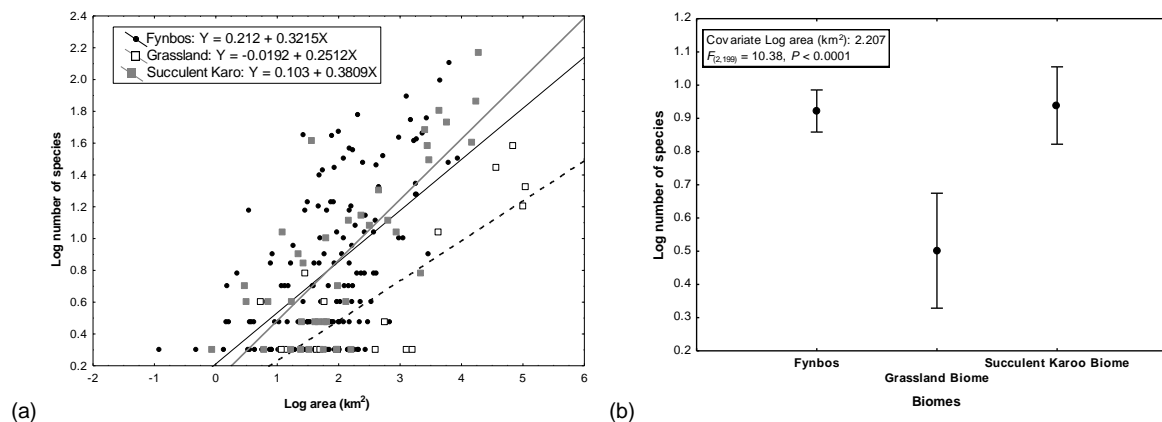


Figure 9. (a) Species-area relationship between monkey beetle species richness and bioregional habitat patch size for the Fynbos, Succulent Karoo, and Grassland biomes. (b) Unplanned multiple comparisons between the three biomes showing unequal intercepts (vertical bars donate 0.95 confidence intervals. Confidence intervals not overlapping indicate significant differences (Sokal and Rohlf 1995)).

Regression models for the Fynbos, Succulent Karoo, and Grassland biomes produced contrasting results. For the Fynbos Biome, area only accounted for 35.4% of explained variance. Whereas, for the Grassland and Succulent Karoo biomes, area explained high proportions (*ca.* 61%) of variance in beetle richness patterns. Regression slope comparisons revealed homogenous slopes ($F_{(2,197)} = 1.238, P = 0.292$) between these three biomes, although their respective *Y*-intercepts were seen to be significantly different ($F_{(2, 199)} = 10.381, P < 0.0001$). The Grassland Biome showed a significantly smaller *Y*-intercept in comparison to the Fynbos and Succulent Karoo biomes (Fig. 9b). Within any given region, within the range of areas in Figure 9a, the Fynbos Biome has 1.7 times more species than Grassland bioregion patches, while the Succulent Karoo has 1.4 times more species. Within the range of areas of Figure 9a, the Fynbos Biome has higher species diversities than the Succulent Karoo, although not significantly so (Fig. 9b).

DISCUSSION

DISTRIBUTION AND DIVERSITY PATTERNS

South Africa, with 63% of the world species, and over a third of the world genera, is clearly the centre of diversity of the tribe Hopliini. Exceptionally high levels of endemism are recorded, with almost all species (98%), and over 80% of genera endemic to South Africa. Diversity patterns seen here for monkey beetles raise interesting questions concerning the drivers of insect speciation in South Africa, particularly in the speciose, winter rainfall regions (Succulent Karoo and Fynbos biomes). For these biomes the exceptional diversity of the Hopliini is matched by congruent patterns of insect diversity across a range of taxonomic groups, highlighting this region as a centre of high evolutionary interest for insect speciation and adaptive radiation. Furthermore, these patterns show concordance with Phytogeographical Centres, suggesting possible co-evolutionary histories between plants and insects, particularly since many of these species-rich insect groups are closely associated with plants and flowers (Hesse 1969, Eardley 1989, Gess 1992, Whitehead and Steiner 2001, Barraclough 2006). This congruent pattern is also suggestive of parallel responses of fauna and flora to historical climatic and geological events.

In broad congruence with Carcasson's (1964) and Endrödy-Younga's (1978) delimited zoogeographic zones, monkey beetle distribution patterns were divided into distinct western and eastern zones, as can be seen from the primary split into two distinct clusters at the > 5% similarity level of the hierarchical cluster analysis using presence data of genera. The western zone showed high monkey beetle species richness and many endemic species, with diversifications concentrated here, thus conforming to a similar pattern shown by many other insect groups (see Introduction). The strong correlations observed between monkey beetle richness and endemism support this region as a centre of diversification. Furthermore, the large

number of range restricted beetle taxa and local endemics highlights the uniqueness of the winter rainfall region and reinforces the suggestion of the existence of a distinct Cape Faunal Zone (Endrödy-Younga 1978). However, a few disjunct (relictual) Cape montane monkey beetle elements are known from areas within the eastern summer rainfall zone (e.g. *Anisonyx* (Andreae 1965)). The high altitude grassland habitats of the Drakensberg Mountains are such an area, and are well known to harbour many shared montane paleogenic invertebrates with the western zone Cape Fold Mountains (Stuckenberg 1962).

In contrast, the eastern zone showed lower richness values, and less endemic species. However, well-collected areas (centered on large towns) showed comparable levels of grid square diversity with some western zone areas, suggesting higher than recorded richness values for this zone, and highlighting the need for more focused collecting within the summer rainfall biomes. However, the same amount of collecting in an eastern vs. a western QDS grid cell would no doubt still show the latter to be richer.

The eastern zone has been shown for several faunal groups to be less zoogeographically distinct than the Cape Zone, sharing Afrotropical elements with southern and central African regions (Ponyton 1961, Lawrence 1952, Balinsky 1962, Van Bruggen 1978, Mansell 1985, Crowe 1990, Tjeder and Hansson 1992, Hamer and Slotow 2002, Alexander et al. 2004, Dijkstra 2007). This pattern is also seen for monkey beetles, with several genera showing shared elements with southern and central African regions (Dombrow 1997d, e, 2002d).

ECOLOGICAL PATTERN - AREA AND HABITAT HETEROGENEITY

Area - often considered a surrogate of habitat heterogeneity (Cowling et al. 1997) – has a long history as an explanatory variable of regional diversity patterns (Connor and McCoy 1979, Rosenzweig 1995). However, the question of whether area *per se* or habitat diversity is more important in influencing species richness is not always clear (Rosenzweig 1995, Tews et al. 2004, Quin et al. 2006, Baldi 2008, Kallimanis et al. 2008). At the biome scale for South Africa, area was a poor explanatory variable of monkey beetle richness and for the measure of habitat heterogeneity (number of vegetation types). Monkey beetle diversity was, however, strongly related to the number of vegetation types found within a biome, suggesting that ecological habitat heterogeneity rather than area size *per se* of a biome is the more important variable in determining beetle richness (see Baldi 2008). The large number of vegetation types, particularly in the Fynbos Biome, represents a rich floristic resource (Goldblatt and Manning 2002) and heterogeneous habitat with the potential to support large numbers of beetle species, thus promoting diversity. In addition, this floristic habitat heterogeneity may be a strong selective force promoting speciation as a result of evolution of habitat (vegetation type) specialisation by beetles, as seen in the high

number of range restricted taxa and local endemics. Furthermore, this floristic habitat heterogeneity is associated with topographic, edaphic, and climatic complexities (Cowling 1990, Cowling et al. 1997, Cowling and Lombard 2002, Linder 2005), often in association with steep physical gradients (Linder 2005). Thus, these factors associated with vegetation types may themselves act as strong drivers of beetle speciation, e.g. through allopatric speciation along steep environmental gradients (cf. South African scorpions (Prendini 2005).

An interesting pattern at the finer ecological scale of bioregion was seen, with larger and smaller sized areas having disproportionately less species in relation to their respective areas (Fig. 4b). Smaller sized bioregions may not offer sufficient resources (abundance of host plants and/or numbers of flowers) to support many beetle species. These small sized bioregions were mostly Fynbos bioregions with low vegetation type diversity (see Appendix 2). The large sized bioregions showing low diversities in comparison to their area sizes were mostly Savanna, Grassland, and Nama-Karoo bioregions, which have low regional diversities. However, area at this ecological scale generally did appear to be an important variable in explaining richness patterns, with larger area sized bioregions generally showing higher richness values (Fig. 4b). Furthermore, at the scale of bioregions, a strong positive relationship was seen between beetle richness and habitat heterogeneity and between habitat heterogeneity and area size. Thus, generally larger bioregions reflect areas with more habitats (and floristic resources) and therefore support more beetle species (cf. habitat heterogeneity hypothesis – Williams 1964, Rosenzweig 1995).

Focussing specifically on Fynbos bioregions (Fig. 4c), close to 60% of variance in beetle richness was explained by area. Area was also positively correlated with habitat heterogeneity; thus, confounding the influences of area and habitat heterogeneity on beetle richness. Nonetheless, habitat heterogeneity is most likely strongly influential on richness patterns, particularly within western fynbos regions, and is the likely underlying reason for the association of richness and area. Positive standardized residuals were generally noted for most western, north-western, south-western and Renosterveld Fynbos bioregions; whereas, all eastern Fynbos bioregions displayed negative standardized residuals. Western fynbos sites are known to be richer in plant species and endemics and show greater differentiation diversities (Levyns 1964, Cowling and Lombard 2002). Thus, western areas will offer greater resources in host plant diversity across finer-scaled (shorter) floristic gradients, which may be promoting higher speciation rates in monkey beetles. It must be noted, however, that within western fynbos regions, the importance of speciation history over and above area/habitat heterogeneity in explaining diversity of western fynbos floristic elements has been strongly debated (Cowling and Lombard 2002, Cowling and Proches 2005), and may also be applicable (assuming shared speciation histories) to the patterns seen of rich beetle

diversity concentrated in western regions of the Fynbos Biome (Fig. 1a). Thus, the strong influence of historical processes (long-term climate stability – Linder 2003, Cowling and Proches 2005) associated with elevated speciation rates may be overemphasising the role of area/habitat heterogeneity in these western areas (see Ricklefs 2006).

The double logarithmic form of the species-area curve revealed significant relationships between habitat area size (vegetation type patch) and richness for the full data range across all biomes, and separately for the Fynbos, Succulent Karoo and Grassland biomes. Comparisons of slopes and intercepts from these curves are useful in relating increases in richness per unit area (Rosenzweig 1995, Cowling et al. 1998, Ouin et al. 2006) and comparing area-controlled regional diversities (Gould 1979, Cowling et al. 1989). Although showing a highly significant relationship ($P < 0.0001$), habitat patch size was a poor explanatory variable of beetle richness accounting for only 3.4% of variance seen in richness. Furthermore, the slope of the curve (0.08) was lower than that predicted for mainland habitat patches (0.1 – 0.2) (Rosenzweig 1995), and for South African plants (0.18) (Cowling et al. 1989). In contrast, Botes et al. (2006) found a strong influence of habitat patch size on ant diversities within the Fynbos Biome across altitudinal gradients. The slope of the curve calculated for monkey beetles is no doubt influenced by the many large sized habitat patches with low beetle richness recorded from the beetle depauperate biomes, e.g. Savanna Biome (see Appendix 2).

Considerably more monkey beetle species are packed into Fynbos landscapes compared to other South African biomes. The slope for the Fynbos Biome curve was the highest (0.27) and comparable to that recorded for plants (0.21) (Cowling et al. 1989). As mentioned above, the Fynbos Biome represents a floristically rich resource for monkey beetles, and the high number of plant species packed into this biome possibly allows for more beetle species occupancy per unit area than other biomes. High species richness values of annuals and geophytes – favoured monkey beetle host plants (Picker and Midgley 1996, Goldblatt and Manning 1998) – have been recorded within the two largest phytogeographical regions of the Fynbos Biome (Goldblatt and Manning 2002). Furthermore, the high beta diversity of the beetles, as seen by the high numbers of narrow range restricted taxa and local endemics, is no doubt influencing the area-richness relationship as with each increase of fynbos habitat patch new beetle species are encountered.

The Succulent Karoo, another resource-rich and plant habitat diverse biome for monkey beetles, did not show significant differences in the slope of species area curves with that of either the Fynbos or Grassland biomes, reflecting an intermediate level of beetle species packing per unit area of habitat. It did, however, show a comparable slope (0.19) to that recorded by Cowling et al. (1989) for plants (0.20). Interestingly

the Grassland Biome showed a significant relationship between beetle richness and habitat area (0.11), whereas the Savanna Biome did not, even though this latter biome showed comparable beetle diversities to the former, and greater number of vegetation types (see Table 1) and plant diversity (Cowling et al. 1989). However, the Grassland Biome shows higher plant alpha and gamma diversity and a higher slope (slope = 0.25) value for its plant species-area curve (Cowling et al. 1989), suggesting greater plant resources per unit area of habitat for beetles. This possibly also explains the non-significant differences between beetle species-area slopes for the Grassland and Succulent Karoo biomes. Furthermore, the Grassland biome had higher beetle species compositional dissimilarities between ecological units than the Savanna Biome (as adjudged from the higher percentage of species restricted to vegetation types – Table 2), and thus, higher beetle species turnover between vegetation types is most likely influencing the positive relationship between area and beetle richness (see Rosenzweig 1995, Scheiner 2003).

The slopes of the species-area curves using bioregional patches as sampling units were noticeably higher than those recorded using vegetation type patches. However, this was expected, as bioregional patches are representative of more environmentally heterogeneous sampling units, and as such, will affect slope values (Rosenzweig 1995, Kallimanis et al. 2008). Nonetheless, area still explained low proportions (*ca.* 30%) of the variances seen in beetle richness. Homogeneous slopes were seen for these curves, and thus area could be factored out and intercept values compared. For any given area, the Fynbos Biome has 1.7 times more species than the Grassland Biome, and 1.28 times more species than the Succulent Karoo. The larger regional beetle diversities seen for the Fynbos Biome are mostly likely the product of the high plant diversities and high habitat diversity (many bioregions – see Appendix 2) seen for this biome (see above). The Fynbos Biome also shows high beetle alpha (Table 1) and beta diversities (Table 2), which are all important contributing components of regional diversity (Whittaker 1972). The Succulent Karoo's regional diversity values are also impressive, and the ecological factors determining regional diversity for the Fynbos, are most likely at play in this biome as well. This is reflected in the shared diversifications of many monkey beetle genera. The Succulent Karoo shows high beetle alpha (Appendix 3) and beta diversity (Colville et al. 2002). Although of short duration (Cowling et al. 1999), the mass spring flowering displays of the latter offer a rich floristic resource. Furthermore, as for most parts of the Fynbos Biome, the climate is favourable in terms of highly predictable winter rainfall (Cowling et al. 1998) and subsequent spring flowering events.

HISTORICAL PATTERNS – VICARIANCE AND SPECIATION

Both contemporary ecology and historical factors should be invoked when explaining biogeographic patterns of extant taxa (Myers and Giller 1988). The approach of using both local (ecological) and

regional (historical) processes when explaining geographic diversity patterns has recently been strongly advocated (Ricklefs 2004, 2006). Modern biogeographic analyses using cladistic-based morphological and molecular phylogenies have postulated several different historical factors accounting for current southern African invertebrate distributional and diversity patterns. A recurrent explanation commonly presented for the fauna of the winter rainfall regions of South Africa is the geographical fragmentation of populations as a result of palaeoclimatic change (Endrödy-Younga 1988, Stuckenberg 1998, 2000, Prendini 2001a, Wishart and Day 2002, Prendini 2005) and geomorphic evolution (Irish 1990, Stuckenberg 1998, Prendini 2001b, 2005, Sole et al. 2005). Such factors have set up barriers to dispersal, isolating populations geographically, and in turn promoting allopatric speciation through vicariant events (Endrödy-Younga 1978, Irish 1990, Prendini 2001a). More specifically, vicariant speciation in the Cape Folded Mountain system has been proposed for various taxa within the Fynbos and Succulent Karoo biomes (Endrödy-Younga 1988, Holm 1990, Perkins and Balfour-Browne 1994, Stuckenberg 1998, Stevens and Picker 1999, Stuckenberg 2000, Wishart and Day 2002, Prendini 2005, Sole et al. 2005, Ribera and Balke 2007). While the current studies have focused largely on montane taxa and have estimated that various populations have been isolated (Wishart and Day 2002), less work has been done on the lowland fauna. The role of historical processes and its relations to high levels of cladogenesis and endemism as observed in the Fynbos and Succulent Karoo biomes would need to be considered in order to fully explain monkey beetle diversity and distribution patterns.

CONCLUSION

The global centre for monkey beetle diversity is clearly centered within South Africa, with a separation of the fauna into two distinct provinces, viz. a high diversity western and lower diversity eastern zone corresponding broadly with the winter rainfall Fynbos and Succulent Karoo biomes and summer-rainfall Grassland and Savanna biomes, respectively. Furthermore, the centre of adaptive radiation and speciation is clearly centered within the winter rainfall biomes of south, which show the highest number of range restricted beetle taxa, high local vegetation type endemism, and concentrations of lineage diversifications. Using area as a prime measure of ecological pattern revealed area to be a poor explanatory variable of beetle richness. Habitat heterogeneity appeared to be of greater importance when explaining richness patterns. The Fynbos Biome showed the highest beetle richness, accumulated species significantly faster than other biomes and showed highest richness per unit habitat area.

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APPENDIX

Appendix 1. Descriptive statistics for bioregions.

Label	Bio-regions	Biome	Bio-region size (km ²)	No. of vegetation types per bio-region	No. of beetle spp.	No. of vegetation types with beetle collection records (% of total)	Average no. of beetle spp. per vegetation type (± sd.)	Average area (km ²) of vegetation types in bio-region (± sd.)
1	Albany Thicket	Albany Thicket Biome	29127.54	14	38	10 (71.43)	5.50 (4.01)	2494.83 (2025.41)
2	Alluvial Vegetation	Azonal Vegetation	8817.01	-	-			
3	Alluvium Fynbos - Southwest Fynbos Bioregion	Fynbos	1035.66	3	72	3 (100.0)	27.67 (2.89)	345.22 (251.92)
4	Alluvium Renosterveld - East Coast Renosterveld Bioregion	Fynbos	498.35	1	13	1 (100.0)	13	498.35
5	Bushmanland Bioregion	Nama-Karoo Biome	95882.3	6	5	2 (33.33)	2.50 (2.12)	26881.44 (26300.87)
6	Central Bushveld Bioregion	Savanna Biome	118373.9	28	27	18 (64.29)	4.33 (4.47)	5321.45 (4675.15)
7	Dolerite Renosterveld - Karoo Renosterveld Bioregion	Fynbos	1007.47	2	34	2 (100.0)	18.00 (9.90)	503.74 (400.17)
8	Drakensberg Grassland Bioregion	Grassland Biome	41930.68	10	32	8 (80.0)	7.88 (5.08)	5218.56 (6269.35)
9	Dry Highveld Grassland Bioregion	Grassland Biome	113485.2	15	15	9 (60.00)	2.78 (2.44)	9760.18 (6738.14)
10	Eastern Kalahari Bushveld Bioregion	Savanna Biome	124263.4	16	6	3 (18.75)	2.67 (2.08)	13323.13 (7465.01)
11	Eastern Strandveld	Azonal Vegetation	471.72					
12	Estuarine Vegetation	Azonal Vegetation	162.58					
13	Ferricrete Fynbos – Southwest Fynbos Bioregion	Fynbos	706.07	2	2	1 (50.00)	2	665.58
14	Freshwater Wetlands	Azonal Vegetation	1325.88					
15	Gariep Desert Bioregion	Desert Biome	6303.34	10	8	3 (30.00)	2.67 (0.58)	1435.55 (1210.52)
16	Granite Fynbos - Namaqualand Cape Shrublands Bioregion	Fynbos	36.39	1	6	1 (100.00)	6	36.39
17	Granite Fynbos - Southwest Fynbos Bioregion	Fynbos	604.65	3	69	2 (66.67)	46.50 (4.95)	293.83 (290.18)
18	Granite Renosterveld - Namaqualand Cape Shrublands Bioregion	Fynbos	706.13	1	42	1 (100.00)	42	706.13
19	Granite Renosterveld - West Coast Renosterveld Bioregion	Fynbos	947.46	1	51	1 (100.00)	51	947.46
20	Indian Ocean Coastal Belt	Indian Ocean Coastal Belt	14281.97	5	47	4 (80.00)	15.25 (20.71)	3322.71 (2340.74)

Label	Bio-regions	Biome	Bioregion size (km ²)	No. Of vegetation types per bio region	No. of beetle spp.	No. of vegetation types with beetle collection records (% of total)	Average no. of beetle spp. per vegetation type (± sd.)	Average area (km ²) of vegetation types in bio-region (± sd.)
21	Inland Saline Vegetation	Azonal Vegetation	17855.35					
22	Kalahari Duneveld Bioregion	Savanna Biome	42628.88	4	2	1 (25.00)	2	36771.68
23	Knersvlakte Bioregion	Succulent Karoo Biome	5061.08	8	79	6 (75.00)	17.17 (17.34)	794.39 (586.42)
24	Limestone Fynbos - South Coast Fynbos Bioregion	Fynbos	2103.96	3	5	1 (33.33)	5	686.52
25	Limestone Renosterveld - Western Fynbos-Renosterveld Bioregion	Fynbos	502.01	1	4	1 (100.00)	4	502.01
26	Lower Karoo Bioregion	Nama-Karoo Biome	31863.45	4	17	2 (50.00)	8.50 (10.61)	10986.40 (13206.63)
27	Lowveld Bioregion	Savanna Biome	66085.2	24	22	11 (45.83)	3.55 (2.77)	4360.60 (5785.34)
28	Mesic Highveld Grassland Bioregion	Grassland Biome	124128.79	29	24	20 (68.97)	3.85 (2.30)	5364.62 (5533.45)
29	Mopane Bioregion	Savanna Biome	25669.49	8	1	1 (12.50)	1	8797.34
30	Namaqualand Hardeveld Bioregion	Succulent Karoo Biome	19352.72	6	155	6 (100.00)	40.17 (35.07)	3225.45 (3992.54)
31	Namaqualand Sandveld Bioregion	Succulent Karoo Biome	9097.18	13	80	12 (92.31)	12.83 (12.61)	726.71 (1036.38)
32	Quartzite Fynbos – Eastern Fynbos-Renosterveld Bioregion	Fynbos	1450.2	2	4	1 (50.00)	4	885.43
33	Quartzite Fynbos - Northwest Fynbos Bioregion	Fynbos	1646.18	1	12	1 (100.00)	12	1646.18
34	Quartzite Fynbos - Southwest Fynbos Bioregion	Fynbos	98.17	1	3	1 (100.00)	3	98.17
35	Quartzite Fynbos – Western Fynbos-Renosterveld Bioregion	Fynbos	1268.07	1	4	1 (100.00)	4	1268.07
36	Rainshadow Valley Karoo Bioregion	Succulent Karoo Biome	27892.95	14	148	11 (78.57)	18.36 (15.79)	2246.15 (2154.43)
37	Richtersveld Bioregion	Succulent Karoo Biome	6463.77	19	55	13 (68.42)	8.69 (6.01)	418.25 (340.63)
38	Sand Fynbos - Eastern Fynbos-Renosterveld Bioregion	Fynbos	153.69	1	2	1 (100.00)	2	153.69
39	Sand Fynbos - Northwest Fynbos Bioregion	Fynbos	3694.78	2	87	2 (100.00)	45.50 (55.86)	1847.39 (1284.11)
40	Sand Fynbos - South Coast Fynbos Bioregion	Fynbos	938.79	2	5	2 (100.00)	2.50 (0.71)	469.40 (337.74)

Label	Bio-regions	Biome	Bioregion size (km ²)	No. of vegetation types per bioregion	No. of beetle spp.	No. of vegetation types with beetle collection records (% of total)	Average no. of beetle spp. per vegetation type (± sd.)	Average area (km ²) of vegetation types in bio-region (± sd.)
41	Sand Fynbos - South Strandveld Bioregion	Fynbos	186.26	1	4	1 (100.00)	4	186.26
42	Sand Fynbos - Southwest Fynbos Bioregion	Fynbos	3215.14	5	61	5 (100.00)	16.00 (10.00)	643.03 (700.70)
43	Sandstone Fynbos - Eastern Fynbos- Renosterveld Bioregion	Fynbos	11612.29	6	64	6 (100.00)	13.67 (13.11)	1935.38 (1339.48)
44	Sandstone Fynbos - Northwest Fynbos Bioregion	Fynbos	8524.83	9	172	9 (100.00)	31.22 (28.49)	947.20 (737.71)
45	Sandstone Fynbos - Southern Fynbos Bioregion	Fynbos	2255.17	2	31	2 (100.00)	17.00 (0.00)	1127.58 (135.88)
46	Sandstone Fynbos - Southwest Fynbos Bioregion	Fynbos	4369.84	7	113	6 (85.71)	25.67 (22.29)	710.42 (385.91)
47	Sandstone Fynbos - Western Fynbos- Renosterveld Bioregion	Fynbos	3343.82	7	24	4 (57.14)	7.25 (4.03)	667.53 (366.51)
48	Seashore Vegetation	Azonal Vegetation	349.17					
49	Shale Band Vegetation - Northwest Fynbos Bioregion	Fynbos	264.32	2	10	1 (50.00)	10	264.32
50	Shale Band Vegetation - Southern Fynbos Bioregion	Fynbos	68.67	1	1	1 (100.00)	1	68.67
51	Shale Band Vegetation - Southwest Fynbos Bioregion	Fynbos	134.66	1	1	1 (100.00)	1	134.66
52	Shale Fynbos - Eastern Fynbos- Renosterveld Bioregion	Fynbos	1081.31	2	30	1 (50.00)	30	566.43
53	Shale Fynbos - Northwest Fynbos Bioregion	Fynbos	428.01	1	9	1 (100.00)	9	428.01
54	Shale Fynbos - Southern Fynbos Bioregion	Fynbos	186.75	1	2	1 (100.00)	2	186.75
55	Shale Fynbos - Southwest Fynbos Bioregion	Fynbos	952.55	4	20	4 (100.00)	5.75 (5.56)	238.14 (103.84)
56	Shale Renosterveld - East Coast Renosterveld Bioregion	Fynbos	7816.01	5	65	4 (80.00)	19.00 (15.43)	1754.89 (799.89)

Label	Bio-regions	Biome	Bioregion size (km ²)	No. of vegetation types per bioregion	No. of beetle spp.	No. of vegetation types with beetle collection records (% of total)	Average no. of beetle spp. per vegetation type (± sd.)	Average area (km ²) of vegetation types in bio-region (± sd.)
57	Shale Renosterveld – Eastern Fynbos-Bioregion	Fynbos	2033.39	4	13	2 (50.00)	6.50 (3.54)	286.86 (112.82)
58	Shale Renosterveld - Karoo Bioregion	Fynbos	4552.42	4	67	4 (100.00)	18.50 (20.63)	1138.11 (1283.09)
59	Shale Renosterveld - West Coast Bioregion	Fynbos	4975.44	2	104	2 (100.00)	57.50 (61.52)	2487.72 (3476.17)
60	Shale Renosterveld - Western Fynbos-Bioregion	Fynbos	4531.81	4	68	3 (75.00)	24.33 (13.65)	1418.47 (838.85)
61	Silcrete Fynbos – Southern Fynbos Bioregion	Fynbos	868.47	1	3	1 (100.00)	3	868.47
62	Silcrete Renosterveld - West Coast Bioregion	Fynbos	99.94	1	1	1 (100.00)	1	99.94
63	Southern Namib Desert Bioregion	Desert Biome	862.32	5	10	3 (60.00)	3.33 (2.52)	281.51 (116.89)
64	Sub-Escarpment Grassland Bioregion	Grassland Biome	75048.84	18	37	14 (77.78)	5.93 (4.23)	5041.21 (3220.05)
65	Sub-Escarpment Savanna Bioregion	Savanna Biome	35523.66	7	64	7 (100.00)	12.29 (14.37)	5074.81 (4077.56)
66	Trans-Escarpment Succulent Karoo Bioregion	Succulent Karoo Biome	15416.3	3	39	2 (66.67)	20.50 (13.44)	6559.55 (1278.47)
67	Upper Karoo Bioregion	Nama-Karoo Biome	120534.19	4	17	4 (100.00)	4.75 (4.27)	30133.55 (18542.89)
68	Western Strandveld - South Strandveld Bioregion	Fynbos	656.89	3	6	2 (66.67)	3.00 (2.83)	298.40 (135.11)
69	Western Strandveld - West Strandveld Bioregion	Fynbos	2343.63	6	70	5 (83.33)	21.20 (7.95)	461.60 (188.88)
70	Zonal & Intrazonal Forests	Forests	4484.85	9	20	6 (66.67)	3.67 (2.50)	669.59 (327.25)

Appendix 2. Descriptive statistics for vegetation type habitat patch sizes for biomes and bioregions. Habitat patch sizes were used in plotting double logarithmic forms of the species-area curve.

Region	<i>n</i>	Mean local beetle richness (±sd.)	Median vegetation patch area (km ²) (25 quantile - 75 quantile)	Mean proportional area size of local patch (±sd.)
Biome				
Grassland Biome	33	4.64 (3.04)	711.82 (217.26 - 1865.94)	0.31 (0.29)
Fynbos Biome	113	10.07 (11.47)	85.66 (31.28 - 188.26)	0.17 (0.20)
Succulent Karoo Biome	76	9.16 (8.67)	154.10 (50.12 - 376.26)	0.28 (0.27)
Savanna Biome	28	6.04 (6.63)	546.33 (176.71 - 1701.16)	0.28 (0.30)
Indian Ocean Coastal Belt	2	6.00 (0.00)	60.93 (4.88 - 116.97)	0.43 (0.55)
Albany Thicket Biome	5	3.80 (1.64)	229.50 (125.97 - 254.42)	0.63 (0.39)
Nama-Karoo Biome	3	2.00 (0.00)	787.15 (107.02 - 1800.06)	0.36 (0.34)
Desert Biome	1	2.00 (0.00)	9.20 (9.20 - 9.20)	0.13 (0.00)
Forests	4	2.75 (0.96)	20.77 (11.55 - 29.39)	0.43 (0.25)
Bioregion				
Mesic Highveld Grassland Bioregion	10	3.10 (1.66)	45.54 (28.56 - 614.73)	0.22 (0.32)
Rainshadow Valley Karoo Bioregion	7	9.57 (13.96)	58.53 (7.05 - 173.80)	0.30 (0.32)
Sandstone Fynbos - Eastern Fynbos-Renosterveld Bioregion	3	2.00 (0.00)	31.70 (1.50 - 55.62)	0.25 (0.23)
Central Bushveld Bioregion	7	4.29 (5.62)	138.87 (50.72 - 394.42)	0.21 (0.24)
Sandstone Fynbos - Northwest Fynbos Bioregion	3	5.67 (2.08)	38.89 (2.26 - 68.81)	0.43 (0.39)
Indian Ocean Coastal Belt	2	6.00 (0.00)	60.93 (4.88 - 116.97)	0.43 (0.55)
Albany Thicket	5	3.80 (1.64)	229.50 (125.97 - 254.42)	0.63 (0.39)
Namaqualand Hardeveld Bioregion	13	10.23 (6.75)	58.51 (12.90 - 74.04)	0.27 (0.20)
Knersvlakte Bioregion	5	5.00 (3.46)	22.23 (12.02 - 25.32)	0.41 (0.28)
Shale Renosterveld - West Coast Renosterveld Bioregion	2	14.00 (0.00)	15.91 (3.43 - 28.38)	0.32 (0.35)
Upper Karoo Bioregion	1	2.00 (0.00)	107.02 (107.02 - 107.02)	0.09 (0.00)
Sub-Escarpment Savanna Bioregion	7	9.14 (11.29)	201.92 (83.66 - 293.54)	0.54 (0.30)
Zonal & Intrazonal Forests	4	2.75 (0.96)	20.77 (11.55 - 29.39)	0.46 (0.26)
Gariep Desert Bioregion	1	2.00 (0.00)	9.20 (9.20 - 9.20)	0.15 (0.00)
Sandstone Fynbos - Western Fynbos-Renosterveld Bioregion	2	4.50 (2.12)	6.47 (6.19 - 6.75)	0.19 (0.01)
Namaqualand Sandveld Bioregion	5	6.00 (2.24)	27.02 (25.70 - 55.37)	0.41 (0.22)
Sand Fynbos - Northwest Fynbos Bioregion	1	2.00 (0.00)	9.19 (9.19 - 9.19)	0.25 (0.00)
Granite Fynbos - Southwest Fynbos Bioregion	1	4.00 (0.00)	1.54 (1.54 - 1.54)	0.25 (0.00)
Richtersveld Bioregion	2	5.00 (4.24)	31.62 (18.37 - 44.86)	0.49 (0.29)
Sub-Escarpment Grassland Bioregion	3	3.67 (0.58)	392.41 (217.26 - 724.38)	0.59 (0.34)
Sand Fynbos - South Coast Fynbos Bioregion	1	2.00 (0.00)	3.57 (3.57 - 3.57)	0.38 (0.00)
Drakensberg Grassland Bioregion	3	3.33 (2.31)	252.55 (209.86 - 420.04)	0.70 (0.26)
Dry Highveld Grassland Bioregion	1	2.00 (0.00)	581.76 (581.76 - 581.76)	0.51 (0.00)
Shale Renosterveld - Eastern Fynbos-Renosterveld Bioregion	1	2.00 (0.00)	10.85 (10.85 - 10.85)	0.53 (0.00)
Granite Renosterveld - Namaqualand Cape Shrublands Bioregion	1	2.00 (0.00)	3.81 (3.81 - 3.81)	0.54 (0.00)
Western Strandveld - West Strandveld Bioregion	2	10.50 (9.19)	13.51 (13.19 - 13.82)	0.58 (0.02)
Sand Fynbos - Southwest Fynbos Bioregion	1	8.00 (0.00)	18.53 (18.53 - 18.53)	0.58 (0.00)
Sandstone Fynbos - Southwest Fynbos Bioregion	1	44.00 (0.00)	26.75 (26.75 - 26.75)	0.61 (0.00)
Shale Renosterveld - East Coast Renosterveld Bioregion	1	6.00 (0.00)	48.24 (48.24 - 48.24)	0.62 (0.00)
Bushmanland Bioregion	1	2.00 (0.00)	787.15 (787.15 - 787.15)	0.82 (0.00)
Shale Renosterveld - Karoo Renosterveld Bioregion	1	6.00 (0.00)	40.18 (40.18 - 40.18)	0.88 (0.00)
Shale Fynbos - Southwest Fynbos Bioregion	1	7.00 (0.00)	8.48 (8.48 - 8.48)	0.89 (0.00)

2 DELIMITING CENTRES OF ENDEMISM FOR SOUTH AFRICAN MONKEY BEETLES AND SEARCHING FOR CONGRUENCE WITH BIOGEOGRAPHIC PATTERNS OF OTHER GROUPS

“The most elementary questions of historical biogeography concern areas of endemism and their relationships” (*Nelson and Platnick 1981*).

ABSTRACT

Centres of endemism – central units of area used in biogeographic and conservation studies – are generally accepted to represent areas of special evolutionary history (centres of diversification and clade origin). Within South Africa, and particularly within the global floristic hotspots of the Cape Floristic Region and Succulent Karoo, biogeographic congruence across faunal and floral groups, in terms of common centres of diversification, has not been investigated. In this context, monkey beetle centres of endemism (CoE) were delimited using an Integrated Weighting technique in conjunction with GIS interrogation and then spatially matched to several other zoogeographic and phytogeographic centres to search for areas of biogeographic congruence. Of the 18 centres of endemism (CoE) retrieved for monkey beetles, the most endemic- and species rich, and largest sized CoEs were retrieved from the winter rainfall western regions that had well-defined Cape and Namaqualand zones. These zones showed good spatial congruence with other zoogeographic and phytogeographic centres, highlighting shared centres of diversification across taxonomic groups within the Fynbos and Succulent Karoo Biomes. In contrast, less well-defined and diverse centres were retrieved within the summer rainfall regions of South Africa. Nonetheless, spatial congruence of monkey beetle CoE matched coastal tropical and montane biogeographic centres. Within CoEs, endemism values were strongly correlated with the richness of non-endemic species ($r^2 = 0.89$, $P < 0.001$), highlighting CoEs as areas of high diversity and high conservation importance. The radiation and diversification of monkey beetles within the winter rainfall region was further explored based on inference from contemporaneous patterns seen in other faunal and floral groups whose phylogenetic histories are better known. The timing and geographical structure of monkey beetle diversifications accords with faunal and floristic evidence, and indicates a coevolved response to, and with, the progression of floral evolution within the winter rainfall biomes in response to periods of climatic change during the Pliocene.

INTRODUCTION

Establishing patterns of areas containing range restricted taxa is one of the fundamental steps in historical biogeography. Such areas are commonly referred to as “centres of endemism”. However, the strict definition of such areas is much debated (Harold and Mooi 1994, Linder 2001, Hausdorf 2002). Generally, centres of endemism are defined by at least two sympatric species with similar restricted

geographic ranges (Morrone 1994, Linder 2001). Furthermore, centres of endemism have been defined based on phylogenetic relatedness of co-occurring species (Harold and Mooi 1994) and the appearance of clear geological and other physical barriers that isolate populations and promote the formation of new species (Morrone 1994, Hausdorf 2002). Despite the discrepancies in definition, centres of endemism are generally accepted to represent areas of special evolutionary history (centres of diversification and clade origin; Croizat et al. 1974, Ricklefs and Schuller 1993, Harold and Mooi 1994, Emerson and Kolm 2005). Centres of endemism are furthermore representative of areas of high conservation importance in that areas containing high numbers of endemics are useful surrogates for global diversity patterns (Lamoreux et al. 2006) and are weighted heavily in conservation assessments when assigning global “hotspot” status (cf. Cape Floristic Region (Myers et al. 2001). Moreover, their underlying character of reflecting historical evolutionary processes highlights their importance in conservation strategies that seek spatial surrogates which capture key processes like classic geographic speciation (Rouget et al. 2003).

In addition, delimiting centres of endemism provides ‘units of area’ (Hausdorf 2002) to work with in searching for congruent biogeographical patterns across taxa (“biogeographic homology” – Morrone 2001) in terms of their respective centres of possible diversification (Rosen 1978, Calsbeek et al. 2003). Patterns of centres of endemism can also be placed within their historical context of landscape evolution (e.g. geomorphic changes – Cowling et al. 2008). Thus, centres of endemism provide insights into the evolutionary history of an area and its associated biota and help explain contemporary patterns of species distributions.

Delimitation of phytogeographic and zoogeographic centres within southern Africa has a long history (Werger 1978). However, early zoogeographic studies generally did not relate distributional patterns in terms of ecology and history (see references in Werger 1978) and rather confined their approaches to historical zoogeography. A further short-coming of these early studies was the largely intuitive approach in examining species distribution maps with the lack of empirical techniques, essentially making these studies unrepeatably (see Linder 2001). Nonetheless, these early studies were invaluable in subdividing Africa into a number of clearly defined phytogeographic (e.g. White 1976) and zoogeographical zones (e.g. Carcasson 1964).

The development of modern analytical techniques has made it possible to analyse large taxonomic and distributional datasets more objectively to identify biogeographic patterns. Geographic information systems (GIS) have further revolutionized the analysis of spatial data allowing more detailed ecological zoogeographic studies (Huang et al. 2008). Progression of techniques utilized for South African faunal groups have evolved from descriptive accounts based on expert knowledge, e.g. Masarine wasps (Gess

1992), through to GIS based empirical analyses using point locality data in conjunction with GIS environmental themes, e.g. scorpions (Prendini 2005). Phylogeography - another modern spatial technique used to study the historical processes that are responsible for contemporary geographic distributions (Avice 2000), has also been widely used (Sole et al. 2005, Price et al. 2007). Advanced clustering techniques for delimiting centres of endemism have further been undertaken for a number of plant groups within southern Africa (Linder 2001, Moline and Linder 2006, Born et al. 2007). However, these recently developed techniques have not yet been utilized for faunal studies in southern Africa. Ironically, the only study delimiting centres of endemism for a South African insect group (Morrone 1994) did not place any biogeographical or ecological context to its findings, but rather used the insect group of choice purely to highlight a methodological approach (parsimony analysis) used in delimiting areas of endemism.

Clustering techniques used in delimitation of centres of endemism have been progressively refined to account for both wide-spread and narrow range restricted taxa (Williams 1992, Linder 2001). Such statistical approaches include the use of various weighting techniques which maximize the valuable information obtained from range restricted taxa, while reducing the noise created by less informative, wide-spread taxa (Nelson and Platnick 1981, Linder 2001, Bradshaw and Linder 2009). Several of these proposed weighting techniques offer different advantages in their contrasting weighting functions used when dealing with high numbers of range restricted or wide-spread taxa (see Linder 2001). Furthermore, other studies have adopted a null model approach to account for possible confounding effects of levels of local richness (Jetz et al. 2004) and to filter out conflicting taxa (Giokas and Sfenthourakis 2008). Recently, Bradshaw and Linder (2009) have developed an integrated weighting technique which uses a range of modern weighting techniques to seek spatial congruence in the results obtained from multiple clustering analyses. Furthermore, they refine delimited centres based on the best results from each technique by investigating results within GIS, which allows areas of congruence and conflict to be highlighted, and subsequently interrogate and resolved (see also Huang et al. 2008). Thus, this approach effectively delimits centres in terms of their physical size and numbers of endemics captured.

Here, I use the integrated weighting technique approach of Bradshaw and Linder (2009). As suggested by these researchers, various weighting techniques to delimit monkey beetle centres of endemism (CoE) for South Africa were used with post-interrogation of results within GIS. Specifically, I investigate (1) the geographic patterns of centres of endemism for an insect group within South Africa (2) the relationship between numbers of endemics within centres and numbers of species (richness) to see whether centres are also reflective of areas of higher richness and (3) the geographical positions and boundaries of monkey beetle CoEs in comparison to centres of endemism for other insect and plant groups, in order to seek

biogeographical congruence possibly highlighting areas of common historical processes and biotic speciation, and of high conservation importance. Furthermore, focussing specifically on the species rich winter rainfall areas identified in Chapter 1, radiation and diversification of monkey beetles in the context of identified CoE patterns, are explored based on inference from contemporaneous patterns seen in other faunal and floral groups whose phylogenetic histories are better established.

METHODS

COMPILATION OF DISTRIBUTIONAL DATA SET

A point locality distributional data set was collated from several sources (see Chapter 1). This data set reflected the most recent taxonomic position of the South African monkey beetles. Monkey beetle distributional data was further obtained from an extensive pinned collection housed at the South African Iziko Museum, Cape Town. Additional locality data was supplemented by field study collections undertaken during spring flowering seasons (1999-2007). Each point locality was geo-referenced using 1:50 000 and 1:250 000 topo-cadastral maps of South Africa (sourced from Chief Directorate: Surveys and mapping (CDSM), Mowbray, Cape Town, www.w3sli.wcape.gov.za) and the GeoNet Names Server gazetteer (http://164.214.2.59/gns/htm/cntry_files.html). Only collection records of sufficient accuracy were used. Obscure and/or vague locality records, such as “Cape of Good Hope” were excluded. Highly disjunct records, suggesting misidentification of a species, or incorrect locality label information were further excluded from the data set. In total, 1040 species and 6959 unique locality records were collated for use in the GIS analysis. Distributional datasets from e.g. museum natural history collections are highly useful in biogeographic studies, although limitations of such presence-only data sets are recognised (Graham et al. 2004).

Monkey beetle point distribution maps were created using Arcmap 9.2 (ESRI 2006) and overlaid onto a Quarter Degree Square (QDS) grid (Edwards and Leistner 1971) of South Africa (including Lesotho and Swaziland).

APPROACHES USED IN IDENTIFYING COES

AREA BASED INPUT UNIT

Following similar biogeographical studies (Olivero et al. 1983, Linder and Mann 1998, Linder 2001, Prendini 2005, Bradshaw and Linder 2009) QDS grid cells were selected as the most efficient geographic area input unit (Crevello 1981) to identify patterns of monkey beetle endemism in South Africa.

Shortcomings have been noted in the use of QDS due to its geographic coarseness (Moline and Linder 2006). However, apart from allowing comparisons with other studies, analytical techniques used in identifying CoE require a defined area based input unit (Rosen 1988, Morrone 1994).

WEIGHTING TECHNIQUES

Traditionally, clustering algorithms, including phenetic similarity (Rosen, 1988) and parsimony analyses (Morrone, 1994) have been used in identifying areas of endemism. Subsequently, taxon weighting techniques have been employed in identifying CoE, specifically emphasising the contributions of range restricted taxa (those taxa most likely to be endemic) (Linder 2001). More recently, Bradshaw and Linder (2009) have further developed this approach to include multiple weighting techniques in conjunction with the use of GIS, in identifying CoEs. Using this approach allows one to identify different patterns of area (QDS) clustering, providing an indication of conflict between different biotic elements and taxa, and thus, more accurate and inclusive CoEs can be delimited (Bradshaw and Linder 2009).

Following the literature (Williams 1992, Linder 2001), I used four recommended weighting techniques. Firstly, the data set was analysed unweighted (Rosen 1998), i.e. all species were equally weighted, irrespective of their distributional range size. Secondly, inverse weighting of species area was used (Williams 1992, Linder 2001). For inverse weighting, the weights are proportional to the inverse of species ranges; therefore, species with small ranges are assigned high weights, whilst species with larger ranges have progressively lower weights (Williams 2000, Linder 2001). Thirdly, the Bell-shaped curve weighting technique of Linder (2001) was used. This method employs more moderate weighting of highly range restricted taxa. Although the Bell-shaped curve weighting can be adjusted, it can only be done *a posteriori* (Linder 2001). Finally, Bradshaw and Linder's (2009) integration weighting technique was also used. This technique adjusts to the spatial properties of individual data sets *a priori* by taking into account the relative frequencies of range restricted and widespread taxa. The integration technique provides a flexible, fast and efficient additional weighting criterion to further test for congruence between biotic elements in the data (Bradshaw and Linder 2009). The results from the different weighting techniques were then combined in a GIS (see below).

CLUSTERING OF QDS INTO CoEs

For each of the weighted data sets, the computer software package PRIMER v6 (Clarke and Gorley 2006) with Bray-Curtis Similarity measures was used in clustering QDS, displayed in group averaged dendrograms. A cut-off phenon-line for clusters was not drawn, as these phenon-lines are essentially

arbitrary (see Linder 2001); instead logical clusters were intuitively grouped, mostly in the region of 20% similarity. This approach maximises the number of clusters and complete clusters, without arbitrary discounting basal clusters on the dendrogram.

For each weighting analysis, clusters (grouped QDS) were then screened in a GIS (Arcmap 9.2) to remove spurious QDS. This screening process has a dual purpose of firstly removing clusters that contain no endemic taxa, and secondly modifying the remaining clusters to include only those QDS that contain at least part of the distributional range of at least one of the endemics in the respective cluster (Bradshaw and Linder 2009). The results from this screening, for each weighting analysis, were then overlaid in a GIS and evaluated following Bradshaw and Linder's (2009) procedures for spatial congruence between the different analyses, resulting in a more optimal arrangement of QDS for delimited CoE (cf. consensus trees in phylogenetics). These consensus CoEs were then mapped in a GIS and displayed with a topographic (Jarvis et al. 2006) background for spatial reference. Spatial and taxonomic (number of species and endemics) properties of the delimited CoE were calculated and tabulated.

Delimited CoEs were further clustered with the four weighting analyses mentioned above based on species compositional similarities between them. Average-weighted Dendrograms were plotted based on Bray-Curtis Similarity resemblance matrices within the software package PRIMER. This essentially combined the CoEs into hierarchical zoogeographic levels, which aided in making comparison to zoogeographic regions in the literature.

TAXONOMIC CORRELATES OF COES

Linear regression analyses were used to relate the number of endemics (for those CoEs with $n \geq 2$ endemics (Linder 2001) found within CoEs to richness (number of non-endemic species) and to area (km^2). To ensure the assumption of independence between variables, (Quinn and Keough 2003), non-endemic species richness was used in regression with endemism, and calculated as the total number of species found within a CoE minus the number of endemic species found in that CoE.

Comparisons of numbers of species between unequalled area sized CoEs was accommodated by calculating area-corrected species densities by solving for c , the coefficient of the species-area curve of $S = cA^z$, where S is species number, A is area, and z is the exponent of the power function (Gould 1979, Rosenzweig 1995). The assumed z value of 0.18, a commonly occurring value for continental areas (Rosenzweig 1995) and for South African biomes (Cowling et al. 1989), was used (see also Born et al. 2007). However, it must be noted that comparisons of area corrected species richness for CoEs may not

be biologically or statistically valid in that the geographical definition of CoEs is based on the commonality of a set of range restricted taxa, whose geological ranges in turn are most likely strongly reflective of evolutionary (historical) processes possibly independent of area effects, being less influenced by the contemporary environment (see Jetz et al. 2004). Furthermore, the non-endemic species diversity component of a CoE may consist of a high number of widespread taxa, or at very least, based on CoE delimitation criteria, taxa whose ranges extend outside of the CoE, and as such, the area size of the CoE is most likely unimportant for such taxa, whose presence within a CoE is possibly coincidental and more reflective of regional processes, e.g. immigration (see Ricklefs 2006). Thus, the assumption that an area delimited for a CoE encompasses a corresponding area of species richness whose extent is influenced by the area size of the delimited CoE has not been validated.

BIOGEOGRAPHIC CONCORDANCE – ZOOGEOGRAPHIC ZONES AND PHYTOGEOGRAPHIC CENTRES

Biogeographic patterns for monkey beetles were compared with two other insect zoogeographic studies (Carcasson 1964, Endrödy-Younga 1978; from here on referenced without dates of publication). Carcasson and Endrödy-Younga both focussed on broad scale zoogeographic patterns, concentrating on faunistic regions across the Ethiopian Region. Zoogeographic regions retrieved by Carcasson were based on close examination of all taxonomic (phylogenetic) levels of the butterfly fauna of Ethiopian Africa, whereas, Endrödy-Younga focussed on higher taxonomic levels (genera and above) of representative beetle families with heavy emphasis on wingless tenebrionid beetles.

Monkey beetle biogeographic zones were further compared to areas of floristic diversity and Phytogeographic centres (Born et al. 2007, Goldblatt and Manning 2002, Mucina and Rutherford 2006, van Wyk and Smith 2002) to search for congruent patterns of biogeographic regions and centres of biotic diversity and evolution, with particular emphasis on the winter rainfall regions. As for earlier zoogeographic studies, above referenced phytogeographic studies were mostly compiled intuitively based on species distribution patterns and expert opinion. An exception is Born et al.'s (2007) study, which utilised hierarchical clustering techniques within a statistical framework to identify centres of endemism and their groupings.

To highlight congruent patterns maps from three of the above mentioned studies (Carcasson 1964, Endrödy-Younga 1978, and Born et al. 2007; the latter also incorporates Goldblatt and Manning's (2002) phytogeographic centres) were digitised within GIS (ArcMap 9.2 (ESRI 2006)) and spatially joined to mapped monkey beetle CoEs. From this, calculations of spatial congruence (percentage geographic

overlap) were calculated within GIS and the results tabulated. Calculating geographic areas of congruence between taxonomic groups would highlight areas of conservation importance, both in their concentrations of endemic species, but further in their possible sharing of ecological and evolutionary (historical) processes.

GENERIC DIVERSIFICATIONS

Firstly, focusing only on those CoEs with ≥ 10 endemic species, genus diversifications were measured as the percentage occurrence of species from respective genera within each CoE. Only genera with ≥ 3 species were used. For the purposes of this analysis, and in the absence of a phylogeny for the South African Hopliini, it was assumed that all taxonomically defined genera are monophyletic – an assumption that is probably not true for all genera (Dombrow pers. comm.). Such a measure should indicate which genera are centered within specific CoEs and the extent of their diversifications across CoEs. CoEs are most likely reflective of areas of centres of diversification (see above) and thus should indicate geographic areas of evolution more accurately. Secondly, focussing on the endemic component within CoEs, the percentage contribution of endemic species was calculated. High percentage contributions of endemic species within CoEs by specific genera should provide further insights into the faunistic uniqueness of CoEs and their endemic character (neo- and paleoendemics).

RESULTS

CENTRES OF ENDEMISM (COE)

Eighteen CoE with $n \geq 2$ endemic species were identified (Table 1). Four multiple QDS CoEs were noted which contained only single endemic taxa. Eighteen QDS that contained single taxa that were endemic to their respective QDS, were mostly seen scattered within areas showing low monkey beetle diversity, and/or areas of under-collecting, e.g. the Nama-Karoo Biome.

Table 1. Spatial and taxonomic properties of delimited CoEs for South African monkey beetles (vegetation unit endemics defined as CoE endemic taxa confined to a single vegetation type; CoEs shaded in grey consist of a single endemic taxon; Outside refers to QDS that were not assigned to a CoE. (Veg = vegetation).

Label	Centres	Area (Km ²)	CoE Taxon diversity (area adjusted) [generic]	CoE Taxa > 50% ^A (%) [genera (%)]	CoE Endemic taxa (%) [genera (%)]	Veg unit endemics (%)	Veg types with ≥ 1 veg unit endemic (%) [no. of veg units]	Σr ^A	con ^B	CON ^B
1	Southern Namaqualand	20253.3	299(50.2) [43]	186(62.2) [11(25.6)]	145(48.5) [6(14)]	67.59	62.16 [37]	224	0.05	0.04
2	South Western Cape	18462.7	261(44.5) [45]	170(65.1) [13(28.9)]	117(44.8) [8(17.8)]	62.39	46.55 [58]	218	0.05	0.05
3	Central Namaqualand	10672.0	140(26.4) [29]	87(62.1) [5(17.2)]	60(42.9) [3(10.3)]	75.00	31.82 [22]	83	0.09	0.07
4	Karoo Mountain	13547.6	151(27.2) [32]	72(47.7) [5(15.6)]	54(35.8) [4(12.5)]	74.07	30.43 [46]	77	0.07	0.05
5	Albany Centre	7131.1	87(17.6) [22]	40(46) [1(4.5)]	28(32.1) [0]	50.00	27.59 [29]	56	0.14	0.11
6	Southern Coastal	7443.71	79(15.9) [20]	27(34.2) [0]	22(27.8) [0]	86.36	26.67 [30]	26	0.09	0.05
7	Central Natal	5866.3	54(11.3) [13]	28(51.9) [2(15.4)]	21(38.9) [0]	80.95	14.29 [14]	31	0.15	0.11
8	West Coast	4918.9	57(12.3) [19]	19(33.3) [3(15.8)]	14[24.6] [2(10.5)]	71.43	41.18 [17]	21	0.17	0.10
9	Drakensberg	11432.4	25(4.7) [7]	13(52) [0]	13(52) [0]	53.85	13.33 [15]	23	0.10	0.03
10	North Eastern Escarpment	8363.1	28(5.5) [14]	12(42.9) [4]	12(42.9) [2(14.3)]	66.67	16.00 [25]	22	0.15	0.08
11	Gariep	6391.2	47(9.7) [17]	14(30) [1(5.8)]	11(23.4) [1(5.9)]	36.36	17.39 [23]	25	0.23	0.15
12	Namaqualand Uplands	2691.8	37(8.9) [14]	12(32.4) [0]	11(29.7) [0]	81.82	40.00 [10]	13	0.30	0.23
13	Central & North Natal	3388.2	13(3.0) [6]	4(30.8) [0]	4(30.8) [0]	25.00	8.33 [12]	7	0.35	0.13
14	Dundee	680.5	5(1.5) [2]	3(60) [0]	3(60) [0]	66.67	25.00 [4]	3	1.00	1.00
15	Pella	674.2	2(0.6) [1]	2(100) [0]	2(100) [0]	100.0	33.3 [3]	2	1.00	1.00
16	Kimberley	677.4	3(0.9) [3]	2 (66.7) [0]	2(66.7) [0]	100.0	100.0 [1]	2	1.00	1.00
17	Carnarvon-Victoria West	1321.9	5(1.4) [4]	2(40) [0]	2(40) [0]	50.0	20.0 [5]	3	0.75	0.50
18	Dikboome	648.7	7(2.2) [6]	2(28.6) [0]	2(28.6) [0]	100.0	100.0 [1]	2	1.00	1.00
19	Wolkberg	705.0	3(0.9) [3]	1(33.3) [1]	1(33.3) [1(33)]	100.0	33.3 [3]	1	1.00	-
19	Fraserburg-Murraysburg	1311.5	2(0.5) [2]	1(50) [0]	1(50) [0]	0	0 [4]	2	-	-
20	Nama Karoo	2743.0	2(0.5) [2]	1(50) [0]	1(50) [0]	0	0 [6]	4	-	-
21	Graskop	1397.8	3(0.8) [3]	1(33) [0]	1(33.3) [0]	100.0	16.7 [6]	2	-	-
22	Outside	308 QDS	178 [38]	45 [3]	22 [0]			26	0.00	-0.04

^ANumber of taxa with at least half of their range found in a respective CoE (Bradshaw and Linder 2009). ^BOptimality criteria used as defined in Linder (2001).

Based on species compositional similarities, delimited CoEs were clustered for all weighting techniques primary into two distinct groups - a winter and all-year-round rainfall group; and a summer-rainfall group (Figs. 1a-d). Several of the species poor CoEs with ≤ 3 endemic taxa, e.g. CoEs Fraserburg/Murraysburg, Nama-Karoo, and Kimberley, showed weak species similarities to other CoEs, and zoogeographic affiliations were difficult to assign.

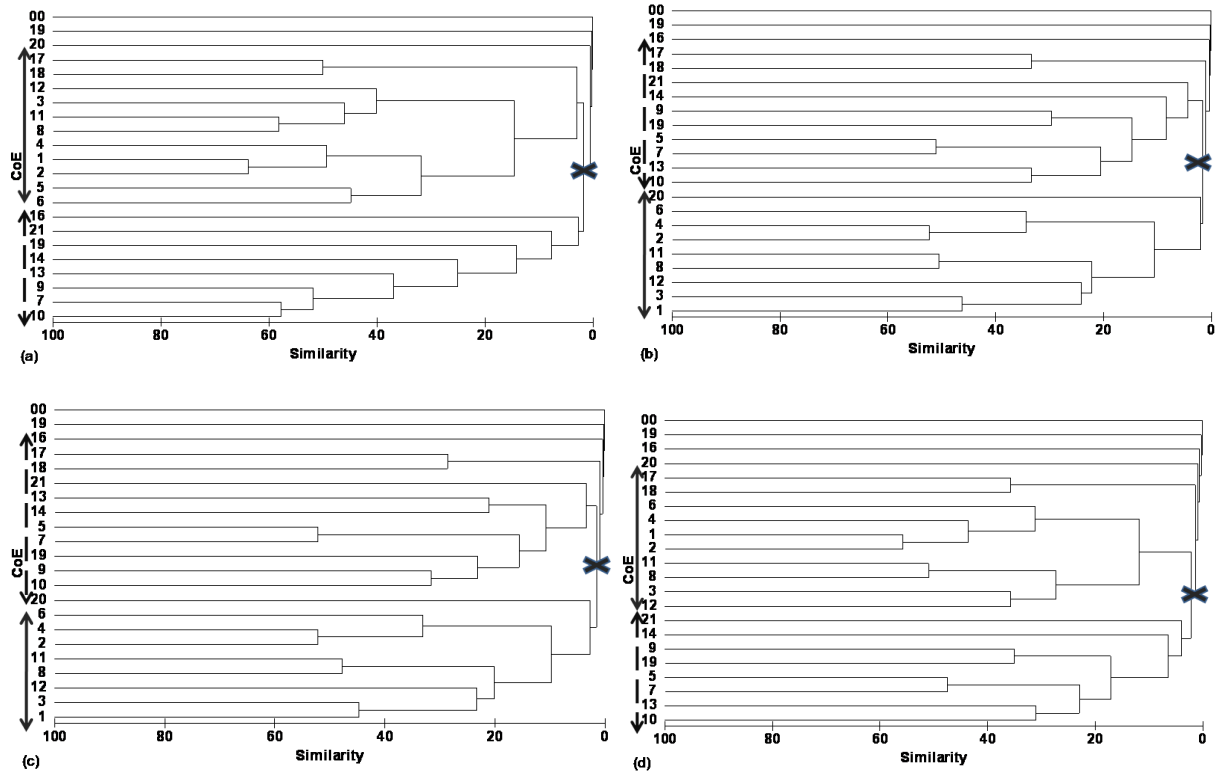


Figure 1. Clustering of monkey beetle CoEs for species data weighted using (a) Unweighted, (b) Inverse, (c) Bell-shaped, and (d) Integrated Weighting techniques. Species compositional similarities between CoEs were calculated using the Bray-Curtis similarity coefficient. (CoE number labels match those of Table 1; 00 on dendrogram is the Wagner rooting (Rohlf 1984)). Two broad groupings of CoEs are seen for each weighting technique (primary break indicated by black cross) - a winter and all year rainfall (solid arrow on y-axis), and a summer-rainfall grouping (dashed arrow on y-axis).

WINTER AND ALL-YEAR-ROUND RAINFALL AREA

Within the species rich winter and all-year-round rainfall zone of monkey beetle distributions two fairly distinct subgroups of CoEs were retrieved for most of the weighting techniques (see Fig. 1). Firstly, a Cape CoE centered within Carcasson’s and Endrödy-Younga’s faunal Cape Zone (Figs. 2 & 3; Table 2 & 3), and Goldblatt and Manning’s Cape Floristic Region (CFR) was retrieved (Table 4). Secondly, a well-defined zone was retrieved within Namaqualand (*sensu* Cowling et al. 1999), centered within Carcasson’s and Endrödy-Younga’s arid Namib and Southwestern Zone, respectively. Strong congruence for this zone was also seen with Born et al.’s (2007) Namaqualand and Namib Desert Regions (Table 4).

Cape Zone

The two best developed CoEs, Southern Namaqualand and South Western (SW) Cape, in terms of levels of endemism (quarter of endemic South African species), diversity, and area were seen within the Cape

Zone. The Southern Namaqualand CoE has the largest taxonomic diversity, highest level of endemism, and is the largest sized CoE. The Integrated and Unweighted Weighting technique linked this CoE to CoEs within the Cape Zone (Figs. 1a & 1d, respectively), whereas, the Inverse Weighting and Bell techniques linked it to the Namaqualand CoEs (Figs. 1b & 1c, respectively). Species and genera typical of Namaqualand were seen to occur within this CoE, especially within its northern areas. The inclusion of the Southern Namaqualand CoE into the Cape Zone was supported by the north-western extent of Endrödy-Younga's Cape Zone capturing the entire extent of this CoE. Furthermore, this CoE showed strong congruence with the northern section of Goldblatt and Manning's Northwestern phytogeographic centre (NWPP – Table 4.). Some biogeographic congruence was also seen for this CoE with Born et al.'s (2007) Hantam-Tanqua-Roggeveld Region. Although the Southern Namaqualand CoE was not retrieved as a defined western extension of the Karoo, as seen in Caracasson's butterfly zoogeographic zones, it did however, show north-eastern extensions into his Karoo Zone.

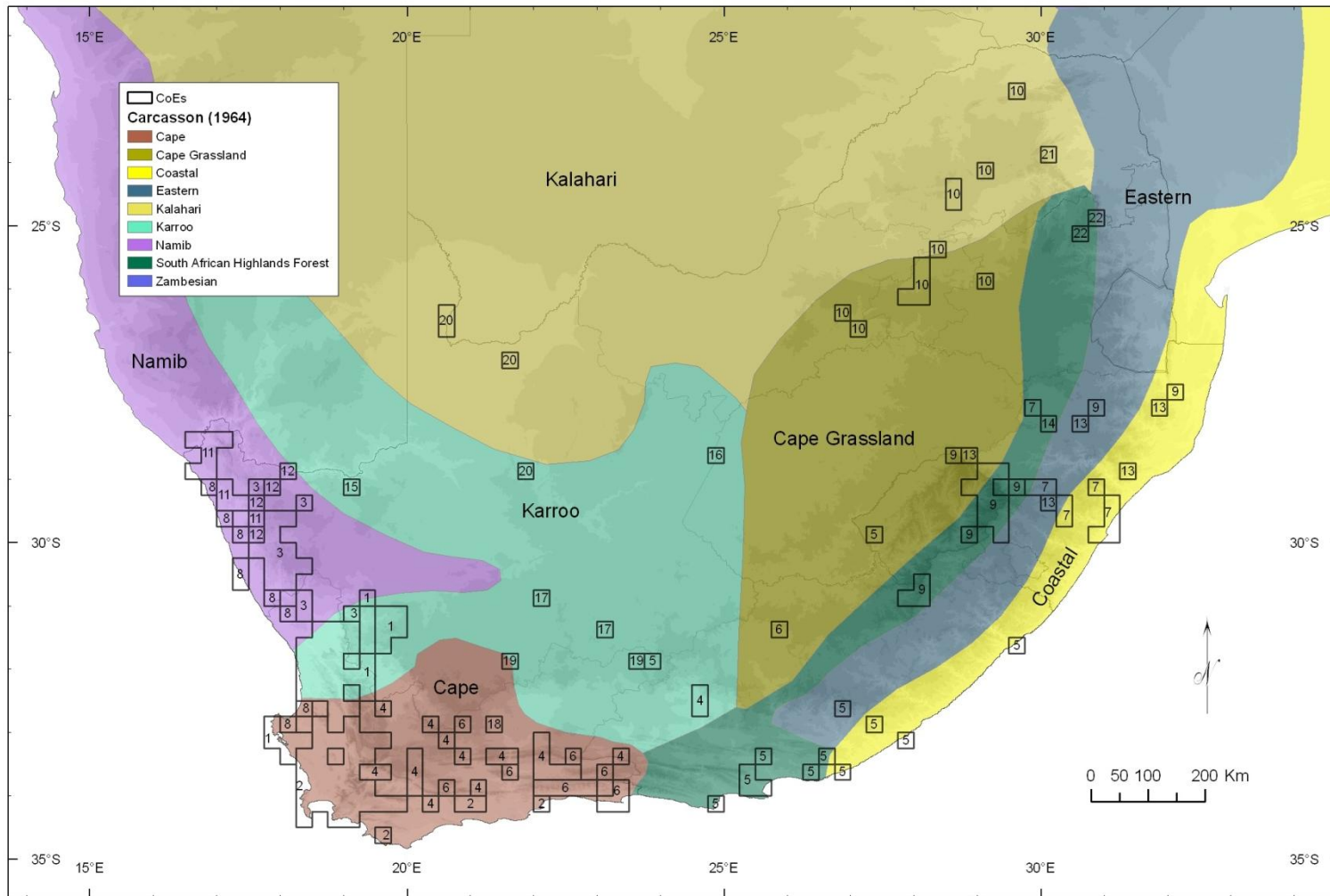


Figure 2. Delimited CoEs for South African monkey beetles overlaid onto Carcasson's (1964) zoogeographic zones for the butterfly fauna of Ethiopian Africa (see also Table 2). CoE 19 – 21 only contain a single endemic taxon and are shown here highlighting areas requiring further investigation.

Table 2. Percentage (%) spatial congruence between monkey beetle CoEs and Carcasson's (1964) zoogeographic zones for the butterfly fauna of Ethiopian Africa.

	Carcasson's Zoogeographic Zones for butterflies							
	Cape	Cape Grassland	Coastal	Eastern	Kalahari	Karoo	Namib	South African Highlands Forest
Monkey beetle CoEs:								
Albany Centre	-	9.4	20.2	9.38	-	9.2	-	51.85
Carnarvon/Victoria West	-	-	-	-	-	100.0	-	-
Central & North Natal	-	20.0	40.07	39.93	-	-	-	-
Central Namaqualand	-	-	-	-	-	5.92	94.08	-
Central Natal	-	-	58.8	24.13	-	-	-	17.07
Dikboome	100	-	-	-	-	-	-	-
Drakensberg	-	20.27	5.98	10.67	-	-	-	63.08
Dundee	-	-	-	2.03	-	-	-	97.97
Fraserburg/Murraysburg	25.17	-	-	-	-	74.84	-	-
Gariep Centre	-	-	-	-	-	-	100.0	-
Graskop	-	-	-	24.01	-	-	-	76.0
Kimberley	-	-	-	-	-	100.0	-	-
Karoo Mountain	90.38	-	-	-	-	9.62	-	-
Nama Karoo	-	-	-	-	75.36	24.64	-	-
Northern Escarpment	-	59.88	-	-	40.12	-	-	-
Southern Namaqualand	20.41	-	-	-	-	75.87	3.72	-
Pella	-	-	-	-	-	100.0	-	-
Southern Coastal	91.14	8.86	-	-	-	-	-	-
Namaqualand Uplands	-	-	-	-	-	2.89	97.12	-
SW Cape	100.0	-	-	-	-	-	-	-
West Coast	23.89	-	-	-	-	-	76.11	-
Wolkberg	-	-	-	-	100	-	-	-

The slightly smaller sized SW Cape CoE showed similar high values of taxonomic diversity and levels of endemism to that of the Southern Namaqualand CoE. This CoE was centered on the south-western Cape, which is the core region of the Cape Faunal Zone, and showed high congruence with Goldblatt and Manning's Southwestern phytogeographic centre, although, in addition, incorporating some areas of their Agulhas Plain and Langeberg centres, with several south-eastern extensions for this monkey beetle CoE retrieved as far east as Mossel Bay.

The Karoo Mountain and Southern Coastal CoEs were further seen to be part of the Cape Zone and were retrieved, incorporating QDS from the south-western, southern, and Eastern Cape. All weighting techniques linked the Karoo Mountain CoE within the Cape Zone. Although falling within the Cape Zone for three of the weighting techniques, the Southern Coastal CoE showed less clear affiliations for the unweighted technique, being linked with the eastern Albany Centre CoE. Both of these centres fell within Carcasson's and Endrödy-Younga's Cape Zones. However, the Karoo Mountain CoE did show two disjunct QDS retrieved from Carcasson's Karoo Zone and Endrödy-Younga's Central Arid Zone, and for the Southern Coastal CoE, a single disjunct eastern QDS was retrieved from Carcasson's Cape Grassland and Endrödy-Younga's Central Arid Zone.

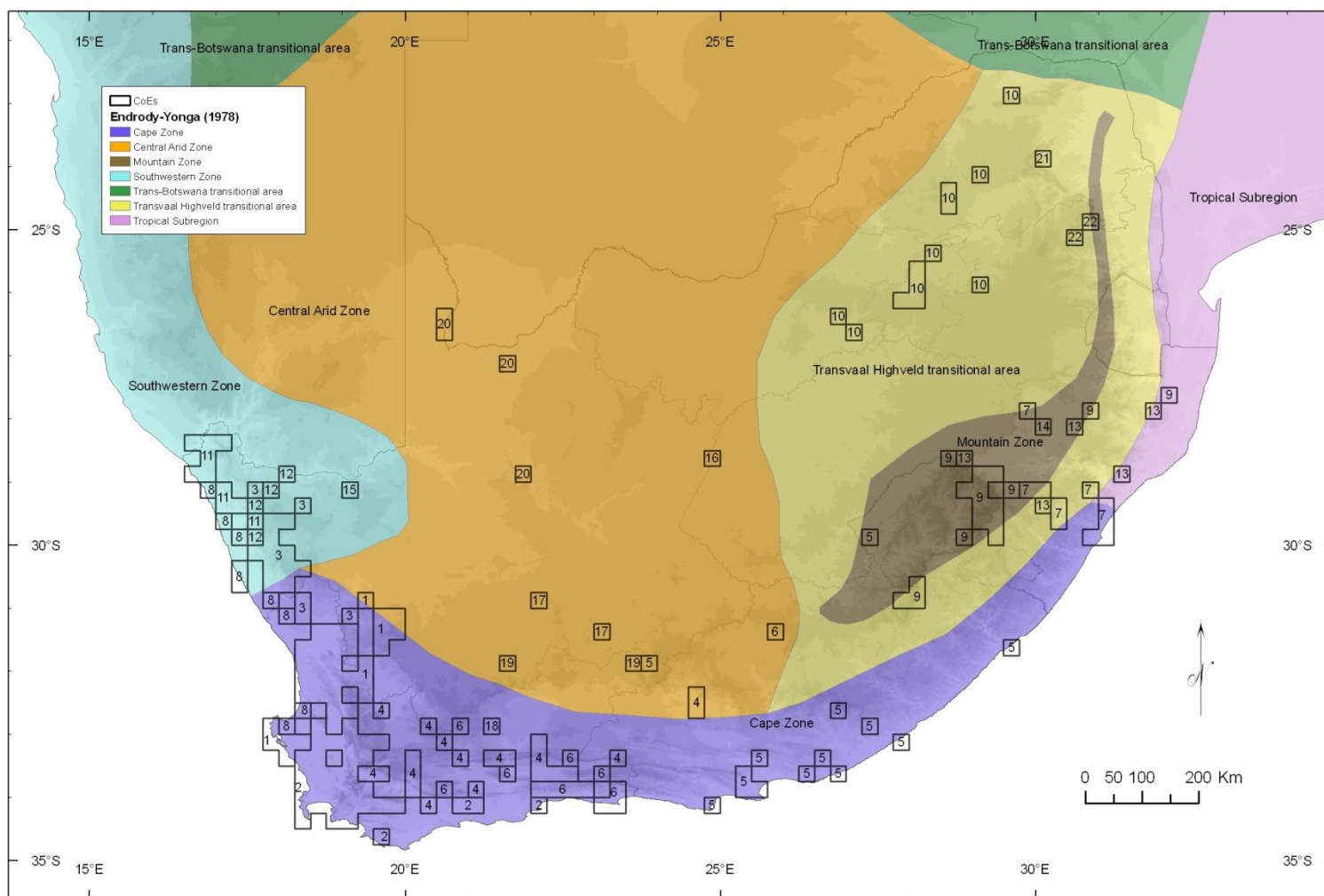


Figure 3. Delimited CoEs for South African monkey beetles overlaid onto Endrödy-Younga's (1978) zoogeographic zones for the Sub-Saharan Africa (see also Table 3). CoEs 19 – 21 only contain a single endemic taxon and are shown here highlighting areas requiring further investigation.

Table 3. Percentage (%) spatial congruence between monkey beetle CoEs and Endrödy-Younga's (1978) zoogeographic zones for the Sub-Saharan Africa.

	Endrödy-Younga's Zoogeographic Zones for beetles					
	Cape	Central Arid	Mountain	Southwestern	Transvaal Highveld Transitional Area	Tropical Subregion
Monkey beetle CoEs:						
Albany Centre	81.42	9.20	9.39	-	-	-
Carnarvon/Victoria West	-	100.0	-	-	-	-
Central & North Natal	-	-	38.33	-	30.86	30.82
Central Namaqualand	30.16	0.99	-	68.85	-	-
Central Natal	27.59	-	22.08	-	44.53	5.81
Dikboome	100.0	-	-	-	-	-
Drakensberg	-	-	71.03	-	22.99	5.98
Dundee	-	-	100.0	-	-	-
Fraserburg/Murraysburg	-	100.0	-	-	-	-
Gariiep Centre	-	-	-	100.0	-	-
Graskop	-	-	24.17	-	75.83	-
Kimberley	-	100.0	-	-	-	-
Karoo Mountain	90.47	9.53	-	-	-	-
Nama Karoo	-	100.0	-	-	-	-
Northern Escarpment	-	-	-	-	100.0	-
Southern Namaqualand	92.04	7.96	-	-	-	-
Pella	-	-	-	100.0	-	-
Southern Coastal	91.14	8.86	-	-	-	-
Namaqualand Uplands	-	-	-	100.0	-	-
SW Cape	100.0	-	-	-	-	-
West Coast	50.80	-	-	49.20	-	-
Wolkberg	-	-	-	-	100.0	-

In terms of congruence with phytogeographic centres, the species rich Karoo Mountain CoE appears to show greatest congruence with Goldblatt and Manning's Karoo Mountain Centre, although QDS retrieved boarded on Born et al.'s (2007) Karoo Region. The Southern Coastal CoE showed a similar range pattern as the Karoo Mountain CoE, although it was centered more on coastal QDS and more congruent with Goldblatt and Manning's Southeastern Centre. Another contrasting feature between these two CoEs was the lack of endemic genera in the Southern Coastal CoE; however, this CoE was seen to house a high diversity of genera with 20 genera found within. Both these CoEs may show greater affinities with eastern zone elements, as suggested by the two eastern outlying QDS delimited. However, increased collecting in these areas is required in order to fully explore their faunal relationship with eastern zone CoEs.

Namaqualand Zone

The Namaqualand Zone consisted of four CoEs (Central Namaqualand, Gariiep Centre, West Coast, and Namaqualand Uplands) and fell strongly within Carcasson's Namib Zone and Endrödy-Younga's Southwestern Zone (Table 2 & 3). The Central Namaqualand CoE – the largest retrieved CoE in the Namaqualand Zone – showed a comparable level of endemism with the above two large Cape Zone CoEs. However, the Central Namaqualand CoE was notably less species rich, with approximately 50% less species recorded (area corrected values showed a similar pattern – Table 1). Good biogeographic congruence was seen with Born et al.'s (2007) Namaqualand Region (c. 80% spatial overlap).

Table 4. Percentage (%) spatial congruence between monkey beetle CoEs and Born et al.'s (2007) phytogeographic regions for the Greater Cape Floristic Region. Columns shaded in grey represent Goldblatt and Manning's (2002) original phytogeographic centres for the Cape Floristic Region. [PP=Phytogeographic Province; AP=Agulhas Plain; HTR=Hantam-Tanqua-Roggeveld; KM=Karoo Mountains; LB=Langeberg; Nam=Namaqualand; NW=North West, SE=South East; SW=South West].

	Born et al.'s (2007) phytogeographic centres for the Greater Cape Floristic Region									
	APPP	HTR	Karoo	KMPP	LBPP	Nam	Namib Desert	NWPP	SEPP	SWPP
Monkey beetle CoEs:										
Albany Centre	-	-	20.4	-	-	-	-	-	79.6	-
Central Namaqualand	-	-	-	-	-	81.2	12.6	6.2	-	-
Dikboome	-	-	-	100.0	-	-	-	-	-	-
Fraserburg/Murraysburg	-	-	100.0	-	-	-	-	-	-	-
Gariiep Centre	-	-	-	-	-	90.0	10.0	-	-	-
Karoo Mountain	-	-	9.6	57.1	9.5	-	-	14.3	4.8	-
Southern Namaqualand	-	17.8	-	-	-	5.9	-	61.8	-	14.5
Pella	-	-	-	-	-	-	100.0	-	-	-
Southern Coastal	-	-	-	41.8	-	-	-	-	58.2	-
Namaqualand Uplands	-	-	-	-	-	49.8	50.2	-	-	-
SW Cape	2.9	-	-	-	5.9	-	-	23.7	-	64.6
West Coast	-	-	-	-	-	78.2	-	10.9	-	10.9

A less diverse West Coast CoE was seen centered along the west coast, capturing a number of coastal QDS from Port Nolloth in the north to Saldanha Bay in the south. However, a disjunction between southern Namaqualand and northern CFR coastal regions was seen (Fig. 2). This disjunction was congruent with the western extension seen for Karoo butterfly elements, which divides Carcasson's Cape Zone from his Namib Zone. Further congruence was seen between the West Coast CoE and with Born et al.'s (2007) coastal Namaqualand Region (c. 78% spatial overlap).

The northern Namaqualand Gariiep CoE fell strongly within Born et al.'s (2007) Namaqualand Region (90%). In contrast, the central Namaqualand Upland CoE was equally divided between Born et al.'s (2007) Namaqualand and Namib Desert Regions. Just west of these northern Namaqualand CoEs, a small (single QDS) Pella CoE was delimited, containing two endemic species from a single genus. This CoE is centered on the old Pella Mission Station and possibly reflects a sampling artefact.

SUMMER RAINFALL AREA

Tropical Subregion

Within the less species diverse eastern zone of monkey beetle distributions, a number of smaller sized CoEs were seen, mostly made up of non-contiguous QDS (Fig. 2). CoEs were mostly clustered by the various weighting techniques into sub-tropical and tropical coastal centres; eastern highland (mountain) centres; and northern grassland and savanna centres (see Fig. 1a-d). Mixed levels of congruence were seen between these broad eastern CoE zones and Carcasson's and Endrödy-Younga's zoogeographic zones

(Table 2 & 3). Eastern monkey beetle CoEs mostly showed extensions across several zoogeographic zones defined by these biogeographers. Endrödy-Younga's extensive north-eastern, mostly coastal Cape Zone, was not retrieved for monkey beetle CoEs, with greater species similarities seen rather with southern extensions of eastern faunal elements, as retrieved for Carcasson's butterflies. Quite strong congruence was seen with the retrieval of CoEs delimited from eastern mountainous areas and with those of Carcasson's South African Highlands Forest Zone, and Endrödy-Younga's Mountain Zone. Northern savanna and grassland CoEs showed better congruence with Endrödy-Younga's Transvaal Highveld Transitional Zone than with Carcasson's Cape Grassland Zone.

The Albany Centre CoE was the most speciose CoE within this eastern zone (87 species, 22 genera), and showed reasonably high levels of endemism (32.1%). This CoE was mostly centered on coastal QDS of the Albany Thicket Biome. The Bell, Inverse, and Integrated Weighting techniques linked the Albany Centre CoE with the Central Natal CoE (Fig. 1b-d). However, some shared species were also seen with Cape Zone CoEs, as seen with the Unweighted Weighting technique linking this CoE with the Southern Centre CoE (Fig. 1a). The Albany Centre CoE fell strongly within Endrödy-Younga's Cape Zone (c. 80% spatial overlap); whereas, congruence with Carcasson's eastern zones were less clear with spatial overlap recorded across several of his eastern zones; however, greatest overlap was seen with his South African Highlands Forest Zone (Fig. 2). In terms of phylogeographic patterns of congruence for this CoE; biogeographic congruence was seen with van Wyk and Smith's (2001) Albany phylogeographic centre.

The next most diverse eastern zone CoE retrieved was the Central Natal CoE. Strong species similarities were seen with the Albany Centre CoE, with three of the weighting techniques linking these two CoEs (see above). The Eastern and Coastal Zones of Carcasson showed the best congruence with this CoE (Table 2). The Central Natal CoE was more-or-less equally spread across three of Endrödy-Younga's zones – Eastern Mountain Zone (c. 38%), Transvaal Highveld Transitional Area (c. 30%), and Tropical Subregion (c. 30%). Biogeographic congruence with phylogeographic centres was seen with the Maputaland-Pondoland phylogeographic centres of van Wyk and Smith (2001).

Mountain Relics and Transitional Faunal Areas

The strongly endemic montane Drakensberg CoE (52% endemism) was centered on the Drakensberg Mountains and showed species similarities with other eastern mountain regions (e.g. Wolkberg Mountain – Fig. 1b). A congruent zoogeographic pattern was seen with Endrödy-Younga's Mountain Zone (c. 70%), and to a lesser extent, with Carcasson's South African Highlands Forest (c. 63%). Biogeographic congruence was seen with van Wyk and Smith's (2001) Drakensberg Alpine phylogeographic centre.

In the northern reaches of the Savanna and Grassland Biomes, a Northern Escarpment CoE was retrieved, and which consisted of a fairly large sized, discontinuous CoE (Table 1). The Northern Escarpment CoE showed 100% congruence with Endrödy-Younga's Transvaal Highveld Transitional Zone and approximately 60% spatial overlap with Carcasson's Cape Grassland Zone. Other, weakly retrieved CoEs were delimited from northern areas of high altitude grassland habitats. These CoEs fell within Endrödy-Younga's Mountain Zone and Transvaal Highveld Transitional Zone; and within Carcasson's Kalahari and South Africa's Highland Forest. Congruence between these weakly delimited CoEs was seen with van Wyk and Smith's (2001) Wolkberg and Soutpansberg phytogeographic centres.

Central Arid Zone

Four CoEs were weakly retrieved within the arid central regions of South Africa with two of these consisting of single endemic species (Table 1). These CoEs were seen overlapping with Endrödy-Younga's Central Arid Zone and Carcasson's Karoo Zone. The four, small sized CoEs retrieved each showed very low species similarities with other CoEs (Fig. 1a-d). A Kimberley CoE with three species (2 endemic) and three genera was retrieved from a single QDS centered on the town of Kimberley. Biogeographic congruence with this centre was seen with van Wyk and Smith's (2001) Griqualand West phytogeographic centre. Furthermore, a CoE was retrieved from two discontinuous QDS from the Carnarvon/Victoria West areas of the arid Nama-Karoo Biome and a CoE with a single endemic taxon was retrieved from three QDS from the north-western regions of the Nama-Karoo Biome. Possible other CoEs within the arid regions were centered on the Fraserberg/Murraysburg regions of the Nama-Karoo Biome (Fig. 2).

GENUS DIVERSIFICATIONS

Percentage occurrence of species for different genera within CoEs revealed genus diversification patterns within a zoogeographic context. Species occurrences for various genera linked CoEs through one of several different patterns (Table 5). The eastern zone CoEs were linked through the genera *Eriesthis*, *Monochelus*, and *Lepitrichula*, which showed occurrence patterns predominantly within and across these eastern CoEs. In addition to this, the former two genera showed occurrences of species within the south-western and Little Karoo CoEs, although of weaker extent. Of these two genera, *Monochelus* showed the more extensive occurrence patterns within western zone CoEs, with species seen occurring as far north as Namaqualand. Further genus occurrence patterns linking eastern zone CoEs with south-western CoEs seen in the Cape montane genus *Anisonyx*, with species occurring on the Drakensberg Mountains and within the Albany Centre CoE. Thus genera centered with the eastern zone showed occurrences within

western zone CoEs, and conversely, genera centered within western zone CoEs showed some occurrences within eastern zone CoEs, e.g. see occurrence patterns of *Heterochelus*.

Table 5. Percentage (%) of species of a genus species found within CoEs with ≥ 10 endemic species. Percentage (%) contribution calculated as the number of species found within a CoE of that genus divided by the total number of species known for that genus. (CoE code: AB= Albany Thicket; CNam= Central Namaqualand; CN= Central Natal; Drk= Drakensberg; GC=Gariep Centre; KM=Karoo Mountains; NE= Northern Escarpment; SN= Southern Namaqualand; SC=Southern Coastal; NU= Namaqualand Uplands; SWC= SW Cape; WC=West Coast).

CoE	AB	CNam	CN	DrK	GC	KM	NE	SN	SC	NU	SWC	WC
Genus:												
<i>Amblymelanoplia</i>	-	-	-	-	-	60.0	-	60.0	20.0	-	60.0	-
<i>Anisocheilus</i>	-	100.0	-	-	33.3	-	-	100.0	-	33.3	66.7	66.7
<i>Anisonyx</i>	7.1	3.6	-	14.3	-	32.1	-	14.3	10.7	-	64.3	-
<i>Chasme</i>	33.3	33.3	-	-	66.7	-	-	66.7	-	-	66.7	66.7
<i>Clania</i>	-	33.3	-	-	16.7	-	-	66.7	-	-	16.7	-
<i>Denticnema</i>	28.6	42.9	-	-	57.1	42.9	-	100.0	-	28.6	28.6	42.9
<i>Diaplocheilus</i>	-	-	-	-	-	20.0	-	60.0	40.0	-	100.0	-
<i>Dicheilus</i>	5.9	5.9	-	-	-	17.6	-	20.6	14.7	-	64.7	-
<i>Dicranocnemus</i>	56.3	-	6.3	-	-	12.5	-	25.0	31.3	-	50.0	-
<i>Dolichiomicroscelis</i>	-	-	-	-	-	-	-	100.0	-	-	66.7	-
<i>Eriesthis</i>	26.3	-	52.6	47.4	-	15.8	42.1	-	-	-	5.3	-
<i>Goniaspidius</i>	-	50.0	-	-	-	33.3	-	16.7	-	-	-	-
<i>Gymnoloma</i>	33.3	22.2	-	-	11.1	44.4	-	55.6	33.3	-	-	11.1
<i>Heterochelus</i>	11.8	13.8	6.7	2.1	1.0	17.9	1.5	34.9	9.2	3.1	30.3	2.1
<i>Hoplia</i>	-	-	20.0	-	-	20.0	-	-	20.0	-	20.0	-
<i>Hoplocnemis</i>	23.5	11.8	-	-	-	47.1	-	41.2	29.4	5.9	35.3	5.9
<i>Ischnochelus</i>	-	26.3	-	-	5.3	42.1	-	42.1	15.8	21.1	5.3	5.3
<i>Khoina</i>	50.0	-	-	-	-	75.0	-	50.0	50.0	-	75.0	25.0
<i>Knysna</i>	-	-	-	-	-	33.3	-	33.3	-	-	100.0	-
<i>Kubousa</i>	-	46.7	-	-	-	6.7	-	26.7	-	-	40.0	13.3
<i>Lepisia</i>	-	55.6	-	-	11.1	-	-	66.7	-	11.1	11.1	22.2
<i>Lepithrix</i>	8.1	37.8	-	-	13.5	13.5	-	81.1	8.1	2.7	29.7	24.3
<i>Lepitrichula</i>	20.0	-	40.0	40.0	-	-	20.0	-	-	-	-	-
<i>Leptocnemis</i>	-	-	-	-	-	12.5	-	87.5	25.0	-	37.5	-
<i>Mauromecistoplia</i>	-	33.3	-	-	33.3	-	-	33.3	-	-	33.3	-
<i>Monochelus</i>	23.3	13.3	50.0	13.3	-	6.7	20.0	6.7	6.7	3.3	10.0	-
<i>Omocrates</i>	10.0	6.7	3.3	-	3.3	16.7	-	20.0	6.7	3.3	30.0	-
<i>Pachycnema</i>	8.3	47.2	-	-	33.3	27.8	-	69.4	11.1	11.1	41.7	27.8
<i>Peritrichia</i>	6.8	12.2	-	-	9.5	27.0	-	52.7	14.9	12.2	51.4	5.4
<i>Platychelus</i>	9.1	25.8	-	1.5	1.5	12.1	-	28.8	7.6	3.0	24.2	12.1
<i>Rectoscutaria</i>	-	-	-	-	-	33.3	-	66.7	33.3	-	-	-
<i>Scelophysa</i>	-	40.0	-	-	40.0	20.0	-	80.0	-	30.0	10.0	30.0
Average	11.3	20.7	5.8	3.7	10.5	21.6	2.7	47.2	12.1	5.3	36.7	11.3
(\pm sd.)	(15.4)	(23.5)	(14.3)	(11.1)	(17.9)	(18.9)	(8.7)	(30.0)	(14.0)	(9.6)	(28.5)	(18.5)

(See Table 1 for total number of genera found in each CoE.)

Within the western zone CoEs genera showed their highest species representation within the Southern Namaqualand and SW Cape CoEs. Many genera were shared between these two CoEs, however, the former CoE showed the highest percent occurrences for the greatest number of genera, with at least 16 genera showing greater than 50% of their species occurring within this CoE. Genera centered within the Southern Namaqualand CoE either showed their next highest, or equal occurrence endemism patterns northwards within the more arid Namaqualand CoEs and West Coast CoE, or rather southwards within the Karoo Mountain CoE and/or SW Cape CoE. Some of these genera (e.g. *Denticnema*, *Gymnoloma*, and

Pachycnema) were also seen to occur south-eastwards into the Albany Thicket CoE. Genera centered within the SW Cape CoE showed their next highest or equal occurrence endemism patterns predominantly within the Southern Namaqualand CoE; or for the genus *Anisonyx*, in the Karoo Mountain CoE. Genera centered within the SW Cape CoE further showed species occurrences northwards into Namaqualand CoEs, and eastwards into the Karoo Mountain, Southern Coastal CoE (e.g. *Diaplochelus*), and Albany Centre CoE (e.g. *Dichelus*).

Within the Namaqualand CoEs, the genera *Goniaspidius* and *Kubousa* showed their highest occurrences of species within the Central Namaqualand CoE. The former genus showed its next highest occurrence patterns within the Karoo Mountain CoE, whereas the latter genus's next highest occurrence patterns were seen within the Southern Namaqualand CoE. No genera showed their highest occurrence of species within the Gariiep Centre and Namaqualand Upland CoE.

The arid-adapted genus *Hoplocnemis* showed its highest species occurrences with the Karoo Mountain CoE. Highest percentage occurrences were also seen for *Ischnochelus* (42%) and *Khoina* (75%); the former showing the same species occurrences within the Southern Namaqualand, while the latter showed equal species occurrences within the SW Cape CoE. The Southern Coastal CoE showed no genera with their highest occurrence of species within this CoE. The Albany Centre CoE had the highest percentage (56%) occurrences for the morphologically unusual genus *Dicranocnemus*, which also showed a high percentage (50%) of its species within the SW Cape CoE. The genus *Monocheilus* - most of its species occurring within the Central Natal CoE, was next well represented (23.3%) within the Albany Centre CoE.

Specific genera characterized the endemic component within those CoEs with ≥ 10 endemic species (Table 6). The most speciose genus *Heterochelus* contributed the most endemic species within almost all of these CoEs. For the Albany Centre, Central Namaqualand, Karoo Mountain, Southern Namaqualand, Southern Coastal, SW Cape, and Central Natal CoEs, this genus accounted for over a quarter of endemic species found within these CoEs. The remaining CoEs showed different genera dominating the endemic component of their respective CoEs. The genera *Peritrichia* and *Pachycnema* recorded high percentages of endemic species (27.3% and 36.4%, respectively) within the Gariiep Centre CoE. The Namaqualand Upland CoE also showed a strong endemic component of *Peritrichia* species (54.4%). The West Coast CoE showed high proportions of *Platycheilus* (42.9%) and *Lepithrix* (21.4%) endemic species. Within the Eastern Zone, the Drakensberg CoE showed high percentage (30.8%) of *Anisonyx* endemic species, while the Northern Escarpment CoE showed equal contributions (16.7%) of endemic species from the genera *Heterochelus* and *Eriesthis*. Other genera showing high contributions of endemic species within CoEs

were seen for *Dichelus* (SW Cape – 13.7%), *Hoplocnemis* (Southern Coastal – 13.6%), *Ischnochelus* (Namaqualand Upland – 18.2%; Karoo Mountain – 9.3%), *Monochelus* (Central Natal – 19.0%), and *Dicranocnemus* and *Omoctrates* (Albany Centre – 10.7% each, respectively).

Table 6. Percentage (%) contribution of endemic species from genera associated with CoEs with ≥ 10 endemic species. (CoE code: AB= Albany Thicket; CNam= Central Namaqualand; CN= Central Natal; Drk= Drakensberg; GC=Gariep Centre; KM=Karoo Mountains; NE= Northern Escarpment; SN= Southern Namaqualand; SC=Southern Coastal; NU= Namaqualand Uplands; SWC= SW Cape; WC=West Coast).

CoE	AB	CNam	CN	Drk	GC	KM	NE	SN	SC	NU	SWC	WC
Genus:												
<i>Anisonyx</i>	3.6	1.7	-	30.8	-	3.7	-	-	9.1	-	6.8	-
<i>Chasme</i>	-	-	-	-	9.1	-	-	-	-	-	-	-
<i>Clania</i>	-	1.7	-	-	-	-	-	2.1	-	-	-	-
<i>Denticnema</i>	-	-	-	-	-	-	-	1.4	-	-	-	-
<i>Diaplochelus</i>	-	-	-	-	-	1.9	-	0.7	-	-	3.4	-
<i>Dichelus</i>	-	1.7	4.8	-	-	7.4	-	2.1	4.5	-	13.7	-
<i>Dicranocnemus</i>	10.7	-	-	-	-	1.9	-	1.4	4.5	-	1.7	-
<i>Dolichiomicroscelis</i>	-	-	-	-	-	-	-	2.1	-	-	0.9	-
<i>Eriesthis</i>	-	-	4.8	23.1	-	-	16.7	-	-	-	-	-
<i>Goniaspidius</i>	-	5.0	-	-	-	3.7	-	0.7	-	-	-	-
<i>Gymnoloma</i>	3.6	-	-	-	-	1.9	-	2.1	4.5	-	-	-
<i>Heterochelus</i>	35.7	26.7	28.6	23.1	9.1	29.6	16.7	33.1	27.3	18.2	28.2	7.1
<i>Hoplocnemis</i>	3.6	-	-	-	-	3.7	-	2.1	13.6	-	0.9	-
<i>Inanda</i>	-	-	9.5	-	-	-	8.3	-	-	-	-	-
<i>Ischnochelus</i>	-	-	-	-	-	9.3	-	3.4	-	18.2	-	-
<i>Khoina</i>	-	-	-	-	-	1.9	-	-	-	-	-	-
<i>Kubousa</i>	-	8.3	-	-	-	1.9	-	0.7	-	-	3.4	-
<i>Lepisia</i>	-	3.3	-	-	-	-	-	2.1	-	-	-	-
<i>Lepithrix</i>	-	8.3	-	-	-	-	-	9.7	-	-	-	21.4
<i>Leptocnemis</i>	-	-	-	-	-	-	-	3.4	4.5	-	0.9	-
<i>Monochelus</i>	7.1	3.3	19.0	-	-	1.9	8.3	0.7	4.5	-	0.9	-
<i>Omoctrates</i>	10.7	3.3	4.8	-	9.1	5.6	-	2.8	4.5	9.1	4.3	-
<i>Pachycnema</i>	-	10.0	-	-	27.3	1.9	-	4.1	-	-	-	-
<i>Peritrichia</i>	3.6	5.0	-	-	36.4	5.6	-	6.9	-	54.5	13.7	7.1
<i>Platychelus</i>	10.7	13.3	-	7.7	-	7.4	-	9.0	18.2	-	8.5	42.9
<i>Scelophysa</i>	-	-	-	-	-	1.9	-	2.1	-	-	0.9	-
Total no. of genera [†]	12	18	9	6	6	22	10	30	11	4	28	7

[†] Includes genera not showed in above table with ≤ 3 endemic taxa

THE RELATIONSHIP BETWEEN SPECIES RICHNESS AND ENDEMISM OF COES

Within CoEs with $n \geq 2$ endemics, non-endemic species richness and number of endemic species were strongly related ($F_{(1,16)} = 123.89$, $r^2 = 0.886$, $P < 0.0001$); with non-endemic species richness explaining nearly 90% of the variance seen in endemism (Fig. 3).

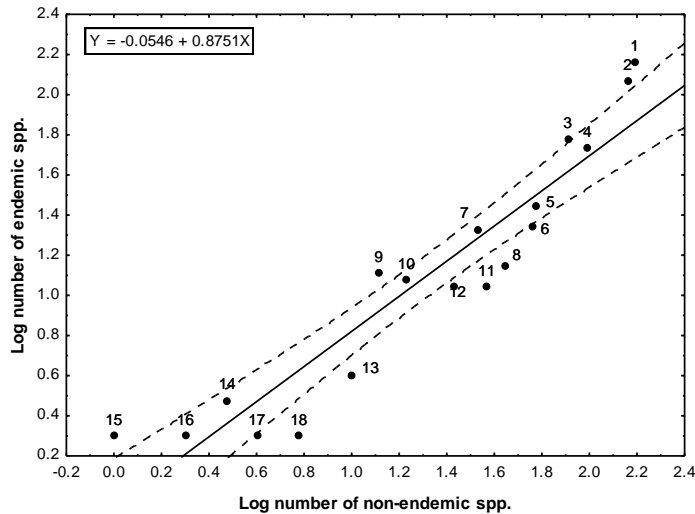


Figure. 3. Relationship between species richness and number of endemic species for CoEs with \geq two endemic species. Dashed lines show 95% confidence intervals. Both variables log transformed to account for non-normality (see Table 1 for CoE names matching to label numbers on above graph).

DISCUSSION

Modern clustering techniques showed several species- and endemic-rich centres of endemism concentrated within the winter rainfall biomes (Fynbos and Succulent Karoo). In contrast, smaller, less well-defined, and less species and endemic rich CoEs were delimited within the summer-rainfall biomes. Much of the discussion that follows places these patterns in biogeographic and historical context; using the two proposed zoogeographical studies (Carcasson 1964, Endrödy-Younga 1978) and several other insect and invertebrate studies which have highlighted areas of zoogeographical interest. Monkey beetle CoEs could be most closely aligned to patterns of “biogeographic zonation” as forwarded by Endrödy-Younga (1978).

MONKEY BEETLE ZOOGEOGRAPHIC ZONES & COMPARISONS WITH BIOGEOGRAPHY OF OTHER TAXA

Cape Zone

The repeated identification of a distinctive Cape Zone centered mostly within the southwestern Cape Province of South Africa has been recorded in a number of studies across a range of faunal taxa (butterflies -Carcasson, 1964, Amphibia - Ponyton 1964, Tabanidae - Usher 1972, flies -Bowden 1978, Tenebrionidae - Endrödy-Younga 1978, mammals – Crowe 1990). This pattern has further been retrieved in phytogeographic studies (Weimarck 1941, Goldblatt and Manning 2002) which have highlighted the Cape Zone as an active centre of speciation (Linder 2003, 2005). Moreover, the high concentration of endemic taxa also suggests that the Cape Zone has been least disturbed by severe historical climatic changes such as glaciation (Stuckenberg 1962, Bowden 1978, Deacon et al. 1992, Cowling and Lombard 2002, Cowling and Proches 2005). The presence of endemism at deep phylogenetic levels (genera and above) (Carcasson 1964, Endrödy-Younga 1978, Picker and Samways 1996, Goldblatt and Manning 2002, Day 2005) provides further proof of the long-term stable nature of the zone. In agreement with the above findings, a well-defined Cape Zone was retrieved for monkey beetles with several species- and endemic rich Cape CoEs delimited; these were dominated by ‘Cape taxa’ (genera which had the majority of their radiation in these CoEs).

The north western and north eastern boundaries of the Cape Zone (“extension lines” of Endrödy-Younga 1978) differ across taxa, as can be seen when comparing Endrödy-Younga’s and Carcasson’s respective Cape Zones. These “extension lines” are reflective of both past, ancient distribution patterns (relictual taxa) and of the younger derivatives of old Gondwanan stock (Stuckenberg 1962, Carcasson 1964, Bowden 1978, Endrödy-Younga 1978, van Wyk and Smith 2001, Sole et al. 2005). The most species- and endemic rich CoE delimited for South Africa (Southern Namaqualand; centered on the northern sections of the CFR and southern parts of Namaqualand) – showed a similar species composition to the southern SW Cape CoE, suggesting that the north western extensions of the Cape Zone as delimited by monkey beetle data is of greater extent than the boundaries defined by Carcasson’s butterfly data, and matches more closely Endrödy-Younga’s Cape Zone boundaries as defined by tenebrionid beetle data and that of jewel beetles (Holm and Marais 1992, Holm and Gussmann 2004), bees (Kuhlmann 2005), and wasps (Gess 1992). The Southern Namaqualand CoE was made up of more arid fynbos and essentially fell within the northern boundaries of the CFR, incorporating areas of southern Namaqualand and the Hantam-Tanqua-Roggeveld centres of Born et al. (2007). However, this CoE also shared species with the Karoo Mountain CoE, showing some support for Carcasson’s western extensions of a zoogeographic

Karoo Zone into the northern CFR. This was not supported by Endrödy-Younga's data, which rather indicated the confinement of Karoo elements to his large Central Arid Region. However, support for Carcasson's Karoo Zone intrusion comes from a molecular phylogeny of the newly-described insect order Mantophasmatodea (Heelwalkers), where a sister taxon to Little Karoo species is found in the areas around Vanrhynsdorp (congruent to northern sections of the Southern Namaqualand CoE) (Damgaard et al. 2008). This faunal link is most likely established across the Hantam Karoo, Roggeveld, and Little Karoo mountains and represents an important biological corridor for insect groups. Some elements of the Southern Namaqualand CoEs were also seen extending into areas of the Karoo and the Hantam-Tanqua Karoo, with arid adapted species of *Hoplocnemis* linking these areas faunistically. Born et al. (2007) also noted strong floristic links between the north western CFR and Namaqualand, Hantam, and Roggeveld. This biogeographic pattern was strongest at their generic level of analysis, and shows strongest congruence with monkey beetle CoEs. Stronger associations have been noted between higher-level floristic taxa and insect species diversity patterns (Novotny 2002, Proches et al. 2009) indicating that biogeographic concordance between plants and insects should show greater geographic matching at these higher-level plant taxonomic groupings.

Further interesting comparative patterns were retrieved between monkey beetle Cape CoEs and Cape phytogeographic centres. In contrast to richness patterns seen for Cape phytogeographic centres where the highest richness was recorded in south-western parts of the CFR (Goldblatt and Manning 2002, Born et al. 2007), the north-western parts of the CFR recorded the highest numbers of monkey beetle species and endemics. The next most diverse area was the south-western areas of the CFR. The higher diversity of the north-western areas may be due to a stronger Karoo (Hantam-Roggeveld-Little Karoo) and Namaqualand faunal influence on this area (see above), increasing insect richness and endemism. Cape Zone monkey beetle CoEs mostly extended across Goldblatt and Manning's (2002) phytogeographic centres, though, they also appear to broadly follow the CFR boundaries. The Agulhas Plain phytogeographic centre of Goldblatt and Manning (see also Born et al. 2007), renowned for floristic endemism and richness was not retrieved as a distinct centre for monkey beetles and was incorporated into the large south-western Cape CoE. It would appear that unusual limestone soils which are basis for the plant endemism have not resulted in a similar evolutionary response in the beetles.

The geographic reaches of eastern and north eastern Cape "extension lines" have also been defined differently by datasets using different taxa (compare Figs. 2 & 3). The south-eastern CoEs of the Cape Zone showed biogeographic similarities to southern areas of the Albany Thicket with typical fynbos monkey beetle genera found here. Fynbos floristic elements are known to extend east of the CFR (Weimarck 1941, Mucina and Rutherford 2006), and these still have their characteristic associated insect

communities. Thus, the Cape Zone for monkey beetles shows a greater eastern extension than when defined by butterflies, extending to the full eastern reaches of the CFR, and with some fynbos-associated beetle species extending along with fynbos plants beyond Port Elizabeth. This pattern has also been retrieved for Acridoidea grasshoppers (Antunes 2003), with several putative Cape origin grasshopper families (with their richness and endemic hotspots concentrated in the winter rainfall region) extending further eastwards than the CFR. This pattern of eastern extensions into the Albany Thicket (see below) is further seen in a range of taxa that have their centres of diversity within the Cape Zone (Dirsch 1965, Hesse 1969, Usher 1972, Bowden 1978, Holm 1978, Gess 1992, Holm and Marais 1992, Holm and Gussmann 2004). Endrödy-Younga (1978) indicated far reaching extension lines for Cape Zone elements, although of gradually weaker extent, reaching almost as far east as the tropical areas of Durban. Support for this pattern is seen in several Cape dragonfly and damselfly elements that show more extensive eastern reaches, some reaching into the far northern regions of South Africa and into southern Zimbabwe and Mozambique (Dijkstra 2007).

Namaqualand Zone

Endrödy-Younga and Carcasson both delimited western arid zones extending from approximately the north western edges of the CFR, incorporating the western sections of the Succulent Karoo and extending north into southern Angola. The biogeographic history of this western arid area is complex, as seen in the three contrasting faunal elements retrieved here; each reflective of a different evolutionary history. Faunal elements found in this region include: (i) younger derivatives of Cape stock that have colonised new, arid landscapes (Endrödy-Younga 1978, Holm 1990, Irish 1990, Sole et al. 2005); (ii) Cape proper elements still confined to temperate habitats such as montane refugia (Stuckenberg 1962, Colville 2006); and (iii) west coast relictual elements of ancient Cape stock origin (Endrödy-Younga 1978), or taxa of independent origin (Endrödy-Younga 1978). Four distinct monkey beetle CoEs were delimited from the Namaqualand region (*sensu* Cowling et al 1999) of this arid western zone, each reflective of the different elements mentioned in (i) – (iii), and discussed further below.

West coastal area

Endrödy-Younga (1978) was convinced that the climatically stable west coastal area with moderate temperatures represented an independent zoogeographic zone of temperate ancestry. He based his conviction on the presence of endemic elements of deeper phylogenetic ancestry (families and sub-tribes) and distribution patterns of relict tenebrionid beetles representative of past temperate climates. Holm (1990) and Irish (1990) retrieved similar results for jewel beetles (Buprestidae) and fishmoths (Thysanura), respectively. Linder (2003) and Cowling and Proches (2005) reiterate the favourableness of

this coastal area during the Pleistocene for northern extensions of temperate Cape floral elements. A clear west coastal CoE was delimited for monkey beetles. This coastal area is a well-recognised phytogeographic centre (Hilton-Taylor 1994, Born et al. 2007). However, whether or not beetle taxa within this CoE are relics is unclear as no phylogenetic analysis of monkey beetles has been attempted. Nonetheless, two endemic (monotypic) genera are found here. This CoE showed closest similarities, in terms of species composition, to other Namaqualand CoEs rather than Cape CoEs highlighting the possible zoogeographic independence of this zone and movement of elements between the west coastal CoEs and inland areas of Namaqualand. Stuckenberg's (1998) cladistic studies on wormlion flies (Vermelionidae) showed a northern movement of fauna from Namaqualand Pleistocene coastal plains into northern Namaqualand areas such as the Gariiep Centre of endemism. The west coastal zoogeographic zone appears at some stage to have become isolated from the south western Cape. Geologically the west coast area (Kalahari and coastal sands) is cut off from the south by a Cape Supergroup geological formation (Meadows and Watkeys 1999). Faunistically, it appears to be cut off by a strong westward intrusion of Karoo faunal elements, as highlighted in Carcasson's map (Fig. 1). The cut off of west coastal elements is seen in the retrieval of two CoE QDS located south of the "Karoo intrusion". This pattern has also been retrieved by Bradshaw and Linder (2009) for phytogeographic centres. Thus, the west coastal areas contain Cape faunal elements that are most likely survivors of ancient Cape lineages. Speciation through vicariance most likely followed after isolation of this coastal group from the south western Cape faunal group, as can be seen in the two genera *Lepithrix* and *Platychelus*, both well represented in the Cape, but showing high endemism within the west coast CoE (see Tables 5 & 6). However, the West Coast CoE showed its greatest affinities rather with the Southern Namaqualand CoE and northern arid Namaqualand CoEs, particular with the Gariiep Centre, possibly indicating a longer, and more independent (from Cape Faunal influences) history of derived arid-adapted groups of the northern Namaqualand biogeographic region, a pattern supported by data of Endrödy-Younga and Stuckenberg (1998) for insects; and Klak et al. (2004) for arid-adapted succulent plants (see also van Wyk and Smith 2001).

Namaqualand CoEs

i) Central Namaqualand

Inland of the west coast, the largest Namaqualand CoE (Central Namaqualand) retrieved for monkey beetles is spatially congruent with several species rich phytogeographic centres (Hilton-Taylor 1994, Born et al. 2007). The high number of endemic monkey beetle taxa associated with this CoE is most likely a reflection of the phylogenetic diversity of floristic elements within these centres - which include

annuals, endemic fynbos taxa on the Kamiesberg and Gifberg Mountains, and high succulent abundance on the arid Knersvlakte (van Wyk and Smith 2001). Furthermore, this CoE showed a phylogenetically complex array of monkey beetles, with montane paleoendemic species restricted to fynbos peaks, e.g. *Anisonyx* (Stuckenberg 1955, van Wyk and Smith 2001, Colville 2006); more adaptive derivatives of Cape taxa, e.g. *Dichelus*; older, arid adapted genera, e.g. *Denticnema*; and elements shared with more eastern CoEs, such as the Karoo Mountains and Albany Thicket, e.g. *Hoplocnemis*.

ii) Namaqualand Upland

This smaller CoE was retrieved south of the Central Namaqualand CoE and fell within the Namaqualand Rocky Hills phytogeographic centre of Hilton-Taylor (1994). This CoE was fairly distinct in its endemic species composition, and highlights the likelihood of Namaqualand consisting of a mosaic of smaller, although clearly defined monkey beetle (insect) CoEs, as seen for Born et al.'s (2007) numerous smaller sized centres delimited for Namaqualand. This CoE also showed faunal links with the Karoo Mountains (e.g. *Ischnochelus*).

iii) Gariep Centre

In the northern reaches of Namaqualand, a well-defined Gariep/Richtersveld Centre was retrieved. A Gariep centre of endemism has also been retrieved in several floral (Hilton-Taylor 1994, van-Wyk and Smith 2001, Born et al 2007) and faunal studies (Gess 1992, Stuckenberg 1998, 2000, Antunes 2003, Prendini 2005). The retrieval of this centre across taxonomic groups indicates the Gariep/Richtersveld area as an area of remarkable biotic diversity and endemism, highlighting its conservation importance. The high biotic diversity and endemism are mostly associated with the ecological variability of the area (climate, topography, and geology, and also for insects, the abundant floristic diversity) (see Hilton-Taylor 1994, Stuckenberg 1998, 2000, and van Wyk and Smith 2001 for discussion on the Gariep Centre).

Tropical Subregion

There is a gradual southward reduction in tropical and sub-tropical elements that are present in the summer rainfall eastern regions of Southern Africa (Ponyton's (1961) "subtraction margin"), with several insect groups showing extensions as far south as the Eastern Cape (summer and all-year rainfall). As mentioned above, Cape faunal elements extend in varying degrees into the Eastern Cape (and beyond), and as such, areas of the Eastern Cape show a juxtaposition of Cape and Eastern tropical and sub-tropical faunal elements. South-west of this area, the climate changes to a winter rainfall, more temperate climate,

and together with the presence of a diverse Cape fauna, sub-tropical and tropical fauna are prevented from further southwards movement.

i) Albany Centre CoE

The monkey beetle Albany Centre CoE, which shares several genera with the more tropical areas of Natal, although showing species occurrences of fynbos, Karoo and Namaqualand genera, is an extreme example of this Eastern Cape zoogeographical merger of various CoE's. A good example of an eastern monkey beetle genus reaching down into the southern parts of the Eastern Cape is seen in the distribution pattern of the essentially sub-tropical genus *Eriesthis* Burmeister 1844 (Dombrow 1997). This genus is found as far north as Tanzania, and as far south as Port Elizabeth, with two species extending into the Little Karoo (Willomore area). Similarly, the savanna/grassland monkey beetle genera (*Microplidus* Péringuey 1902 and *Monochelus* Burmeister 1844) whose distributions extend from East Africa through Zimbabwe into South Africa reaches this CoE. A similar pattern is also seen for other insect groups, e.g. bladder grasshoppers (Pneumoridae), with a tropical species recorded from as far north as Uganda, and extending as far south as the Albany Thicket (Dirsh 1965).

The direct and indirect zoogeographical links between the Albany Centre and several surrounding CoEs highlight the interesting and complex faunistic composition of this centre. Some Cape Fynbos genera have species extending through the Southern Coastal CoE eastwards into the Albany Centre, e.g. *Dichelus*, while others, e.g. *Dicranocnemus* appear to be derived from the neighbouring Fynbos Biome, but have subsequently diversified in the Albany Centre. Namaqualand genera appear to have entered the Albany Thicket through the Karoo Mountains, e.g. *Denticnema*. Karoo Mountain genera which have diversified within this CoE also show species occurrences within the Albany Centre, e.g. the arid adapted, non-flower feeding genus *Hoplocnemis*.

The occurrence of fynbos, Karoo, Namaqualand, forest, grassland, and savanna insect elements within the Albany Centre CoE is further mirrored by the floristic elements of the phytogeographic Albany Centre (van Wyk and Smith 2001, Cowling et al. 2005, Mucina and Rutherford 2006). Cowling et al. (2005) indicate a very old (Eocene) phytogeographic origin for the Albany Centre, which is possibly reflected in the delimitation of this centre as a monkey beetle CoE, and in the occurrence of (regional) endemic and relic butterfly (Carcasson 1964), damselfly (Dijkstra 2007; Tarboton and Tarboton 2005), grasshopper (Dirsch 1965, Antunes 2003), and fly (Stuckenberg 1997, 2000) taxa.

An apparent monkey beetle species depauperate section is evident north of the Albany Centre CoE is evident. This section, extending from 26°E, up towards the coastal town of Durban, may well be a true

reflection of a region of low insect diversity rather than a reflection of poor collection. Endrödy-Younga (1978) noted a similar pattern in several tenebrionid beetle tribes: a rich Cape Fauna extending to about 26° E, with a distinct drop-off in species in the Transkei region of the Indian Ocean Coastal Belt Biome, although with a re-emergence of diversity made up of tropical elements around 31° E. Similar patterns are seen in Usher's (1972) study on tabanid flies showing a diverse all-year round rainfall fauna, an approximate 40% decrease in diversity within the Transkei area, followed by a rapid 60% increase in diversity after 31° E. This patterns is also reflected in diversity hotspots of South African dragonflies and damselflies (Oelofse 1996; Tarboton and Tarboton 2002, 2005) and in South African land snails (van Bruggen 1978). The Transkei region most likely represents an effective climatic barrier for both the eastern extension of the more temperate Cape elements and the southern extension of more sub-tropical and tropical eastern faunal elements. Carcasson (1964) relates the general species depauperateness of butterflies in the Eastern Zone to an early loss (Miocene) of connection to the species rich western forests after uplifting of the eastern plateau, and forest fragmentation and reduction during Pleistocene interpluvial phases.

ii) Central Natal CoE

The tropical Central Natal CoE retrieved for monkey beetles is positioned on and about the coastal town of Durban. Several genera found in this tropical CoE are also recorded from tropical areas of Zaire, Uganda, and Tanzania, e.g. *Ceratochelus* Dombrow 2002, *Congella* Péringuey 1902, and *Lepitrichula* Schein 1959. Inland extensions for this CoE, reach into the Sub-escarpment Grasslands (Mucina and Rutherford 2006), although still within the Maputaland-Pondoland phytogeographic region. However, this pattern of tropical forest elements shared between grassland and savanna habitats has been noted for a number of forest dwelling taxa (Lawrence 1952). Endrödy-Younga (1978) stated that "...the coleopteran fauna of the coastal forest belt could best be characterised as [that of] a forest adapted savanna biome..." The monkey beetle genera *Eriesthis* and *Monochelus* are well represented in these habitat types, and link the Natal CoE with the Central & North Natal and Northern Escarpment CoEs.

Mountain Relics and Transitional Faunal Areas

The three other monkey beetle CoEs delimited within the eastern zones are seen to be made up of contrasting elements of sub-tropical, tropical, savanna/grassland, and relictual species. The CoEs are mostly congruent with Carcasson's Highlands Forests and Eastern (Coastal) Zone, which consists of highland (relictual forest taxa) and lowland forest elements that have penetrated southwards from Eastern and Central Africa. As mentioned above, conflict is seen with Endrödy-Younga's Cape Zone. However, his Mountain Zone, Transvaal Highveld Transitional Area, and Tropical Sub-region match with the

monkey beetle CoEs of the Drakensberg, Northern Escarpment + Central & North Natal, and Central Natal, respectively. The phytogeographic Maputaland-Pondoland Region (van Wyk and Smith 2001) is generally congruent with these zoogeographic zones. Congruence may diminish between these two biotic centres towards the areas of Transkei, as this section represents a faunistically poor region (see above), although still classified as a phytogeographic centre of endemism (Pondoland Centre – van Wyk and Smith 2001).

i) Drakensberg CoE

The Drakensberg CoE delimited for monkey beetles shows some congruence with Carcasson's Highlands Forest, but greater congruence is seen with Endrödy-Younga's Mountain Zone. The Drakensberg Mountains are a known refuge for a number of palaeoendemic taxa (Stuckenberg 1962, 2000; Tarboton and Tarboton 2005), which comprised the 'Eastern Highlands' part of Stuckenberg's Cape Zone, based on montane paleoendemic taxa. Relictual elements for the Drakensberg monkey beetle CoE include five endemic species of the essentially Cape montane monkey beetle genus *Anisonyx* (see below). The Drakensberg CoE shows strong congruence with the phytogeographic Drakensberg Alpine Centre, which houses paleoendemic plant taxa (van Wyk and Smith 2001). Furthermore, a likely centre of diversity exists centered on the Drakensberg Mountains. Although not strongly captured in this study in terms of QDS with high diversity values, indications are that this temperate montane area most likely supports a higher diversity of monkey beetles. The area, particularly within the region of Lesotho, has been largely under-collected. A collection trip to this area in 1959 by the dipterist Brian Stuckenberg unearthed three new species of *Anisonyx*, (Andreae 1965), while more recently (2004), opportunist collecting along the road verge of a mountain passes in Lesotho revealed a further three new species of this genus (Dombrow, unpublished data). The Drakensberg Mountains also house a rich diversity of potential monkey beetle host plants, including several fynbos elements (van Wyk and Smith 2001). Furthermore, the Drakensberg Mountains are known as centres of adaptive radiation for two other pollinating groups, long-tongue flies (Potgieter et al. 1999, Goldblatt and Manning 2000, Potgieter and Edwards 2005, Barraclough 2006), and oil-collecting bees (Whitehead and Steiner 2001). These two groups have shown concordant adaptive radiations and speciation with monkey beetles in the winter rainfall regions of South Africa, suggesting the Drakensberg Mountains should show similar patterns.

ii) Grassland Biome CoE's

The remaining north-eastern monkey beetle CoEs fall mostly within the high altitude plateaus of the Grassland Biome. Endrödy-Younga considered these areas as transitional, bordering between several

main zoogeographical zones and containing a diverse array of elements from all neighbouring zones. In general, the species diversity of monkey beetles within these areas of Grassland and Savanna Biomes is patchy and mostly depauperate. Once again, this pattern is most likely a combination of under-collecting and a general true reflection of diversity patterns. The radiation of species within the Savanna and Grassland Biomes has most likely been limited, as most monkey beetle species are associated with flowers, with only a limited number of species shifting (or retaining) their phytophagous (grass-feeding) nature. Furthermore, the source-pool of species from northern savannas regions appears to be depauperate, and thus the extent of movement of southern extensions of this fauna into South Africa would only constitute a limited contribution, unlike that seen in other insect groups e.g. antlions, which show high diversities in northern savanna regions, and strong affiliations with diverse savanna elements in South Africa (Mansell 1985). However, certain floristically rich areas within these two large biomes most likely contain greater diversities than currently recorded. These north-eastern biogeographical areas are represented by Endrödy-Younga's Transvaal Highveld Transitional Area and Trans-Botswana Transitional Belt (Fig. 3). Carcasson's Cape Grassland and Kalahari Zones are mostly congruent with these two transitional areas, respectively; although, Carcasson's Kalahari Zone shows a greater southern extent linking eastern and western areas of South Africa.

iii) Mpumalanga/ Drakensberg CoE's

The Northern Escarpment, Wolkberg, and Graskop monkey beetle CoEs show their greatest congruence with the northern reaches of Endrödy-Younga's Transvaal Highveld Transitional Area. Monkey beetle CoEs within this Transvaal Highveld Transitional Area mostly occupy areas of high altitude grasslands and show species compositional similarities with each other and with the Central Natal and Drakensberg CoEs, highlighting the mixture of tropical (lowveld tropical taxa) and high altitude (relictual) elements characteristic of this zoogeographical area. Congruence of these CoEs is further seen with van Wyk and Smith's (2001) phytogeographic centres of the Wolkberg, Sekhukhuneland, and Soutpansberg.

Miscellaneous CoE's

Endrödy-Younga's Trans-Botswana Transitional Belt and Carcasson's Kalahari Zone is weakly retrieved for monkey beetles. This important faunal exchange route links western southern continents with their eastern counterparts allowing for cross-continental dispersal to occur (Endrödy-Younga 1978, Prendini 2001). In addition to this transitional belt being retrieved for tenebrionid beetles and butterflies, many other disparate insect groups mirror this pattern, e.g. ascalaphid owlflies (Tjeder and Hansson 1992), nemopterid lacewings (Tjeder 1967), bombyliid bee-flies (Greathead and Evenhuis 2001), mydas flies (Hesse 1969), anthophorid bees (Eardley 1994), buprestid jewel beetles (Holm 1978), acridoid

grasshoppers (Antunes 2003) and cetoniid fruit chafer beetles (Holm and Marais 1992). Within monkey beetles, this transitional belt is only retrieved with a single grass-feeding genus (*Outeniqua* Péringuey 1902). This genus is further represented in the northern savanna regions of South Africa and in north-central Namibia. The probable sister genus (*Pseudouteniqua* Dombrow 2001) is found in, and endemic to, Botswana. The distribution pattern of this genus and its sister genus, most likely represents past movement through the Trans-Botswana Transitional Belt. The weakness of this pattern retrieved in monkey beetles is probably a result of poor collecting, particularly within the isolated areas of the Kalahari and northern Namibian regions. In addition to the western-eastern continental connection, this transitional belt falls within an arid corridor, which connects arid southern faunal and floral elements to arid regions of north-eastern Africa through a well defined drought corridor (Balinsky 1962, Carcasson 1964, Van Zinderen Bakker 1962, Endrödy-Younga 1978, Holm 1978, Werger 1978, Prendini 2001). Although not discussed by Damgaard et al. (2008), the disjunct distribution of a single Tanzanian species of mantophasmatid Heelwalker is easily explained, and connected to, south-western occurring Heelwalkers through this arid corridor. The distribution pattern of monkey beetle species of the genera *Eriesthis* and *Inanda* - found in northern Namibia and western Tanzania – is most likely explained through faunal interchange via the arid corridor connecting these areas.

Central Arid Zone

A further distribution pattern seen in monkey beetles, and shared with many other invertebrate groups is the lack of any meaningful extensions from surrounding biogeographic regions into the central arid zone of South Africa. Characteristically low values of species richness and endemism are seen for many insect and invertebrate groups for this arid zone (Vernon 1999). However, some insect groups, such as the grasshopper families Pamphagidae and Lentulidae (Antunes 2003) and termites (Coaton 1963) are reasonably well represented here. Endrödy-Younga delimited an extensive Central Arid Zone, incorporating much of the Nama-Karoo Biome of South Africa. He considered this zone difficult to define faunistically based on the beetle groups he used. However, generally, coleopterous fauna found within this arid zone show a clear South African origin, with strong links with Cape stock (Endrödy-Younga 1978, Holm and Gussmann 2004, Sole et al. 2005). Elements of this fauna are thus likely to be arid-adapted, western coastal and Namaqualand derivatives (Endrödy-Younga 1978, Holm 1990), which are mostly wingless, psammophilous and ultrapsammophilous species (Endrödy-Younga 1978, Irish 1999, and Prendini 2001). However, north eastern African elements - from a range of ground-living, wingless beetle families (see Endrödy-Younga 1978) – are also evident in this zone, having moved through the arid corridor connecting these areas (see above).

Carcasson recognized two separate zones within this central arid region - a Karoo and a Kalahari geographic zone (mostly equivalent to the Nama-Karoo Biome); with the latter showing a distinctly impoverished butterfly fauna, and the former zone still retaining a number of endemic species. However, both these zones appear to be meeting grounds for the impoverished extremities of neighbouring zoogeographic regions. For monkey beetles the arid zone is poorly retrieved and showed weak affinities to surrounding zoogeographic zones. A single species of *Outeniqua* linked the Kimberley CoE with the Savanna Biome. This faunal link is seen in termites, with savanna species retrieved from the Nama-Karoo (Vernon 1999). The Nama-Karoo also appears to be linked with the Kalahari through an arid adapted species of *Peritrichia*, a monkey beetle genus usually associated with the Fynbos and Succulent Biomes. Generally, dispersal from the western zone into this region is limited by the aridity and contrasting summer rainfall pattern, and floristically poorer habitats (Cowling and Hilton-Taylor 1999). Thus, as Endrödy-Younga mentions, this central arid zone is difficult to define faunistically. However, it must be noted that several studies (Cowling et al. 1989; Hesse 1969; Stuckenberg 1998; Usher 1972; Vernon 1999) have highlighted the Nama-Karoo as being poorly collected for both fauna and flora, and thus, patterns of richness and endemism are possibly obscured by this lack of biogeographic data.

EXPLAINING THE MEGARADIATION OF MONKEY BEETLES IN WINTER RAINFALL COES

An obvious question arising from the patterns of CoEs delimited here is to ask why the winter rainfall areas support the greatest species richness and endemism of monkey beetles in Africa. Since monkey beetles are strongly linked with flowers, it could be expected that diversification of the fynbos and succulent Karoo, with their great variety and profusion of flowers, would bring about co-adaptational and speciation responses among monkey beetles. Several other pollinating insect groups in the region show clear co-adaptations with their host plants. This relationship has also been shown to be a strong biogeographical determinant, with close matching between host and pollinator distributions closely. In comparison to other Hopliini (Lovell 1915), the vast majority of South African monkey beetles are adapted specifically towards anthophily (Picker and Midgley 1996, Goldblatt et al. 1998, Steiner 1998a,b). Thus, the evolution of key adaptations allowing the exploitation of the floristic proliferation of the fynbos and succulent Karoo may have been the adaptive step in promoting radiation of certain genera. The relationship between beetle radiation and evolution of the fynbos and succulent Karoo flora is discussed below. However, it must be noted that phylogenetic information and fossil evidence on monkey beetles is lacking, and as such, explanations put forward here are based on inference from contemporaneous patterns seen in other faunal and floral groups whose phylogenetic histories are better known.

Considering the antiquity of beetles (Grimaldi and Engel 2005) and early history of associations with angiosperms (at least since the Cretaceous - Grimaldi 1999) - ancestral species of monkey beetles were most likely present well before the radiations of Cape plant genera. However, their anthophilic behaviour may have already been well established (Grimaldi and Engel 2005), thus preadapting them for the exploitation of the impressive radiation of the Cape flora. Based on recent plant molecular phylogenies, fortuitously of plants involved in co-evolutionary relationships with monkey beetles, insights into possible floral-induced radiation events in monkey beetles might be inferred. These events may have already begun in the Oligocene with the radiation of the Proteacea (Linder 2003), followed in the early Miocene with Iridaceae diversification (Reeves et al. 2001), and in the late Miocene with the radiation of the large genus *Moraea* (Iridaceae) (Goldblatt et al. 2002). However, Cape floral clades (which today have monkey beetle-pollinated members) may have even longer histories, dating back to the Tertiary (Linder 2003, 2005, Linder and Hardy 2004), suggesting a possibly longer evolutionary association between some of these plants and monkey beetles, or their earlier ancestors. Members from each of the plant groups mentioned above display plant-pollinator relationships with monkey beetles (Goldblatt and Manning 1998; Colville, unpublished data). A good example of this is seen in the genus *Moraea*, which have co-evolved complex pollinating relationships with monkey beetles (Steiner 1998b, Goldblatt et al. 2002).

These earlier plant radiations appear to have occurred in the forest and open woodlands of the warm, humid early Miocene (Deacon et al. 1992). With the onset of climatic cooling in the middle Miocene, which initiated proliferation of the Cape flora (see above), an initial (first) monkey beetle adaptive radiation possibly occurred with genera rapidly diversifying, forming a species-rich source pool (still evident today). The onset of a winter rainfall climate from around the middle Pliocene (Deacon et al. 1992), opened up new geographic and floristic habitat in the Succulent Karoo, from which “Cape original” (Endrödy-Younga 1978) elements radiated into as they adapted to more arid habitats. Here, the apparently rapid and recent radiations (Goldblatt et al. 2002, Klak et al. 2004, Linder 2005) of seasonally abundant, large bowl-shaped flowers of Asteraceae, Iridaceae, and Mesembryanthemaceae would have created floristically favourable niches providing a considerable (second) evolutionary impetus for diversification of several monkey beetle genera. However, it is quite possible that repeated northern extensions occurred in the past from the fynbos into the Succulent Karoo during cool (wet) periods of the cool-warm climatic cycles of the Pleistocene (Deacon et al. 1992). Many taxa are shared between these two biomes, although at least 6 genera and 130 species are endemic to the arid parts of the winter rainfall regions. Furthermore, the presence of several monkey beetle CoEs in the northern parts of the Succulent Karoo Biome (Namaqualand – see above) is suggestive of a fairly long-term, stable evolution by genera

that had adapted specifically to the arid conditions and diverse succulent flora. However, another possibility is that some monkey beetle genera within the arid winter rainfall areas were well established before the advent of the winter rainfall climate. Klak et al. (2004) suggest such a possibility for some Aizoaceae clades, whose members appear not to have radiated in response to the establishment of the seasonally arid climate. Aizoaceae species are favoured host plants for monkey beetles, and thus beetles may have already established co-evolutionary relationships with these clades, and merely tracked the extensions of their plant hosts.

The hypothesis that some genera radiated initially in the Fynbos and then subsequently invaded the Succulent Karoo is supported by the radiations of other insect groups. As Endrödy-Younga (1978) noted of Cape tenebrionid beetles “...the Cape proper retained most of its original character and original biome whilst the [northern] extension areas are occupied by the younger, more adaptive derivatives”. Furthermore, the Cape Zone is renowned for high levels of endemic, higher taxa (genus and above) (Carcasson 1964, Endrödy-Younga 1978, Picker and Samways 1996, Goldblatt and Manning 2002, Day 2005) providing further proof of the primary character of the Cape Zone. Holm (1978, 1990) provides support for this pattern based in his systematic studies of jewel and fruit chafer beetles, with northern extensions seen in southern Namibia clearly of Cape (and Namaqualand) origin. Sole et al.’s (2005) phylogeographic study of flightless dung beetles showed that the more derived taxa were distributed in northern Namibia, whereas plesiomorphic taxa were situated in coastal areas of Namaqualand and the Western Cape. Other insect groups show similar patterns, with several bee families (and many species) showing clear Fynbos – Succulent Karoo extensions, with an adaptive centre (95% endemism) found in the arid areas of the western, winter rainfall regions (Eardley 1989, Kuhlmann 2005). Stuckenberg’s (1998) detailed cladistic study on wormlion flies (Vermileonidae) showed the evolution through cladogenesis of a basal south western fynbos genus splitting into more adaptive (for anthophily) Succulent Karoo clades. Furthermore, Stuckenberg (1998, 2000) and others (Barraclough 2006, Greathead and Evenhuis 2001, Usher 1972) have highlighted the adaptive responses in mouthpart morphology of anthophilic genera found in at least seven other fly families. These adaptations are significant in that they are mostly specific to species located in the Fynbos and Succulent Karoo Biomes, indicating the diversification of the Fynbos and Succulent Karoo flora acted as a strong adaptive force in a number of insect groups. Extensive adaptive radiations are also seen within other insect groups whose members show anthophilic associations; with high diversification seen in oil-collecting bees (Eardley 1989, Whitehead and Steiner 2001), bees (Kuhlmann 2005), wasps (Gess 1992), long tongues flies (Barraclough 2006), nemopterid lacewings (Tjeder 1967, New 1989), and jewel beetles (Holm 1976, 1978, Holm and Gussmann 2004). Clearly not all invertebrate taxa will follow this pattern, and the

carnivorous Heelwalkers (Mantophasmatodea) have basal taxa in Namibia and derived clades in the fynbos biome (Damgaard et al. 2008).

The proposed timing of these radiations is to some extent supported by lineage ages obtained by molecular dating methods used in studies on southern African flightless dung beetles (Sole et al. 2005) and phytophagous cicadas (Price et al. 2007). These studies indicate radiation events dating back to the late Pliocene and early Pleistocene, contemporaneous with climatic, geomorphic, and floristic changes happening at these geological time scales (Linder 2003, 2005, Cowling et al. 2009).

CONCLUSION

This study represents the first attempt at using modern weighting techniques to delimit insect centres of endemism within South Africa. Eighteen CoEs were delimited across South Africa with clear concentrations of well-defined CoEs located along the western extent of South Africa, extending from the south western Cape into northern Namaqualand. These western zone CoEs contained the highest levels of endemism and species richness. Strong concordance between biogeographic centres of endemism reported for other taxa and those defined in this study was seen within this zone. Thus, the western, winter rainfall zone is highlighted as an evolutionary region of diversification, with the two largest south western CoEs possibly reflective of more established evolutionary centres. This was reiterated in the strong positive correlation recorded between beetle richness and endemism, highlighting the biotic importance of this zone. Speciation of monkey beetles within the winter rainfall zone appears to have followed or has co-evolved with the evolution of the flora of the winter rainfall biomes. Less well-defined, less diverse, and smaller sized CoEs were retrieved from the summer rainfall eastern zone of South Africa. Spatial congruence for these CoEs was mainly seen between tropical and sub-tropical coastal and montane biogeographic regions, highlighting areas such as the Drakensberg Mountains as centres of diversification. The need for phylogenetic data is highlighted, as this would allow a deeper understanding of the evolution of the group and a means of testing the hypothesis raised here. Furthermore, the possibility of dating lineage diversifications would allow cladogenetic events to be related to the geological and climatic evolutionary history of the winter vs. summer rainfall regions of South Africa.

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PART 2

MODELLING SPECIES RICHNESS AND TURNOVER

3 SPECIES RICHNESS OF MONKEY BEETLES IN SOUTH AFRICA: ENVIRONMENTAL AND PLANT CORRELATES AND THE SPATIAL NON-STATIONARITY IN RELATIONSHIPS

“The richness in species... is clearly due to the presence of an extraordinary combination of factors promoting speciation in the Cape Centre. Among these factors might be mentioned the antiquity of the landscape..., varied nature of the topography, mountain ranges of considerable relief..., the floristic trichotomy..., and the climate, characterized by winter rainfall in the south-west and more or less perennial rains in the east...the zones of high rainfall being confined to the summits and sea-facing slopes of the Fold Mountains, with marked rain-shadow effects in the intermontane valleys” *B. R. Stuckenberg (1962)*.

ABSTRACT

Regional species richness gradients are often explained in terms of habitat heterogeneity, climatic factors such as ambient energy, water-energy balances, and climatic stability. Regional patterns of species richness emerge from localized differences in heterogeneity and climate, but until recently the issue of non-stationarity (the spatial variation in modelled relationships) was often neglected or poorly explored. The development of use of Geographically Weighted Regression (GWR) allows modelling of the relationship between locally heterogeneous variables and regional patterns of species richness. In southern Africa, studies explaining regional insect richness patterns are noticeably lacking. In this study, I use GWR and distributional data for greater than 1000 monkey beetles at the scale of quarter degree grid squares (QDS), to investigate the power of environmental and plant variables in explaining species richness. Model results indicate wide spatial variation in the explanatory power of selected variables. Within the beetle rich winter rainfall areas; for arid parts of Namaqualand, plant diversity was an effective predictor of beetle diversity (positive relationship), as was rainfall (positive relationship) and summer temperature (negative relationship), whereas in the Cape Floristic Region (CFR), summer temperature (positive relationship) and beetle turnover (negative relationship) were found to be more important. In addition, habitat heterogeneity was an important explanatory variable for transitional areas between CFR phytogeographic centres. For the species poor, eastern, summer rainfall areas, generally weak relationships were retrieved for explanatory variables used in the model. However, summer temperature (positive relationship) showed the strongest relationship with beetle richness. GWR models, by incorporating these spatial differences in explanatory power, performed better in predicting species richness than global models that assume a constant spatial relationship between richness and environmental and climatic factors. The wide variation in the predictive power of the variables, indicates that not one model can fit all areas of the highly heterogeneous landscapes of South Africa, and further highlights the importance of using a modelling approach that can relate regional richness patterns with smaller scale variations in explanatory variables.

INTRODUCTION

Insects are a megadiverse and an essential functional component of all terrestrial and freshwater ecosystems (Wilson 1992, Grimaldi and Engel 2005). Attempts at explaining this enormous diversity have related the success of insects, in terms of species diversity, adaptive radiations, and biomass, to that of their physiological, morphological, behavioural, and ecological adaptations (Gullan and Cranston 2005, Schowalter 2006, Hunt et al. 2007). Furthermore, insects are an extremely ancient group, with some modern lineages dating back to the Late Triassic (Grimaldi and Engel 2005). Thus, insects have an exceptionally long and successful evolutionary persistence, having built up a huge biomass and bewildering number of species and functional forms.

The ecological literature is replete with studies focusing on the explanatory variables associated with regional richness gradients (Currie et al. 1999, Gaston 2000). Regional richness of plants and animals appears to be strongly influenced primarily by climate (energy and water (Pianka 1967, Currie 1991, Wright et al. 1993, Hawkins et al. 2003, Rodríguez et al. 2005) and habitat heterogeneity (Rosenzweig 1995, Kerr 2001). Five, well-known hypotheses have been shown to be the most important variables in explaining regional richness patterns: three associated with energy (ambient energy, water-energy balances, and for animals, plant productivity), one with habitat heterogeneity, and one associated with climatic stability (Wright et al. 1993, Gaston 2000, Rodríguez et al. 2005). However, the spatial scale at which these abiotic and biotic variables are investigated often determines their explanatory power (Foody 2004). Furthermore, the geographic range sizes of species under study can influence observed species richness patterns (Jetz and Rahbek 2002).

Energy, heterogeneity and climatic stability are commonly explored broad scale ecological processes that have been shown to be good explanatory variables for insect richness patterns (Turner et al. 1987, Wright et al. 1993, Kerr 1999, Kerr and Currie 1999, Kerr and Packer 1999, Kerr 2001, Kerr et al. 2001, Gotelli and Ellison 2002). Studies focusing on ecological determinants explaining insect species richness, however, most notably seek explanatory variables from the close association many insect groups have with the plant environment (Murdoch et al. 1972, Strong et al. 1984, Miller 1987, Gaston 1992, Hawkins and Porter 2003, Novotny et al. 2006, Condon et al. 2008). Almost half of all insects appear to have co-radiated with angiosperms (Grimaldi and Engel 2005), and as such, the plant environment is hypothesized to be strongly influential in insect diversifications. A host of studies have shown that various plant variables, including taxonomic diversity (Barraclough et al. 1998, Hawkins and Porter 2003, Novotny et al. 2006); phylogenetic diversity (Symons and Beccaloni 1999, Proches et al. 2009); architectural (fractal) complexity (Strong et al. 1984); host specificity (Ehrlich and Raven 1964, Schoonhoven et al. 1998, Dyer

et al. 2007) host geographic range (Southwood 1961, Cornell 1985); and the evolutionary arms race between insects and plants (Mitter and Farrell 1991, Mello and Silva-Filho 2002) are able to explain in varying degrees of success insect richness patterns. However, there are many insects groups that are not associated with plants (although they are often associated indirectly, e.g. predacious groups which prey on phytophagous insects and inhabit plants) and, even amongst phytophagous insect groups, plant explanatory variables have not always correlated with insect richness patterns (Hawkins and Porter 2003, Hunt et al. 2007, Condon et al. 2008). Moreover, convincing evidence of reciprocal diversifying co-evolutionary relationships between plants and insects has as yet not been established (see Schoonhoven et al. 1998 for discussion on strengths and weaknesses of current hypotheses; see also Miller 1987, and Hawkins and Porter 2003). In addition to above mentioned explanatory variables (see also Appendix 6.1 of Wright et al., 1993), studies have shown the importance of topography and edaphic requirements as being important in explaining insect richness patterns (Irish 1990, Gess and Gess 1998, Gervais and Shapiro 1999, Prendini 2001b, Sole et al. 2005, Colville 2006, Botes et al. 2007). Thus, as for other faunal and floral groups, insect richness patterns appear to be determined by a complex, and often interacting suite of ecological factors.

South Africa houses a remarkably speciose and endemic-rich insect fauna (Scholtz and Holm 1985, Scholtz and Chown 1995, van Jaarsveld et al. 1997). Two centres of insect diversity are evident: a western centre found within the winter-rainfall Fynbos and Succulent Karoo Biomes, characterised by high species richness and pronounced endemism; and an eastern tropical and subtropical centre showing high species richness, although with noticeably lower levels of endemism (see Chapter 1). In comparison to eastern biomes of South Africa, the Fynbos and Succulent Karoo biomes in the west are overly species rich for a number of insect groups (Tjeder 1967, Mansell 1985, Gess 1992, Kuhlmann 2005, Colville 2006). This pattern of diversity in relatively low energy and water-poor biomes is in contrast to several ecological axioms which indicate that areas of high energy and abundant water should predicatively contain higher species richness than areas of lower energy, or high energy associated with higher water stress (Currie 1991, Hawkins et al. 2003). Furthermore, the importance of area size and associated habitat heterogeneity in determining species richness would also predict greater richness associated with the larger sized and habitat diverse eastern Savanna and Grassland biomes (Rosenzweig 1995, Cowling et al. 1997).

The Fynbos and Succulent Karoo biomes receive predominantly winter-rainfall biomes (although some areas at the south-eastern edge of the winter-rainfall regions receive all year rainfall) and are comprised of temperate, mesic, and semi-arid to arid habitats (Cowling et al. 1999, Mucina and Rutherford 2006). They make up approximately only 14% of the relative biome area of South Africa, whereas the eastern biomes

make up roughly 60%, the rest being the arid biomes of the central part of the region (Mucina and Rutherford 2006). Furthermore, in terms of standard climatic variables related to high energy and favourable environments conducive to high species richness, the Fynbos and Succulent Karoo biomes show noticeably lower values, with a clear east-west gradient in the severity of summer drought conditions extending across South Africa (O'Brien 1993, Cowling et al. 1997, Schulze 1997). However, these two winter rainfall biomes show remarkably high levels of plant richness and endemism (Cowling et al. 1989, Cowling et al. 1998, Cowling et al. 1999) and highly heterogeneous habitats with characteristically steep environmental and floristic gradients (Cowling et al. 1997, Goldblatt and Manning 2002, Latimer et al. 2005). Furthermore, these two biomes appear to be reasonably climatically stable (Cowling et al. 1997, Cowling et al. 1998, Cowling et al. 1999), with western fynbos areas showing climatic stability extending over evolutionary time (Cowling and Lombard 2002, Linder 2003). Thus, the winter rainfall biomes provide interesting global and local contrasts in terms of standard hypothesised explanatory variables determining insect richness patterns.

Studies explaining regional insect richness patterns within southern Africa are noticeably lacking (van Rensburg et al. 1999, Botes et al. 2007). Due to the high biotic interest and global biodiversity importance of their associated phylogeographic centres of plant richness and endemism (Myers et al. 2000, Goldblatt and Manning 2002, Born et al. 2007), a handful of studies have focussed their attentions on explaining insect richness patterns within the Fynbos and Succulent Karoo Biomes. Of particular interest appears to be the insect - plant diversity relationship within the Cape Floristic Region (CFR) (Picker and Samways 1996, Wright and Samways 1998, Giliomee 2003, Proches and Cowling 2006, Proches et al. 2009). Findings to date suggest that overall plant species richness (Wright and Samways 1998, Proches and Cowling 2006), plant phylogenetic diversity (Proches et al. 2009), host plant diversity (Gess 1992, Wright and Samways 2000), parasitic host diversity (Gess and Gess 1998), soil type (Gess and Gess 1998) and temperature (Stuckenberg 1969, Botes et al. 2006, Botes et al. 2007) are important ecological factors explaining insect richness. High species turnover (Beta diversity – a potentially strong influential component of regional diversity – (Whittaker 1972)) further appears to be a significant explanatory variable (Colville et al. 2002).

Almost all of these studies, however, have focussed on sub-sets of insect distributions and richness patterns, using correlations between local insect richness calculated from field study site data and associated localised ecological variables, thus limiting their findings for testing processes effecting regional richness patterns across a taxon's entire distributional range (Currie et al. 1999). Moreover, the single study incorporating a full distributional data set (Gess 1992) did not statistically relate richness

patterns with ecological variables, but instead used expert natural history knowledge and matching broad based host plant patterns in explaining masarine wasp richness.

Here I explore how environmental (rainfall, temperature, habitat heterogeneity, host plant richness) and diversity measures (beta diversity of monkey beetles and associated host plants) explain regional beetle richness patterns, using a relatively comprehensive (see Chapter 1) distributional dataset set for South African monkey beetles (Hopliini). Monkey beetles are a speciose group of pollinating and non-pollinating beetles, occurring throughout South Africa, although showing a clear centre of adaptive radiation within the winter rainfall biomes. Furthermore, at least 63% of the world's species are found in South Africa, with 98% of these being endemic to this country (see Introductory Chapter). Beyond the ecological interest of how insect richness varies through space, understanding the drivers of insect richness is of high conservation urgency: firstly, by allowing an increase in our limited knowledge of an ecologically essential component within two global biodiversity hotspots, and secondly to increase our knowledge to allow more inclusive conservation decisions and understanding of the possible threats of global climate change (Kerr 2001, Samways 2005, Botes et al. 2006).

Specifically, I attempt to understand patterns of monkey beetle richness in terms two main issues: (i) the occurrence of high beetle richness and endemism in a low-energy and low- moisture environment, contradictory to current ecological theory; and (ii) the predictive power of plant diversity in determining insect richness.

MATERIAL AND METHODS

DATABASES

Monkey Beetle Distributional Data Set

A point locality distributional data set was collated from several sources (see Chapter 1). Monkey beetle distributional data was further obtained from an extensive pinned collection housed at the South African Iziko Museum, Cape Town. Additional locality data was supplemented by field study collections undertaken during spring flowering seasons (1999-2007). Each point locality was geo-referenced using 1:50 000 and 1:250 000 topo-cadastral maps of South Africa (sourced from Chief Directorate: Surveys and mapping (CDSM), Mowbray, Cape Town, www.w3sli.wcape.gov.za) and the GeoNet Names Server gazetteer (http://164.214.2.59/gns/htm/cntry_files.html). Only collection records of sufficient accuracy were used. Obscure and/or vague locality records, such as “Cape of Good Hope” were excluded. Highly disjunct records, suggesting misidentification of a species, or incorrect locality label information were

further excluded from the data set. In total, 1040 species and 6959 unique locality records were compiled for use in a geographic information system (GIS).

Monkey beetle point distribution maps were created using Arcmap 9.2 (ESRI 2006) and overlaid onto a Quarter Degree Square (QDS) grid (Edwards and Leistner 1971) of South Africa (including Lesotho and Swaziland). QDS grid cells have been commonly used as operational geographic units (Crovello 1981) in studies exploring species richness patterns within south Africa (van Rensburg et al. 2002, van Rensburg et al. 2004, Richardson et al. 2005, Thuiller et al. 2006). Shortcomings have been noted in the use of QDS due to its geographic coarseness (Williams 2000, Moline and Linder 2006). However, apart from allowing comparisons to other studies mentioned, the GWR modelling approach used in this study requires a defined area based input unit (Fotheringham et al. 2002). Furthermore, using approximately equal area operational units should reduce the area effect on modelled relationships (Rosenzweig, 1995, and see results of van Rensburg et al. 2002 which show lack of underlying species-area effects when using approximately equal area QDS).

Species richness (number of species) was calculated for each QDS. Only QDS with ≥ 5 unique locality records were used to counter the problems of collector bias. Unlike in previous studies (O'Brien 1993, van Rensburg et al. 2002), QDS which included both land and sea were retained for analysis. The reasoning for this was (i) only $< 4\%$ of QDS showed $< 30\%$ of their area covered by land; (ii) the strength of area effects on comparisons between unequal area sized QDS is mostly likely marginal in comparison to the inherent problem of collector bias (Graham et al. 2004) and the strength of other environmental variables across the data set (see Hawkins and Porter 2003); (iii) the statistical robustness of applying land-area corrections to QDS richness scores are unclear (see Lennon et al. 2001); and (iv) South Africa has an extensive coast line and the exclusion of coastal QDS from analyses would hinder our understanding of richness processes within the important coastal biogeographic areas (see Endrödy-Younga 1978, and Mucina and Rutherford 2006). QDS extending across into neighbouring countries ($< 2\%$ of QDS in this study) were assumed to have richness scores equivalent to that found in the South African area component of the QDS (cf. van Rensburg et al. 2002).

Explanatory Variables Data Set

Environmental (Schulze 1997) and vegetation (Mucina and Rutherford 2006) themes were spatially joined in Arcmap 9.2 (ESRI 2006) to the compiled beetle point locality data set and a QDS grid overlay. For each QDS values were calculated for a number of *a priori* selected variables (abiotic and biotic). Variables were selected from those shown, from a range of studies (invoking respective hypothesis), to be

important in explaining regional richness patterns (Whittaker 1972, Currie 1991, Gaston 1992, O'Brien 1993, Cowling et al. 1997, Gaston 2000, Kerr et al. 2001, Lennon et al. 2001, Cumming 2002, van Rensburg et al. 2002, Hawkins et al. 2003, Hawkins and Porter 2003, Rodríguez et al. 2005, Ollerton et al. 2006). Furthermore, several other explanatory variables were selected specifically in the context of explaining monkey beetle richness patterns (Picker and Midgley 1996, Goldblatt and Manning 1998, Colville et al. 2002). Explanatory variables are shown in Table 1 – either with derivation and source data explained for variables specific to this study, or with respective references for source data and derivation for those variables commonly used in richness studies. The latter mentioned variables will not be further discussed in this methods section (see references cited in Table 1). However, variables used specifically in the context of hypothesising processes influencing monkey beetle richness will be discussed further.

Firstly, the obligate anthophilic lifestyle of almost all South African monkey beetles naturally suggests that host plant diversity should be hypothesised to be a good explanatory variable of beetle richness (Hawkins and Porter 2003, Ollerton et al. 2006). In this regard, host plant richness was extracted from the National Herbarium (PRE) Computerised Information (PRECIS) data base (Germishuizen and Meyer 2003, Richardson et al. 2005, Thuiller et al. 2006) – a data base comprising data for over 24 000 southern African plant taxa. From a handful of pollination studies (Picker and Midgley 1996, Goldblatt and Manning 1998, Steiner 1998, 1998, Goldblatt et al. 2001, Goldblatt et al. 2002, van Kleunen et al. 2007) and extensive field observations and collections (Colville unpublished data), six key plant families (see Table 1), which appear to contain a high percentage of their respective species acting as host plants for monkey beetles, were extracted from the PRECIS dataset for calculation of richness scores per QDS for each family separately, and for the sum of all species from the seven plant families. In addition to focussing specifically on host plant diversity, total flowering plant diversity per QDS was also extracted from PRECIS. Several species of monkey beetle are non-anthophilic, feeding on leaves and grasses, e.g. species of *Monochelus* (Péringuey 1902). Furthermore, other species from several genera (*Anisonyx*, *Lepithrix*, *Heterochelus*, and *Peritichia*), have been observed feeding on flowers of plant families not usually associated with commonly occurring monkey beetle pollination guilds, e.g. Restionaceae, Fabaceae, Selaginaceae, Ericaceae, Lamiaceae, Bruniaceae, and Neuradaceae (Colville unpublished data). Thus, to account for the full floral diversity utilised by monkey beetles, total plant diversity per QDS was also considered as an explanatory variable.

Secondly, a notable feature of monkey beetle diversity patterns is the high species compositional dissimilarity (species turnover or beta (β) diversity (Whittaker 1972) seen between communities (Péringuey 1902, Picker and Midgley 1996, Colville et al. 2002). High β diversity has been noted in floral diversity patterns, particularly within the winter-rainfall biomes (Cowling et al. 1989, Cowling 1990,

Simmons and Cowling 1996, Cowling et al. 1998, Cowling et al. 1999), the heartland of monkey beetle diversity within South Africa (see Chapter 1). This β diversity component has been shown to be an important determinant of regional plant richness (Cowling et al. 1989, Cowling et al. 1992) and has been hypothesised to be an important component influencing monkey beetle richness (Colville et al. 2002). In this regard, β diversity was calculated for both monkey beetle and plant occurrence data using Lennon et al.'s (2001) turnover index (β_{sim}) – an index which highlights compositional differences between a focal QDS and all its immediate QDS neighbours, whilst accounting for local richness gradients, which can inflate dissimilarity values between QDS (Lennon et al. 2001, see also van Rensburg et al. 2004). A β_{sim} value for plants and monkey beetles was calculated for each QDS (averaged across all pairwise comparisons with neighbouring QDS) using a program written in the programming language *Python* (version 2.3; www.python.org). These β_{sim} values were used as explanatory variables within the GWR model. To further investigate β diversity, local richness gradients based on Lennon et al.'s (2001) local richness gradients index β_g was calculated for both plant and monkey beetle occurrence data using a similar script written in the programming language *Python*. β_g is a measure of the proportional difference in richness between a focal QDS and all its neighbours. β_g has an upper limit of two (when the focal QDS or its neighbours have no species in common), and a lower limit of zero (identical richness between neighbours) (see Lennon et al. 2001 and van Rensburg et al. 2004).

MODEL DEVELOPMENT

Selection of Variables

In order to decrease the erroneous effects of colinearity within the regression models (Quinn and Keough 2003), all variables were correlated (Pearson's r) against all other variables creating a correlation matrix. Variables with Pearson's $r \geq 0.65$ were not considered for the analyses (see table 1) unless they were used as a surrogate for a range of co-correlated variables (Shi et al. 2006). This helped reduce the number of predictor variables considered and ensured independence of predictor variables (see equations for calculations of measures of precipitation in Schulze 1997 for lack of independence).

Spatial Non-Stationarity and Spatial Autocorrelation

In this study, relationships between regional monkey beetle species richness and selected explanatory variables at the local scale were modelled using geographically weighted regression (GWR) (Brunsdon et al. 1998, Fotheringham et al. 2002).

GWR allows the modelling of local spatial relationships within a regression framework by using the locational information for each observation. Thus, the model allows parameter estimates (slope and intercept) to vary in space. This feature of GWR permits one to account for, and explore the important concept of spatial non-stationarity (local variations) in relationships between the independent and dependent variables. Parameters of the model estimated by fitting the model to spatial data are specific to a given location, and thus, the relationship between variables differs at different locations (see Brundson et al. 1998, 2002, Fotheringham et al. 2002 for a detailed mathematical and theoretical description of GWR). This is in contrast to regression models which apply global parameter estimates across the geographic extent of a dataset. Global regression models can conceal the ecological processes been studied because they give an average picture of the relationships between explanatory and independent variables (Fotheringham et al. 2002, Foody 2004)

Recent findings have shown the importance of local spatial modelling techniques in accounting for spatial non-stationarity and spatial autocorrelation (Lennon 2000, Fotheringham et al. 2002, Diniz-Filho et al. 2003, Foody 2004, Jetz 2005, Wang et al. 2005, Bickford and Laffan 2006, Osborne et al. 2007). Accounting for spatial non-stationarity in regression models describing monkey beetle richness relationships across the highly heterogeneous South African landscape (see Mucina and Rutherford 2006) was thus considered essential. Several studies have highlighted the steep ecological gradients occurring within and across South Africa's biomes (Linder 1985, Cowling et al. 1989, Cowling 1990, Gaston et al. 2001, Cowling and Lombard 2002, van Rensburg et al. 2004, Thuiller et al. 2006) and at least one study has highlighted the importance of considering spatial structure of environmental explanatory variables across South Africa (van Rensburg et al. 2002). Some studies have focussed modelling richness relationships independently within biomes (Cowling et al. 1997, Thuiller et al. 2006). Although limitations in identifying ecological processes at this biogeographical scale are apparent - the degree of spatial non-stationarity within biomes appears to be high (Cowling et al. 1997, Cowling and Lombard 2002, Botes et al. 2006, Colville 2006, Thuiller et al. 2006, Botes et al. 2007), and as such, even at the finer scale of biome, models need to be more spatially sensitive.

GWR further shows its utility for spatial modelling in that it is effective in accounting for problems of spatial autocorrelation (Legendre 1993, Lennon 2000, Brundson et al. 2002, Fotheringham et al. 2002, Wang et al. 2005, Propastin et al. 2006, Cassemiro et al. 2007, Osborne et al. 2007, Propastin et al. 2007, Zhang et al. 2008). However, some concerns have been expressed with this statistical component of GWR (Leung et al. 2000, Jetz 2005, Austin 2007). Spatial autocorrelation was measured for explanatory variables and model residuals using Moran's *I* coefficient within the software Spatial Analysis in Macroecology (SAM v3.0) (Rangel et al. 2006) to determine if GWR accounted for spatial

autocorrelation within the beetle data set analysed herein. Under the null hypothesis of no spatial autocorrelation, Moran's I has an expected value close to zero; with positive and negative values indicating either positive or negative autocorrelation, respectively (Legendre and Legendre 1998). Spatial correlograms (Legendre and Legendre 1998) were plotted for each selected variable and for the GWR and OLS (see below) model residuals to check for patterns of spatial autocorrelation (Diniz-Filho et al. 2003, Wang et al. 2005, Dormann et al. 2007). The significance tests of Moran's I was calculated using Monte Carlo permutation tests (1000 randomisations). Significance levels were adjusted using progressive Bonferroni corrections (Legendre and Legendre 1998).

GWR model calculations were undertaken using the GWR 3.0 software available at <http://ncg.nuim.ie/ncg/GWR/software.htm> (see also Fotheringham et al. 2002). Estimated parameters from GWR are dependent on the choice of weighting function and especially bandwidth (Brunsdon et al. 1998, Foody 2004, Bickford and Laffan 2006). Following the procedures outlined in Fotheringham et al. (2002), a Gaussian model with an adaptive (bi-square) kernel type (spatial weighting function) was selected. The adaptive kernel function selects a certain number of nearest neighbours to adapt the spatial kernel to ensure a constant size of local samples. An adaptive kernel was used to try and ameliorate edge effects on the boundary of the study area, account for any spatial gaps in the data, and to maintain equal sample size where data points were not uniformly spaced. Selection of the kernel bandwidth was optimised through Akaike Information Criterion (AIC_c) minimisation (Quinn and Keough 2003). Finally, in order to test for spatial non-stationarity within local parameter estimates, a Monte Carlo approach (1000 randomisations) was used with the null hypothesis that the parameters do not vary over space.

A standard approach when using GWR is to test the applicability and strength of the GWR (locally variable / non-stationary) results in comparison to those of a global model (Fotheringham et al. 2002, Foody 2004, Wang et al. 2005, Osborne et al. 2007, Zhang et al. 2008). Thus, explanatory variables were further modelled using conventional ordinary least squares (OLS) in GWR 3.0 and in the statistical package STATISTICA 8.0 (StatSoft 2007). The relative improvement of the GWR model in comparisons to the OLS model was compared using an F -test within the GW 3.0 software. Models performance was also compared based on AIC_c (see below) and R^2 values, and on spatial correlograms of model residuals.

Model Selection and Performance

Variables retained after testing for colinearity were then included individually and in various combinations within the model. Akaike Information Criterion (AIC_c) was used for variable and model selection (Fotheringham et al. 2002). The lower the AIC_c value the better the model reflects reality

(Quinn and Keough 2003). A rule of thumb of at least a decrease of the AIC_c value by 3 was used (Fotheringham et al. 2002). Model selection followed five general steps; within each step and between steps various combinations of variables were tested:

- 1) Total plant diversity was considered the most parsimonious explanatory variable in that the vast majority of monkey beetles are anthophilic
- 2) Host plant families were tested (*sensu* Hawkins and Porter 2003) individually and in combination to see whether or not the relationship between beetle richness was particularly strong for certain plant families
- 3) Floral beta diversity was tested to determine whether or not plant diversity *per se*, or rather species turnover of plants was influencing richness patterns through increased speciation rates across steep floristic gradients
- 4) The influence of beetle species turnover on regional beetle diversity was explored
- 5) Environmental variables specifically targeted at monkey beetle biology were tested.

Mapping of Local Parameter Estimates from GWR Model

In order to effectively visualise, and to place within an ecological biogeographic context, spatial variation (or lack thereof) in local parameter estimates were mapped in Arcmap 9.2 (ESRI 2006). In conjunction with the local parameter estimates, local pseudo-*t* statistics (Fotheringham et al. 2002) were also displayed on maps (Mennis 2006, Wimberly et al. 2008). Pseudo-*t* statistics provide additional information about the variability of parameter estimates (non-stationarity). However, the calculation of pseudo-*t* statistics uses neighbouring spatial units repetitively, and as such, is normally not used for formal hypothesis testing (Fotheringham et al. 2002). Nonetheless, they generate useful insights into the spatial variability of explanatory variables used within the model.

RESULTS

VARIABLES USED IN MODELS

As was expected several of the explanatory variables were highly correlated with each other. Twenty two variables were retained for testing within the models and are shown in Table 1. Colinearity was seen between plant richness variables - the speciose family Asteraceae inter-correlated with total plant richness (PLR), monkey beetle host plant richness (MPLR), and Hyacinthaceae richness (Hycan). The speciose

Iridaceae was correlated with Proteaceae, Haemodoraceae, and MPLR. As such, Asteraceae and Iridaceae were used as separate plant variables and not in conjunction with MPLR or PLR.

Abiotic variables also showed colinearity - mean annual rainfall (MAR) was correlated with a number of the water-based explanatory variables (e.g., RCV, PEV, and PET), and thus was retained while its inter-correlated variables were excluded. MAR was also correlated with GRS and PRO, suggesting for this dataset that MAR was a good surrogate of water and energy variables. However, this assumption may not hold for all areas, such as for low-rainfall areas in the western parts of South Africa (see Cowling et al. 1997).

Table 1. Explanatory variables explored for use in GWR models at the QDS scale across South Africa. Grey highlighting indicates variables not used in the model due to high ($r > 0.65$) colinearity. Abbreviations as used throughout text. (See Cowling et al. (1997) for grouping of variables into different frequently invoked hypotheses explaining regional richness patterns).

Explanatory Variable	Abbreviation (units)	Derivation of data and/or reference(s) for derivation and source data of variables - [examples of South African species richness studies using similar variables]
Topographic diversity	TDCV (%)	Calculated for each QDS derived from 90 m SRTM Digital Elevation Model (DEM) (van Rensburg et al. 2002). Cowling ^a et al., 1997- [(van Rensburg et al. 2004, Richardson et al. 2005)]
Length of rainfall gradient	RAR (mm)	Schulze, 1997, Cowling ^a et al., 1997
Length of temperature gradient	RWT (°C)	Schulze, 1997, Cowling ^a et al., 1997 – [(van Rensburg et al. 2002, Thuiller et al. 2006)]
No. of Vegetation types	Veg	Mucina and Rutherford, 2006 – [(van Rensburg et al. 2002, Botes et al. 2007)]
Vegetation type evenness cover	VegE (%)	van Rensburg ^a et al., 2002
Vegetation habitat heterogeneity	Hetero	Mucina and Rutherford, 2006. Calculated for each QDS. Hetero = no. of vegetation types X no. of bioregions X no. of biomes. Multiplicative approach used to maximize the heterogeneity score by increasing the contribution of higher hierarchical habitat units, such as biomes and bioregions. Furthermore, this approach highlights areas of ecotonal diversity. Bioregions defined as in Chapter 1. Scores for Albany Thicket, Indian Ocean Coastal Belt negatively biased due to lack of bioregional categories for these biomes.
Geology	Geo	Number of different geomorphic types (ENPAT 2001) found within a QDS
Geology cover	GeoE (%)	Evenness covers of geomorphic types within a QDS. Calculated as for VegE
Mean annual rainfall	MAR (mm)	Schulze, 1997, Cowling ^a et al., 1997 – [(O'Brien 1993, van Rensburg et al. 2002)]
Summer temperature regime	MST (°C)	Schulze, 1997, Cowling ^a et al., 1997 – [(van Rensburg et al. 2002, Richardson et al. 2005, Botes et al. 2007)]
Winter temperature regime	MWT (°C)	Schulze, 1997, Cowling ^a et al., 1997 – [(Richardson et al. 2005)]
Mean absolute monthly minimum temperatures averaged over the year	Min (°C)	Schulze, 1997 – [(van Rensburg et al. 2002, Richardson et al. 2005, Botes et al. 2007)](Stuckenber 1969)
Mean absolute monthly maximum temperatures averaged over the year	Max (°C)	Schulze, 1997 –[(van Rensburg et al. 2002)]
Effective Temperature	ETemp (°C)	Bailey, 1960 – [(Richardson et al. 2005)]
July solar radiation	SRAD (MJ m ⁻² yr ⁻¹)	Schulze, 1997 – [(van Rensburg et al. 2002)]
July soil water stress (percent days under stress)	H ₂ O (%)	Schulze, 1997– [(Thuiller et al. 2006)]
Potential evaporation	PEV (mm)	Schulze, 1997, Cowling ^a et al., 1997 – [(Richardson et al. 2005)]
Primary production	PRO (t ha ⁻¹ yr ⁻¹)	Schulze, 1997, Cowling ^a et al., 1997 –[(Thuiller et al. 2006)]
Duration of growing season	GRS (days)	Schulze, 1997, Cowling ^a et al., 1997
Rainfall concentration	RCO (%)	Schulze, 1997, Cowling ^a et al., 1997
Annual Temperature range	RAS (°C)	Schulze, 1997, Cowling ^a et al., 1997
Rainfall reliability	RCV (%)	Schulze, 1997, Cowling ^a et al., 1997
Total plant richness	PLR	Germishuizen and Meyer, 2003 – PRECIS data. Number of flowering plant species per QDS
Monkey beetle host plant richness	MPLR	Species richness per QDS for seven plant families identified as containing a high percentage of their species as monkey beetle host plants. Species richness calculated as the sum of the number of species for each family in each QDS (see rows below for plant families).
Asteraceae	Ast	Number of species per QDS (PRECIS)
Iridaceae	Irid	Number of species per QDS (PRECIS)
Hypoxidaceae	Hypox	Number of species per QDS (PRECIS)
Hyacinthaceae	Hycan	Number of species per QDS (PRECIS)
Haemodoraceae	Haem	Number of species per QDS (PRECIS)
Proteaceae	Prot	Number of species per QDS (PRECIS)
Mesembs	Mesemb	Sum of number of species of Mesembryanthemaceae and Ruschoidea per QDS (PRECIS)
Host plant Beta diversity	Pβ _{sim}	Lennon et al., 2001
Monkey beetle Beta diversity	Bβ _{sim}	Lennon et al., 2001

^a In addition to showing variable derivation and/or source data, the reference further acts as an example for the use of a variable in a species richness study within South Africa.

SELECTED MODELS

The best GWR model determined from AIC_c is shown in Table 2 (see Appendix 2 for AIC_c and R^2 values for models with single independent variable. Monkey beetle host plant richness (MPLR) recorded a lower AIC_c value than for total plant richness (PLR) ($AIC_c = 207.56$ ($R^2 = 0.61$) vs. $AIC_c = 211.08$ ($R^2 = 0.54$)). MPLR further performed better than the three plant families tested individually (family Iridaceae the best of the three) and in various combinations. Thus, MPLR was retained as the best plant diversity explanatory variable. Plant beta diversity showed one of the highest AIC_c values ($AIC_c = 274.51$, $R^2 = 0.53$) of all independent variables. In contrast, beetle beta diversity showed the second lowest AIC_c value ($AIC_c = 208.45$, $R^2 = 0.64$) and further showed low AIC_c values with a combination of other variables. Although showing high AIC_c values in comparison to some of the other variables, rainfall gradients (RAR), summer temperature (MST), and vegetation habitat heterogeneity (Hetero) in combination gave the lowest values.

Table 2. AIC_c and R^2 values for best selected combination of explanatory variables for GWR and OLS models. F -test results show a significant improvement of GWR model in predicting beetle richness over the OLS model. (DF = degrees of freedom; see Table 1 for full variable names and descriptions).

Data Set	Selected Model	Regression	AIC_c	R^2	DF	F	P
QDS	MPLR, $B\beta_{sim}$, Hetero, RAR, MST	OLS ^E	292.52	0.31	6	7.96	<0.001
		GWR ^B	147.93	0.66	283.11		

^EOLS model equation: Log_{10} Monkey beetle richness = $-0.469 + 0.002\text{MPLR} - 0.426B\beta_{sim} + 0.0001\text{Hetero} + 0.047\text{MST} + 0.001\text{RAR}$.

^BBandwidth = 54 QDS (16% of total QDS); selected through AIC_c minimisation (see methods).

After running a number of different combinations, the five explanatory variables of monkey beetle host plant richness (MPLR), monkey beetle beta diversity ($M\beta_{sim}$), habitat heterogeneity (Hetero), length of rainfall gradient (RAR), and summer temperature regime (MST) gave the lowest AIC_c and highest R^2 value. Mean annual rainfall (MAR) gave similar results to RAR, but had a slightly higher AIC_c value (269.92 vs. 267.19) and lower R^2 (0.44 vs. 0.57) value.

As can be seen from Table 2, GWR gave better model performance than the equivalent OLS model, with a substantially lower AIC_c value and higher R^2 , explaining 66% of the variance seen in beetle richness. The superiority of the GWR model was confirmed with the F -test, which showed a significant improvement over the OLS model. The GWR model also showed better predictive abilities, particularly at low beetle richness scores (compare Fig. 1 (a) and (b)).



Figure 1. Scatter plot between measured monkey beetle richness and values predicted by (a) GWR and (b) OLS models. (Note: Axes are \log_{10} transformed values. The independent variable of beetle richness was \log_{10} transformed to account for right skewness of the data (Sokal and Rohlf 1995). The standard deviation of OLS model residuals was 2.3 beetle species; and for GWR the standard deviation was 1.8 beetle species).

Furthermore, the GWR model for this study was able to account for spatial autocorrelation within model residuals (compare Fig. 2 (a) and (b)). The GWR model showed no significant spatial autocorrelation under the null hypothesis of Moran's I values either showing no positive or no negative spatial autocorrelation. In contrast the OLS model showed significant spatial autocorrelation across distance classes. (Also see Appendix 3 for spatial correlograms for all variables).

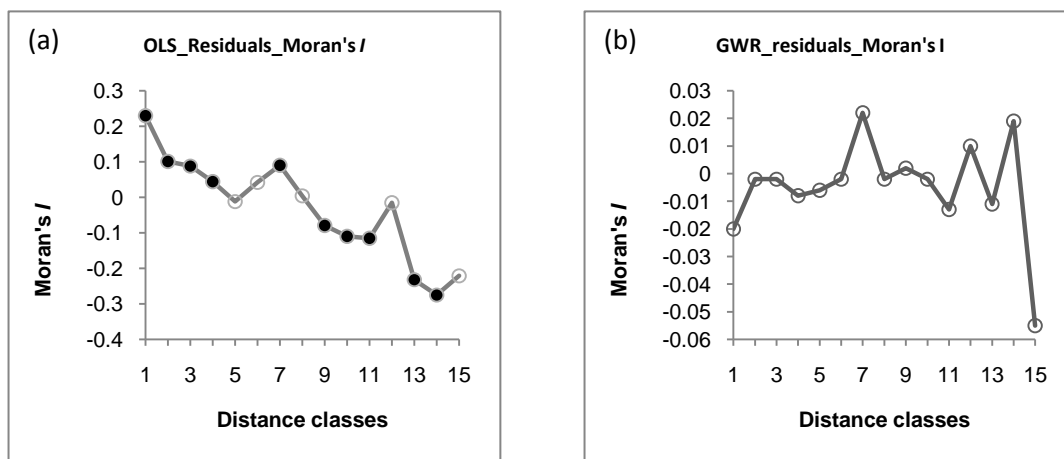


Figure 2. Spatial correlograms for (a) OLS model residuals and (b) GWR model residuals. Dark circles: Moran's I values that remain significant after progressive Bonferroni correction ($P < 0.05$); clear circles represent non-significant values. (Note difference in scale of y-axis between graphs).

PRESENCE OF SPATIAL NON-STATIONARITY

The informal test of spatial non-stationarity whereby the interquartile range is greater than ± 1 standard deviations of the respective global estimate suggests that spatial non-stationarity exists within the parameters under study herein (Table 3; and see Fotheringham et al 2002 and Wang et al. 2005). The presence of significant spatial non-stationarity was confirmed by a Monte Carlo significance test (1000 randomisations) for spatial non-stationarity (Brunsdon et al. 1998, Fotheringham et al. 2002) in five of the six parameters (Table 4). Only the single variable of habitat heterogeneity (Hetero; see Table 1) showed a stationary relationship (highlighted in grey) across the geographical extent of the data (although see Fig. 3 (d)).

Table 3. Descriptive statistics for parameter estimates for OLS and GWR models.

Regression Model	Statistics	Intercept	RAR	MST	HETERO	MPLR	$B\beta_{sim}$
OLS ^S	Parameter estimates	0.0339	0.0000	0.0467	0.0007	0.0020	-0.4263
	Standard error	0.2669	0.0001	0.0086	0.0003	0.0002	0.1523
	<i>t</i>	-1.7562	-0.2899	5.4451	2.2808	8.8322	-2.7994
	<i>P</i> value	0.0800	0.7721	0.0000	0.0232	0.0000	0.0054
	-95% Confidence Interval	-0.9938	-0.0001	0.0298	0.0001	0.0016	-0.7260
	+95% Confidence Interval	0.0564	0.0001	0.0636	0.0013	0.0025	-0.1267
GWR ^G	Mean	7.6577	0.0004	0.0247	0.0003	0.0014	-1.2766
	Minimum	2.1033	-0.0003	-0.1219	-0.0028	0.0003	-3.5725
	25% quartile	5.7756	0.0000	0.0042	-0.0005	0.0007	-2.2778
	Median	5.4739	0.0001	0.0345	0.0002	0.0010	-1.1337
	75% quartile	30.5140	0.0002	0.0707	0.0009	0.0017	-0.2697
	Maximum	787.0832	0.0024	0.1174	0.0025	0.0033	0.6442

^S Statistics for OLS calculated in STATISTICA 8.0; ^G GWR statistics from GWR 3.0. Software.

Table 4. Monte Carlo significance test for spatial variability of GWR model parameters. Grey highlighting indicates single parameter showing a mostly stationary relationship. (See Table 1 for explanations of variables).

Parameter	<i>P</i> value
Intercept	< 0.0001
MPLR	<0.05
$B\beta_{sim}$	< 0.0001
HETERO	0.29
RAR	< 0.0001
MST	< 0.0001

MAPS OF VARIATION OF LOCAL PARAMETER ESTIMATES FROM GWR MODEL

The spatial variation in local parameter estimates are shown in the maps (a) – (f) of Figure 3. It can be clearly seen that across the geographic extent of the data, relationships between independent variables and beetle richness varies spatially. Furthermore, the strength and direction of these relationships (R^2 , slopes, and pseudo- t values) varies spatially. Areas of interest showing variable model parameter estimates are discussed in terms of biogeographical units: phytogeographic centres (Cape Floristic Region (CFR) (Goldblatt and Manning 2002); Succulent Karoo and Namaqualand (Hilton-Taylor 1994)) and/or ecological areas of biomes (Mucina and Rutherford 2006).

Locally estimated R^2 values

Figure 3a shows the spatial variation in the locally estimated R^2 values derived from GWR analysis. Local coefficients of determination had a median of 0.75 and a range of 0.64 to 0.80. The model explained the highest amounts of variance in beetle richness for the North Western (NW phytogeographic centre) sections of the CFR, although including some areas of southern Namaqualand, e.g., Vanrhynsdorp phytogeographic centre. A clear northern gradient from this area of high R^2 was seen with decreasing amounts of variances explained by the model. The model only explains medium to low amounts of variance in beetle richness in the arid northern section of Namaqualand (Gariep Centre), while central Namaqualand shows medium to high amounts of variance explained. The GWR model explained moderately high amounts of variance seen in beetle richness (R^2 values between 0.59-0.67) for South Western (SW) sections of the CFR. The eastern regions of South Africa showed low amounts of variance explained by the model, with local R^2 ranging from 0.29 to 0.48.

Monkey beetle host plant richness (MPLR)

The parameter estimate of monkey beetle host plant diversity showed a positive relationship with beetle richness across the geographic extent of the data (Fig. 3b) and had a median of 0.0010 with a range of 0.0007 to 0.0017. Particularly strong positive relationships between host plant diversity and beetle richness were seen for the arid northern areas of Namaqualand, eastern areas of the CFR, and Albany Thicket. Strong relationships were also seen for most other areas of the Succulent Karoo (Namaqualand and Vanrhynsdorp Centre), and northern sections of the South Western (SW) sections of the CFR. The northern sections of Grassland and Savanna (Johannesburg/Pretoria) also showed a reasonably strong relationship. In contrast to this small area, the majority of the eastern distribution of monkey beetles showed a weak relationship with plant diversity. Interestingly, the Cape Peninsula, Stellenbosch, and areas of the Worcester-Robertson Karoo also showed weak relationships between beetle richness and

plant richness, even though these areas are known to be particularly rich in beetles and monkey beetle host plants.

Monkey beetle species turnover (β_{sim})

Beetle species turnover showed mostly a negative relationship with beetle richness across the geographic extent of the data (Fig. 3c) and had a median of -1.1337 with a range of -2.2778 to -0.2697. This was particularly strong in the areas of highest beetle richness, within the SW and NW sections of the CFR and southern sections of Namaqualand. The central and northern areas of Namaqualand showed a weakly positive relationship with low pseudo-*t* values, indicating that turnover is possibly only weakly influencing beetle richness in these beetle rich areas. Similar weak relationships are seen for the majority of the eastern areas of beetle distribution, although these areas are generally depauperate in species, unlike the Namaqualand areas. However, eastern areas around Durban and extending towards the Drakensberg Mountains showed quite strong negative relationships with beetle richness.

Vegetation habitat heterogeneity (Hetero)

The parameter estimates for habitat heterogeneity (Hetero) showed the highest degree of stationarity (Fig. 3d) and had a median of 0.0002 with a range of -0.0005 to 0.0009. Most areas within the geographic extent of the data showed a weak relationship with low pseudo-*t* values. However, areas which are transitional between biomes (and phytogeographic centres – see Hilton-Taylor 1994 and Goldblatt and Manning 2002) showed significant positive relationships with habitat heterogeneity, e.g., Namaqualand-Bushmanland transitional zone, CFR Langeberg – Karoo Mountain transitional zone.

Rainfall gradient (RAR)

Length of rainfall gradient (RAR) showed fine-grained levels of spatial non-stationarity across the geographic extent of the data, with both positive and negative relationships being recorded (Fig. 3e). Slope values for RAR had a median of 0.0001 with a range of 0.0000 to 0.0002. The winter and all year round rainfall areas showed positive relationships, with Namaqualand showing the strongest positive relationship with this parameter estimate. Other areas showing a positive significant relationship (based on pseudo-*t* values) were the southern sections of the southwestern CFR. The eastern areas around Durban, Drakensberg Mountains, and northern Savanna areas showed weak positive relationships. Negative relationships were seen for the Albany Thicket (particularly areas around Grahamstown and Somerset East) and for small areas extending from the tropical eastern coastal regions inland towards Pretoria.

Summer temperatures (MST)

Mean summer temperature (MST) was also seen to be a highly non-stationary parameter with both positive and negative relationship seen (Fig. 3f). MST parameter had a median of 0.0345 with a range of 0.0042 to 0.0707. A strong negative relationship was seen for northern Namaqualand, while weaker negative relationships were seen at its southern boundary with the CFR. A clear switch is seen at this boundary, with the CFR areas showing a positive relationship between beetle richness and MST. A particularly strong relationship is seen for the southern areas of the SW and Agulhas Plain (AP). Other areas with positive (although weak) relationships include the eastern areas around Durban and extending towards the Drakensberg Mountains, and northwards including the grassland and savanna areas. Three other areas showed negative relationships, that of the areas around Johannesburg and Pretoria, the tropical areas north of Durban, and parts of the Transkei.

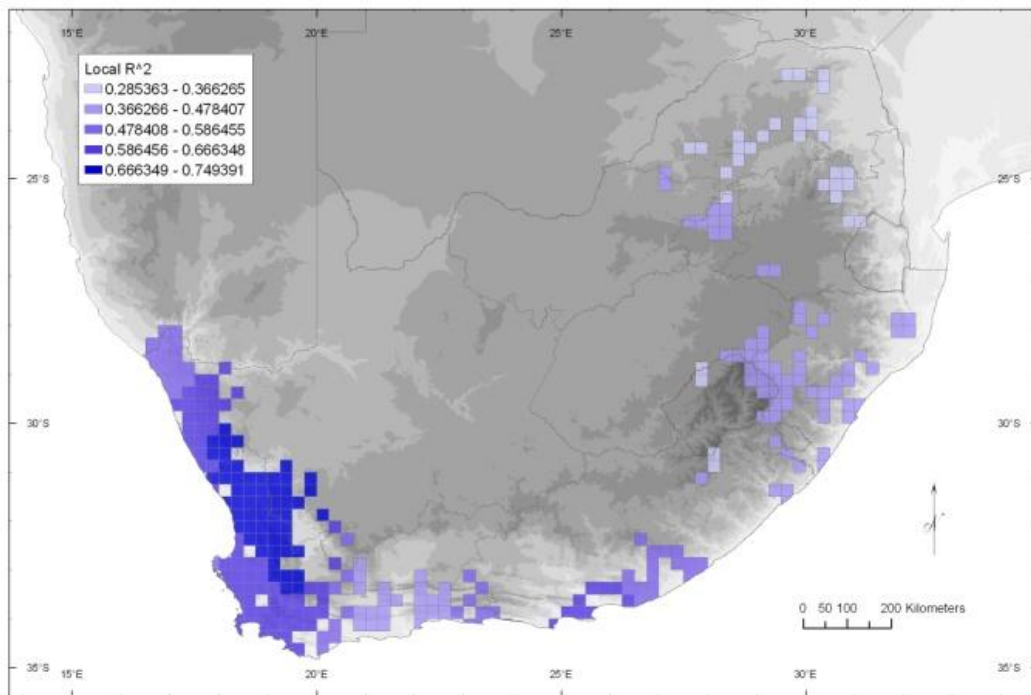


Figure 3a. Locally estimated R^2 values from GWR model.

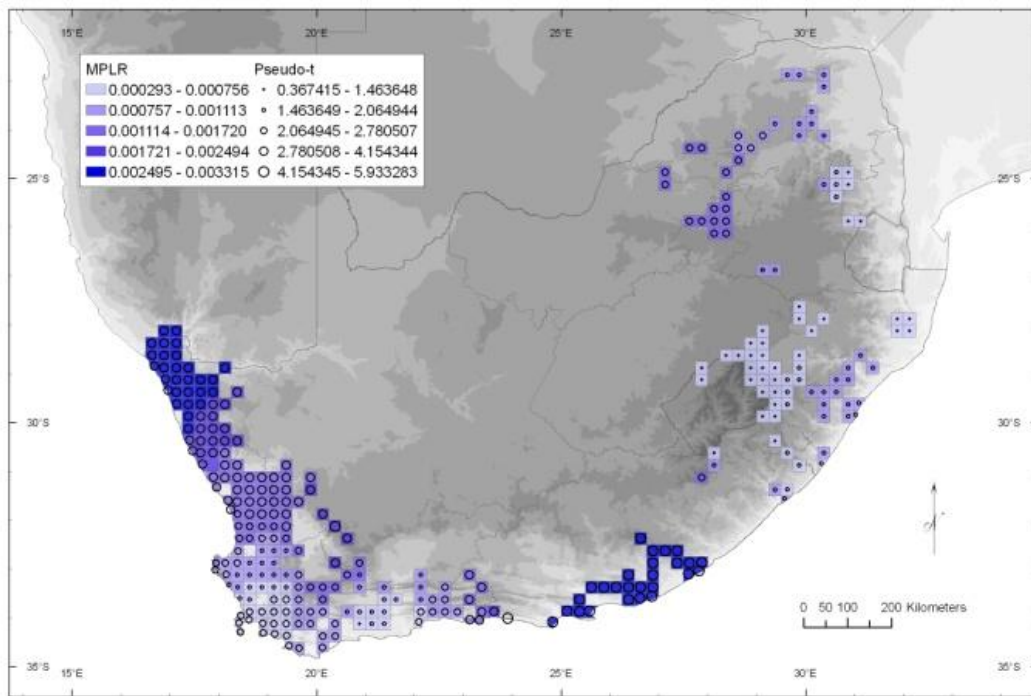


Figure 3b. Model parameter estimates (slope) derived from data for plant richness (MPLR). Pseudo- t values superimposed on slope maps to highlight variation in explanatory strength of variables; larger dots (for positive relationships) or large squares (for negative relationships) correspond to stronger pseudo- t values.

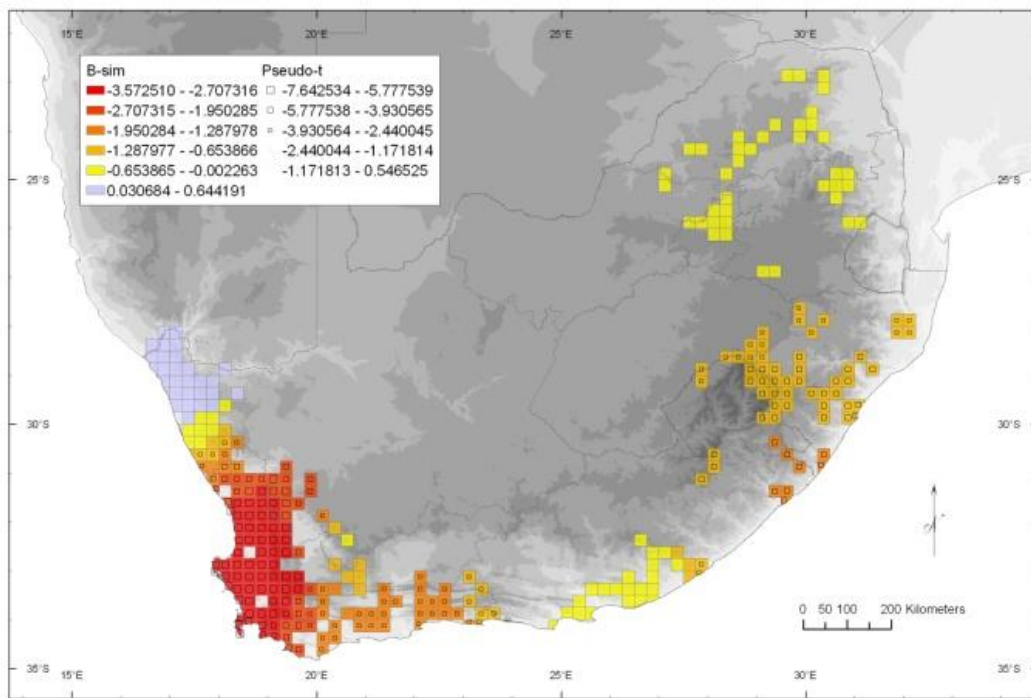


Figure 3c. Model parameter estimates (slope) derived from data for beetle turnover (β_{sim}). Pseudo- t values superimposed on slope maps to highlight variation in explanatory strength of variables; larger dots (for positive relationships) or large squares (for negative relationships) correspond to stronger pseudo- t values.

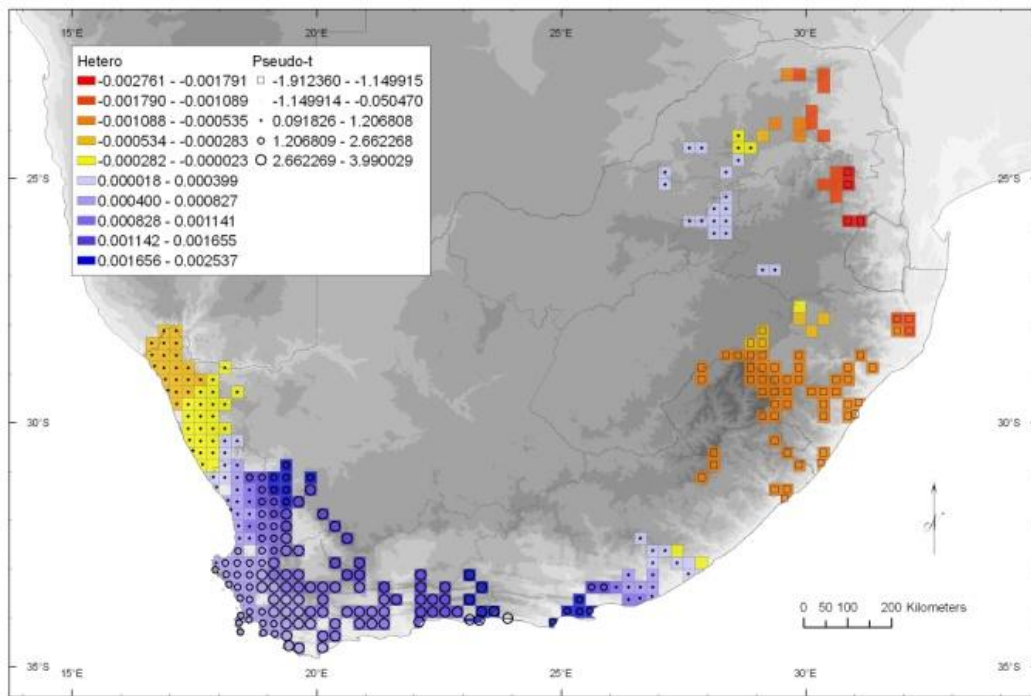


Figure 3d. Model parameter estimates (slope) derived from data for habitat heterogeneity (Hetero). Pseudo-*t* values superimposed on slope maps to highlight variation in explanatory strength of variables; larger dots (for positive relationships) or large squares (for negative relationships) correspond to stronger pseudo-*t* values.

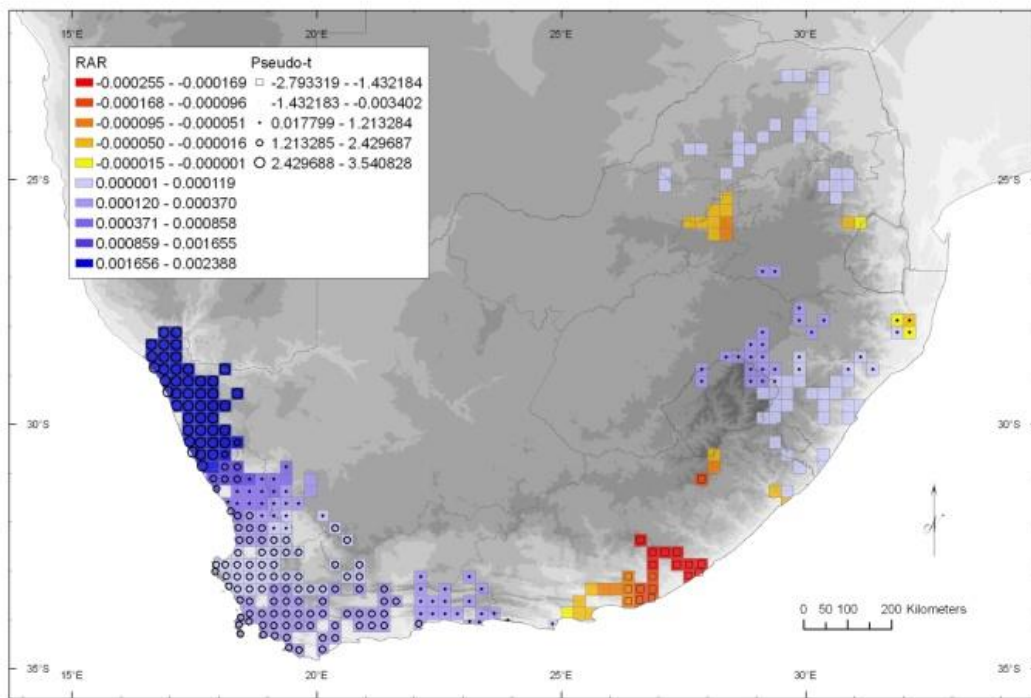


Figure 3e. Model parameter estimates (slope) derived from data for rainfall gradient (RAR). Pseudo-*t* values superimposed on slope maps to highlight variation in explanatory strength of variables; larger dots (for positive relationships) or large squares (for negative relationships) correspond to stronger pseudo-*t* values.

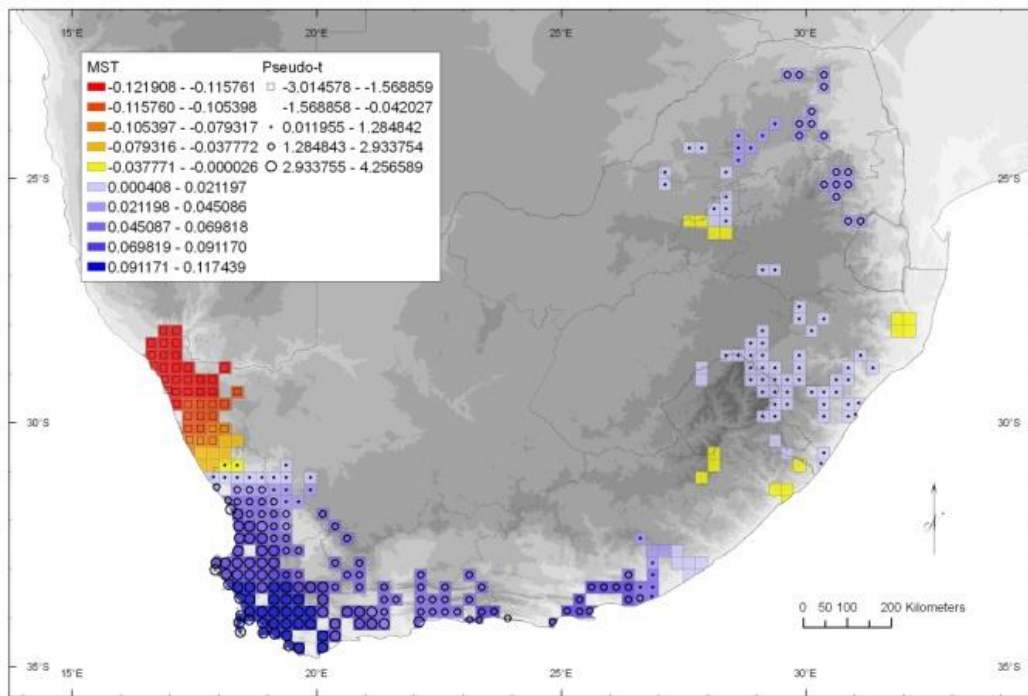


Figure 3f. Model parameter estimates (slope) derived from data for summer temperature (MST). Pseudo-*t* values superimposed on slope maps to highlight variation in explanatory strength of variables; larger dots (for positive relationships) or large squares (for negative relationships) correspond to stronger pseudo-*t* values.

DISCUSSION

JUSTIFICATION FOR USING A SPATIALLY WEIGHTED REGRESSION TECHNIQUE

GWR revealed five explanatory variables (host plant richness, beetle species turnover, vegetation habitat heterogeneity, length of rainfall gradient, and summer temperature) as best describing regional monkey beetle richness across South Africa. The GWR model ranked the strength of the relationships between beetle richness and these explanatory variables and revealed the geography of the relationships. It further showed that the variables explaining richness varied geographically (strong spatial non-stationarity), and are fundamentally different between the winter rainfall areas (*sensu lato*) and the summer rainfall areas. The same pattern is held for plants (see Cowling et al. 1997, Thuiller et al. 2006).

In addition, the GWR model was a better model in comparison to its Global equivalent in explaining variances in beetle richness patterns (lower AIC_c and higher R^2) highlighting spatial differences between beetle richness and explanatory variables, and it accounted for the common problem in spatial data sets of spatial autocorrelation. The results of this study are in accordance with several other studies (Lennon

2000, Fotheringham et al. 2002, Diniz-Filho et al. 2003, Foody 2004, Jetz 2005, Wang et al. 2005, Bickford and Laffan 2006, Osborne et al. 2007) that show that use of a regression technique that allows local parameters (slope, R^2) to vary in space is justified.

The most obvious broad pattern seen in this study was the predominance of species richness within the western, winter rainfall regions of South Africa. Monkey beetles follow the regional pattern highlighted for plant richness by Cowling et al. (1997) and reinforced by Thuiller et al. (2006), of an extraordinary high concentration of species within areas of generally low-moisture and low –energy. For plants, within these winter rainfall areas periods of growth occur during the cool winter months (Pierce 1984, Cowling et al. 1999). In contrast, summer rainfall areas have warm season (summer) growing periods (Schulze 1997). Insects within winter rainfall areas appear to mirror the growth phases of plants, especially hemimetabolous insect assemblages (e.g. Orthoptera), with egg hatching and nymphal stages (cf. growth phase in plants) coinciding with the new winter growth of plants (Picker et al. 2002). Both phytophagous and predacious insects show emergence in the cool winter months – juvenile phytophagous insects feed on the new plant growth and nymphal predators feed on the phytophagous juveniles (pers. obs.).

For both insects and plants, this pattern of high diversity in low-moisture and low –energy environment is mostly in contrast to that of other studies (Wright et al. 1993, Kerr and Packer 1999, Kerr et al. 2001). However, at least one other megadiverse group of pollinating insect (bees) matches this pattern of highest diversity in warm, seasonally dry environments – bee species hotspots are known from Israel, south western United States, and the Sonora Desert (Buchmann and Nabhan 1997). Bees also show high richness within the arid and semi-arid western regions of South Africa (Eardley 1989, Kuhlmann 2005), as do several other insect groups (see Chapter 1). This pattern of concentrations of species within areas of low energy and low water, is in contrast to the majority of other world habitats, and further highlights the global biotic uniqueness of the Cape regions of South Africa.

The bulk of the discussion that follows will be focused on the ecological interpretation of the spatial non-stationarity in parameter estimates seen for the five selected variables within the best performing GWR model. Furthermore, the absence of certain variables within the final model will also be placed in an ecological context.

EXPLANATORY VARIABLES AND THEIR ASSOCIATED SPATIAL VARIABILITY

Three of the five variables used in the final model are broadly related to commonly evoked hypotheses used in explaining regional richness patterns (Currie 1991, Cowling et al. 1997). The variables of length

of rainfall gradient (RAR) and habitat heterogeneity (Hetero) fall within the environmental spatial heterogeneity hypothesis. Mean of daily maximum summer temperature (MST) is linked to the favourable/energy hypothesis and host plant richness has been explored as a measure of resource diversity (Wright et al. 1993, Kerr and Packer 1999, Hawkins and Porter 2003).

Despite its obvious importance as a component of regional richness, beta diversity appears to have been infrequently used in regional richness studies (Kerr et al. 2007). Beta diversity relates to both ecological theory and speciation, in that it reflects areas of limited gene flow and steep ecological gradients (Linder 1985) and high habitat diversity (Shmida and Wilson 1985); thus, reflecting a diverse array of evolutionary processes, such as habitat specialisation, dispersal abilities, and speciation. Spatially limited gene flow and steep ecological gradients have been shown as important drivers of plant speciation in the winter rainfall regions (Linder 2005, Latimer et al. 2005).

PLANT RICHNESS AS A PREDICTOR OF MONKEY BEETLE RICHNESS

In contrast to other studies using a range of environmental variables (Kerr and Packer 1999, Kerr et al. 2001, Hawkins and Porter 2003) in explaining insect richness patterns, plant richness was recorded to be the strongest predictor of monkey beetle richness. This trend was seen at several plant taxonomic levels with total plant diversity and host plant diversity the best predictors of beetle richness, although the latter variable was strongest. Two other studies also have found positive relationships between fynbos species richness and insect richness (Wright and Samways 1998, Proches and Cowling 2006), although their respective investigations of influences from other environmental variables were limited. The relationship appears to be direct and causal with substantial increases in AIC_c (>50) values when host plant richness was excluded in all tested model combinations.

The strength of host plant richness as a predictor variable showed high spatial non-stationarity across the geographic extent of the data. Interestingly, within some areas of the beetle and plant rich western biomes, host plant richness did not project significant influence on beetle richness. South and south eastern areas of the CFR showed such a pattern. These areas harbour high numbers of plant species (Goldblatt and Manning 2002, Helme and Trinder-Smith 2006, Thuiller et al. 2006) and monkey beetles (Chapter 1), and as such, a positive relationship would be expected. However, lower numbers of species of annuals and geophytes - the main floristic resource component for most monkey beetles, have been recorded from more eastern areas of the CFR (Goldblatt and Manning 2002), effectively de-coupling the relationship between plant and beetle richness.

In terms of monkey beetle richness, these South and south eastern areas of the CFR appear to be influenced more by environmental heterogeneity and summer temperatures (see below). Similar findings in terms of environmental heterogeneity have been shown for plants (Cowling et al. 1997, Thuiller et al. 2006). Furthermore, the mountainous areas of these sections of the CFR are known as refugia for stenothermic paleoendemic invertebrate taxa, whose distribution patterns are determined by strict climatic conditions (Stuckenberg 1962, 1969). The high numbers of species from these phylogenetically unique groups are a consequence of the high topographic diversity inducing high geographic speciation (Stuckenberg 1962, Endrödy-Younga 1988, Wishart and Day 2002, Prendini 2005). A significant, but weak ($R^2 < 3\%$) relationship was found between numbers of Cape Peninsula invertebrate endemics and plant richness (Picker and Samways 1996), highlighting the independence of relic taxa on floristic resource diversity. Several relictual monkey beetle genera (Péringuey 1902) are found within the mountainous areas of the southern CFR. In these cases, high topographic diversity, associated with steep climatic gradients and the presence of relictual taxa appear to possibly over-ride plant diversity as the main drivers of beetle species richness.

In contrast, in the more dry/xeric fynbos sections of the CFR, and semi-arid to arid reaches of the Succulent Karoo, host plant richness appears to be a significantly influential predictor of beetle richness. Within these seasonally arid environments, adult monkey beetle life history requirements are intricately connected with mass spring flowering displays. Male and female beetles feed on pollen, nectar, and floral ovaries (Picker and Midgley 1996). Moreover, beetles use bowl-shaped flowers as platforms for mating and male-male combat (Chapter 5), especially species of Mesembs (Aizoaceae), Asteraceae, and Iridaceae. Several broad feeding guild strategies have been recorded indicating the adaptive responses by beetles in response to this abundant and diverse feeding resource (Picker and Midgley 1996, Goldblatt and Manning 1998, van Kleunen et al. 2007). Furthermore, this floristic resource appears to be quite predictable, although of short duration, with high predictability recorded in annual winter rainfall events (Cowling et al. 1999). In contrast to adult beetles, larvae appear to be broad generalist feeders (Colville unpublished data), similar to many other scarab larvae, which live in the soil feeding off small particles of organic matter. Thus, the degree of both feeding and mating specialisation in adult beetles revolving around flowers suggests that beetles have responded directly to floristic resources. Whether the beetles have responded in terms of plant species richness *per se*, or rather, in terms of high abundance of bowl-shaped flowers is unclear. A high number of plant species does not necessarily indicate a high resource niche (many bowl-shaped flowers), as a large number of plant taxa within these areas are not utilised by beetle species.

A similar pattern of high host plant richness influencing beetle richness was seen for the Albany Thicket, and can be explained in terms of the availability of bowl shaped floristic resources. Diverse areas of monkey beetle species are located within the arid Succulent Karoo regions, with some species showing range distributions extending from Namaqualand, through the Karoo regions and into the Albany Thicket (Chapter 2). Furthermore, many of these species resemble Namaqualand species in their morphology and behaviour, suggesting that their reliance on bowl shaped flowers is mirrored in areas of the Albany Thicket which have high numbers of Mesemb flowers (see Gess 1992), as seen in, and utilised extensively by species in the Albany Thicket and areas of Namaqualand. Thus, the importance of bowl-shaped floristic resources for Succulent Karoo derivative species found within the Albany Thicket is possibly reflected in the strong predictive value of host plant richness recorded for thicket areas.

The weak influence of host plant richness on beetle richness patterns seen for the north eastern sections of monkey beetle distribution patterns is expected, and relates to climatic extremes as well as the relictual nature of the beetle fauna. Beetle richness within these areas is generally low (Chapter 1, 2) and is generally reflective of genera which show East African affiliations, suggesting that they are of tropical origin. Cowling et al. (1997) and Thuiller et al. (2006) both showed that richness of floral regions of tropical origin in South Africa are mostly influenced by climatic variables (energy and water). The highest known number of monkey beetle species that feed on non-floral components of plants (leaves) is located in these areas, suggesting that not all beetles found here are reliant on seasonal occurrences of disc flowers for feeding and mating, again decoupling the relationship between plant and beetle richness. The beetle rich communities of the Drakensberg Mountains show a strong element of relictual monkey beetle species, which show disjunctions with montane fynbos Cape species (Andreae 1965). The Drakensberg is known to house a number of paleoendemic taxa (Stuckenberg 1962). As mentioned above, relictual taxa are strongly influenced by strict climatic variables, so the reduction in the explanatory power of plant richness as a predictor of beetle richness is expected.

PLANT AND BEETLE TURNOVER

A surprising finding of this study was the extraordinary high levels of species turnover (beta diversity) for both beetles and plants, and the relationship between these two variables and beetle richness. Climate, environmental heterogeneity and plant variables all show significant relationships with beetle turnover (see Appendix 4), and climatic variables appear to be of primary importance for beetle turnover (see van Rensburg et al. 2004 for contrasting finding for birds).

Beetle turnover and richness

Beetle species turnover had a mostly strongly negative influence on beetle richness, with areas of high richness showing lower turnover. A similar finding was recorded by Lennon et al. (2001) for beta diversity and richness in birds, however, the relationship weakened with increasing scale, with non-significant relationships recorded above 10 km grid scales. Furthermore, Lennon et al. (2001) indicate that at coarse scales (geographic ranges of species confined within a grid) a positive relationship should be seen between turnover and richness. This relationship makes intuitive sense, since one might expect high turnover of species to be associated with low local richness, but that this relationship would be reversed when overwhelmed by the effect of increasing area on species richness. Thus, the scale of observation is a critical factor when exploring the relationship between richness and turnover.

At the operational geographic unit scale of a quarter degree (*c* 25 km x 25km) grid cell, used in the current study, turnover was for most areas significantly negatively associated with richness. Thus, my QDS scale of analysis used here may be small enough to avoid the overwhelming effect of species area. However, a graduated pattern of the influence of beetle turn over on beetle richness is noticeable (Fig. 3c) with a weakly positive relationship seen for northern Namaqualand, grading into a stronger negative relationship in southern Namaqualand and northern CFR, and an even stronger negative relationship within NW and SW parts of the CFR. The eastern sections of the CFR show similar negative influences as seen for the northern sections of the NW CFR. These spatial differences in the relationship between beetle turnover and beetle richness are largely congruent with phyto and zoogeographic centres (see Chapter 2). Thus, comparing influences of species turnover on richness within biogeographic centres may reveal clearer patterns of the relationship between species turnover and richness (see also Cowling et al. 1997). These centres also house large numbers of endemics and high proportions of species' ranges (see Chapter 2), and thus, as suggested by Lennon et al. (2001), using quadrature scales which capture high proportions of species ranges would possibly reveal positive species turnover relationships with richness for at least some areas.

An alternative approach to teasing out the influence of turnover on richness may be considered. At the QDS scale, high turnover ($\beta_{sim} = 0.79 (\pm 0.1)$, i.e. on average a QDS only shares 20% of species with its neighbours) appears to be ubiquitous across the geographic occurrence of monkey beetles within South Africa. This pattern is most noticeable within the beetle rich western regions, suggesting localised adaptation and steep ecological / climatic gradients. Plant turnover patterns across the same set of beetle QDS grid cells also showed similar high levels of beta diversity ($\beta_{sim} = 0.75 (\pm 0.17)$). The spatial grain of turnover within the western regions has not been studied in great detail; however, turnover patterns may

possibly be revealed at even a finer scales than QDS (Cowling 1990, Simmons and Cowling 1996, Colville et al. 2002, Colville 2006). Thus at fine scales, high turnover may be associated with lower richness (negative relationship) while these very high turnover scores no doubt increase richness at the regional scale. Species turnover has been shown to be highly influential on regional richness patterns within the fynbos biome (Latimer et al. 2005). Thus, what appears of importance from this study is how the extraordinary high levels of species turnover interact with the spatial scale of observation. Understanding the relationship between scale and turnover is of primary importance in understanding richness patterns for beetles and plants. Unlocking the key to explaining high patterns of species turnover should in turn highlight the mechanism through which a specific environmental variable, or suite of variables influences regional beetle richness, through the interaction between scale, turnover and regional species richness (see Kerr et al. 2007).

Beetle-plant turnover relationship

Of interest in terms of insect – plant relationships is the weakly positive relationship ($r_s = 0.18$; $P < 0.01$) between plant and beetle turnover patterns (Appendix 4). Plant turnover did not improve the fit of the GWR model (see above) and was a poor substitute for plant richness as an explanatory variable for beetle richness. The above relationship was expected, as most beetle species show low host specialisation with most species visiting a wide range of plant taxa within their preferential feeding guild, thus decoupling the relationship between plant and beetle species turnover. Beetle richness would most likely show stronger positive relationships with plant resource gradients e.g. numbers of flowers, rather than species richness. The lack of a significant relationship ($r_s = 0.02$; $P = 0.730$; Appendix 4) seen between beetle species turnover (β_{sim}) and local plant richness gradients (Plant β_g) reinforces the view that resource abundance may be more important than plant species richness *per se*.

The weak positive relationships between plant and beetle turnover measures have important implications for conservation strategies, particularly within the floristic hotspots of the CFR and Succulent Karoo. Recent conservation approaches for these global hotspots have highlighted the importance of capturing ecological and evolutionary processes, many of these reflected in areas of high species turnover, e.g., lowland – upland gradients (Cowling et al. 2003). As mentioned above, species turnover reflects a complex array of historical and evolutionary processes and contemporary ecological processes. Thus, the mismatch of variables influencing plant and beetle turnover (see Appendix 4), and the poor relationship between them, possibly suggests a different suite of ecological and evolutionary processes specific to each taxonomic group. As such, caution should be exercised when selecting such processes for targeted conservation strategies.

ENVIRONMENTAL VARIABLES – HETEROGENEITY AND TEMPERATURE

Habitat Heterogeneity

Of the four measures of vegetation heterogeneity tested here (Table 1); vegetation habitat heterogeneity (Hetero) performed the best within the model. Vegetation type count and Vegetation type proportional representation per QDS performed consistently poorly in different model combinations. This is in contrast with butterfly studies which have highlighted the importance of land-class heterogeneity (equivalent to number of vegetation types (Veg) variable in this study) in determining regional butterfly species richness (Kerr 2001, Kerr et al. 2001). Topographic diversity was also seen to give weaker model predictions than vegetation habitat heterogeneity (see Kerr et al. 2007).

The measure of vegetation habitat heterogeneity, showed its highest influence on beetle richness within the eastern borders of the of the NW and SW sections of the CFR. Further CFR areas also showed high parameter slopes for this variable i.e. a rapid increase of beetle richness with heterogeneity, as seen in the Langeberg (LB) and western sections of the SE CFR bordering on the Karoo Mountains (KM). These areas have been highlighted in plant studies as being exceptionally high in plant species richness (Goldblatt et al. 2001) and endemism (Bradshaw and Linder 2009), and steep environmental gradients (Campbell 1993), with a diverse array of fynbos floristic elements (montane and lowland) (Mucina and Rutherford 2006). Furthermore, areas with high positive vegetation habitat heterogeneity slopes are located in transitional zones between biogeographic regions, e.g. Namaqualand – Bushmanland interface, CFR – Little Karoo interface, and CFR – Albany Thicket interface (see Fig.3 map (d)). Transitional areas have been shown to be areas of high bird beta diversity (van Rensburg et al. 2004) and important areas of speciation (Smith et al. 1997).

Rainfall Gradients

The heterogeneity measure of length of rainfall gradient (RAR) was seen to be strongly influential within the arid to semi arid areas of Namaqualand (Fig. 3e). A similar result was found by Cowling et al. (1997) for plants. Here steep rainfall gradients are seen extending from low rainfall lowland areas to high rainfall mountain peaks, e.g. steep rainfall gradient seen from low rainfall coastal lowlands to high rainfall fynbos peaks (Desmet 2007). Beetle richness tracks these rainfall gradients, with depauperate coastal communities switching to species rich Upland communities (Colville 2006).

A decreasing gradient in the influence of RAR is noticeable as one moves from Namaqualand into the northern and west central areas of the CFR. This essentially tracks the mean annual rainfall pattern for

this region (Schulze 1997). Here RAR is only a weakly influential predictor of beetle richness. This relationship is mostly due to the stronger influence of Hetero in this region (see above) and, although mapped RAR values (not shown here) show some steepness, the general levels of aridity for this area are far less than for Namaqualand (Schulze 1997). Thus, unlike for Namaqualand, RAR gradients do not span areas of extreme differences in rainfall, possibly reducing their influence on beetle richness. This may be a measurement flaw of RAR in that it does moderate extreme measures from areas ranging from high to very high rainfall. Perhaps using range between upper and lower quartiles may be a more accurate reflection of RAR.

A second transition into areas of RAR importance as a predictor variable is seen for southern areas of the SW CFR including the southern Agulhas Plain (Fig. 3e). Floristic richness in this area has been positively related to the climatic heterogeneity measure of RAR (Linder 1993, Cowling et al. 1997). Some of the highest mapped RAR values for beetle QDS data were seen here. Both semi-arid (Succulent Karoo) to highly mesic areas are found here; with high fynbos peaks recorded to receive exceptionally high levels of mean annual rainfall (Schulze 1997). Host plant richness appeared to be less of an influence in this area (see above). Thus, the role of rainfall heterogeneity appears to have superseded the role of plant diversity.

The influence of RAR diminishes within the eastern sections of the CFR, as the rainfall climate changes to all year round. Here the influence of RAR would be expected to be less influential due to the possibly greater ecological stress of the unpredictability of rainfall (in comparison to winter rainfall areas – see Schulze 1997) and to its aseasonality. Climatic stability has been suggested as an important influence on species richness (Currie 1991). Further eastwards, a weakly negative relationship between RAR and beetle richness was seen for areas of the Albany Thicket. Mapped RAR values for this area are high, although rainfall is unpredictable (Schulze 1997). However, beetle richness in this area appears to be strongly influenced by plant richness and habitat heterogeneity.

The north eastern regions of South Africa show a confusing pattern of both weakly positive and negative relationships for RAR and beetle richness. The positive areas are seen in areas of steep altitudinal gradients with high RAR, while the areas showing negative relationships are areas of mild RAR and altitudinal gradients. Richness patterns for three other insect groups (dung beetles (Davis et al. 1999), dragonflies and damselflies (Samways 1989)) have been associated with altitudinal gradients within eastern KwaZulu-Natal, suggesting altitude and related rainfall gradients as important determinants of insect community patterns

Temperature

Generally mean summer maximum temperature (MST) had a positive influence on beetle richness patterns, as expected based on predictions from the energy–richness hypothesis (Wright 1983). In contrast to Cowling et al.'s (1997) findings for plants, both negative and positive relationships between MST and beetle richness were found within the Fynbos and Succulent Karoo biomes. The northern parts of Namaqualand, including the hyper-arid Gariep Centre, showed a strongly negative relationship. Within this area beetle richness is highest on mountain peaks which have lower summer temperatures (Desmet 2007). The importance of coastal fog in ameliorating summer temperatures in this hot desert region is no doubt of importance (Desmet 2007), as seen in the high species richness recorded from the arid Vyftein Myl se Berg Mountain in northern Namaqualand, whose plant communities are strongly influenced by fog. Furthermore, these cooler refugia from hot summer temperatures may be important for soil-dwelling larvae.

As with several other variables used in the model (see above), a southerly gradient in slope parameter estimates for MST is seen from northern Namaqualand (negative slope), moving into a transitional area at the junction of Namaqualand and the northern CFR (weakly positive slope), and then changing to significantly positive within the CFR (Fig. 3f). In the CFR MST values are generally less extreme than in the arid and semi-arid areas. Furthermore, summer flowering resources within the fynbos are still available (Pierce 1984, Johnson 1992). Beetle emergence times from the CFR show bias towards the late spring and summer months (Chapter 4). The moderate to high (22-30 °C –Schulze 1997) summer temperatures are most likely important and ideal for the thermodynamic requirements of adult monkey beetles. Adult beetle require warm temperatures (Steiner 1998) and sunshine (for sun basking) for feeding and mating activities. In contrast to Namaqualand, September maximum temperatures for large parts of the CFR are possibly still too cool for efficient beetle activity (compare Schulze's (1997) daily maximum temperatures for September between the CFR and Namaqualand).

Of surprise was the weak influence mean summer temperature had on eastern monkey beetle richness patterns. Within these energy rich areas (high temperatures and water) the predominance of sub-tropical and tropical derived fauna would suggest a strongly positive relationship. However, these areas may reflect that part of a curvilinear relationship between energy and water availability where species richness declines in response to this unbalance (Currie 1991, O'Brien 1993). In addition, a number of species within the eastern zone appear to be relicts, confined to cooler, montane peaks.

OTHER EXPLANATORY VARIABLES OF CONSIDERATION

As can be seen from the local R^2 values (Fig. 3a), the model was not able to fully explain the variance seen in beetle richness patterns. Cowling and co-workers (Cowling et al. 1997, Cowling et al. 1998, Cowling and Lombard 2002) have highlighted the need to affirm the evolutionary influences of increased rates of speciation (or decreases in extinction rates), over and above those implied by models using contemporary ecological measures in areas showing higher than expected richness patterns. Such an evolutionary process that may help explain, in addition to ecological measures, the high species richness seen in the western and south eastern areas of South Africa may be the process of sexual selection. Sexual selection has been shown to be an important selection force in promoting increased rates of speciation (Andersson 1994, Arnqvist et al. 2000, Panhuis et al. 2001, Gage et al. 2002). Monkey beetles show strong sexual hind leg and colour dimorphisms. Male beetles have grossly enlarged hind legs festooned with spikes and claws, which are used in intense male-male combat over females. This interesting avenue of explaining species richness of monkey beetles will be explored in Chapter 5.

CONCLUSIONS

Geographically Weighted Regression (GWR) techniques were used to relate regional beetle richness patterns to smaller scale environmental (rainfall, temperature, habitat heterogeneity, host plant diversity) explanatory variables and diversity measures (beta diversity of monkey beetles and associated host plants). A reasonably comprehensive beetle data set was used, which covered a hugely species rich area with wide variation in richness (at the regional – QDS – scale), and wide variation in the spatial patterns of explanatory variables (e.g. arid, winter rainfall areas to subtropical summer rainfall areas).

Plant richness was an important predictor of regional beetle richness, but the predictive power of explanatory variables (rainfall, temperature, habitat heterogeneity, host plant diversity) varied spatially and was fundamentally different between the winter rainfall and the summer rainfall areas. This spatial non-stationarity in the explanatory power of variables as predictors of beetle richness highlights the importance of using a modelling approach that can relate regional richness patterns with smaller scale variations in host plant diversity, rainfall, temperature, and habitat heterogeneity. The wide variation in the predictive power of the variables, indicates that not one model can fit all.

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APPENDIX

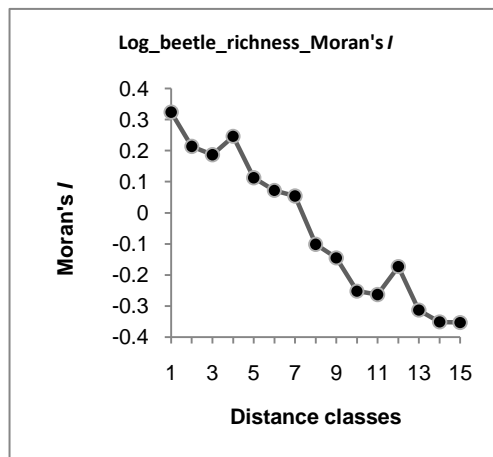
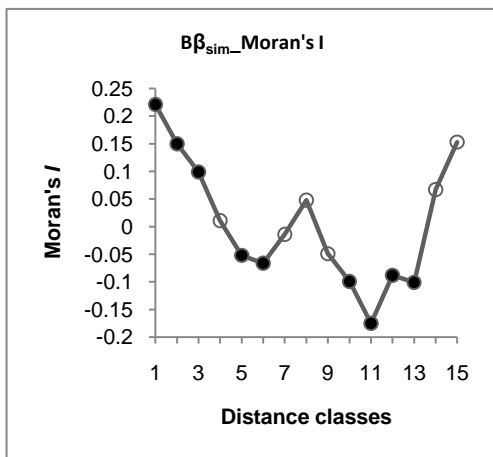
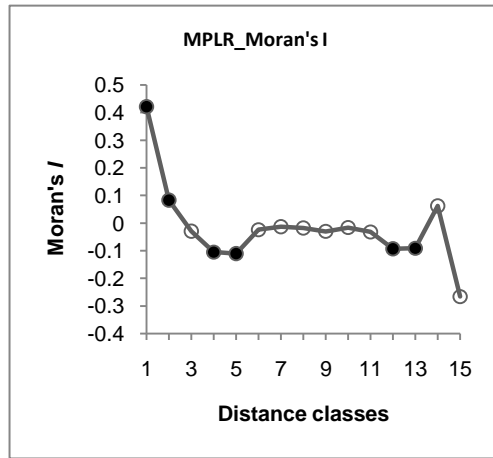
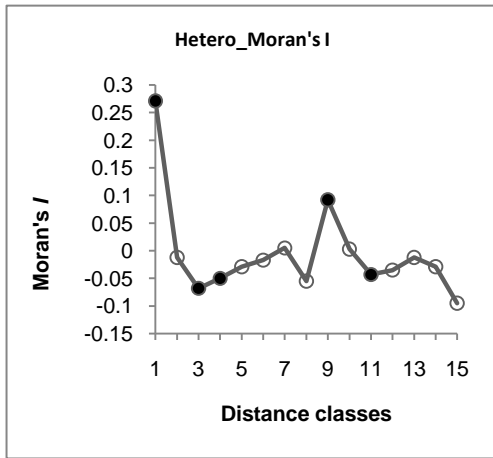
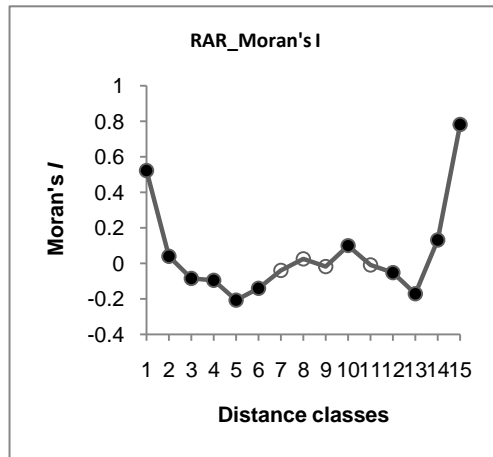
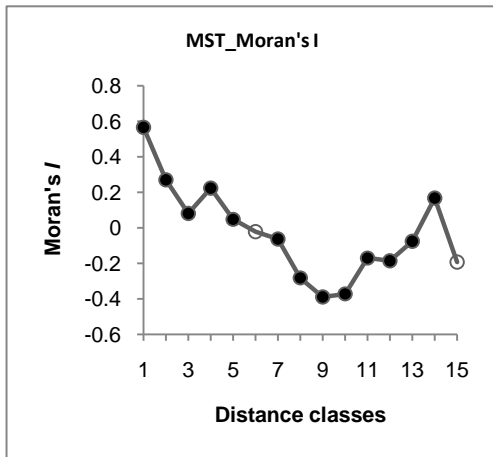
Appendix 1. Descriptive statistics for explanatory variables listed in Table 1. (See Table 1 for explanations for variable abbreviations. $N = 326$ QDS.)

Variable	Mean	Standard deviation	Median	Minimum	Maximum	Lower quartile	Upper quartile	Range
TDCV	0.35	0.25	0.31	0.01	1.54	0.15	0.50	1.53
MAR	517.82	309.63	504.84	24.91	1392.27	232.38	745.60	1367.36
RAR	485.63	492.82	305.0	10.0	2867.0	169.0	639.0	2857.0
RCV	30.26	6.78	30.51	16.29	41.0	25.04	36.53	24.71
RCO	45.41	17.21	51.96	3.32	68.48	36.96	57.66	65.17
MST	27.54	2.63	27.62	15.25	32.87	25.99	29.36	17.62
MWT	4.67	2.78	5.05	-6.56	10.52	2.81	6.78	17.08
RAS	22.87	3.21	22.96	15.25	30.43	20.65	25.19	15.18
RWT	3.26	2.33	3.0	0.0	16.00	2.0	4.0	16.0
MIN	9.38	2.36	9.71	-1.49	15.13	8.13	10.70	16.62
MAX	22.62	2.32	22.76	10.60	27.63	21.42	23.97	17.04
ETemp	14.61	1.33	14.80	0.00	17.10	14.08	15.08	17.10
SRAD	23.08	1.93	23.22	18.31	26.78	21.92	24.53	8.47
Veg	6.76	2.83	6.00	1.00	17.0	5.0	9.00	16.0
VegE	61.30	17.37	63.98	3.73	100.0	51.84	73.42	96.27
Hetero	40.82	72.39	16.0	1.00	575.0	8.00	42.00	574.0
Geo	5.97	2.86	6.0	1.00	18.0	4.00	7.00	17.00
GeoE	67.47	19.22	69.99	7.03	100.0	58.33	82.01	92.97
H ₂ O	67.22	19.74	67.47	15.40	92.0	52.59	87.02	76.60
No. beetle species	10.43	13.68	5.00	1.0	92.0	3.00	12.00	91.00
PLR	467.97	394.53	351.50	7.0	2423.0	161.0	719.0	2416.0
MPLR	130.13	110.23	97.0	1.0	684.0	53.0	177.0	683.0
Ast	65.42	53.55	50.0	0.0	297.0	24.0	97.0	297.0
Irid	29.69	36.14	16.0	0.0	194.0	7.0	37.0	194.0
Mesemb	13.31	14.87	7.50	0.0	93.0	2.0	23.0	93.0
P β_{sim}	0.75	0.08	0.75	0.54	1.00	0.69	0.80	0.46
B β_{sim}	0.76	0.14	0.77	0.50	1.00	0.67	0.87	0.50

Appendix 2. AIC_c and R² values for regression models for single and combinations of independent variables. Grey highlighting indicated variables with low AIC_c values. Results of test for significant spatial non-stationarity also shown (****P* < 0.001; ***P* < 0.01; **P* < 0.05). (Note: not all model combinations tested shown).

Models	Method	AIC _c	R ²	Non-stationarity
MPLR	OLS	386.83	0.54	
	GWR	211.08	0.05	***
PLR	OLS	329.28	0.21	
	GWR	207.56	0.61	***
Asteraceae	OLS	378.94	0.08	
	GWR	224.67	0.59	*
Iridaceae	OLS	308.75	0.25	
	GWR	221.16	0.59	***
Mesemb	OLS	303.22	0.27	
	GWR	257.22	0.56	***
Iridaceae+Asteraceae	OLS	308.89	0.26	
	GWR	224.54	0.57	
Iridaceae+Mesemb	OLS	260.48	0.36	
	GWR	222.19	0.52	
Iridaceae+Asteraceae+Mesemb	OLS	259.64	0.37	
	GWR	230.11	0.59	
Pβ _{sim}	OLS	404.48	< 0.001	
	GWR	274.51	0.53	***
MPLR+ Pβ _{sim}	OLS	292.09	0.3	
	GWR	221.21	0.57	
Bβ _{sim}	OLS	397.91	0.02	
	GWR	208.45	0.64	***
MPLR+ Bβ _{sim}	OLS	325.0	0.22	
	GWR	181.39	0.67	
TDCV	OLS	356.51	0.14	
	GWR	290	0.48	***
RAR	OLS	395.5	0.03	
	GWR	267.19	0.57	***
RWT	OLS	396.01	0.03	
	GWR	265.19	0.51	***
Veg	OLS	375.96	0.08	
	GWR	276.51	0.46	**
Hetero	OLS	393.01	0.04	
	GWR	283.25	0.45	*
VegE	OLS	400.02	0.01	
	GWR	279.36	0.51	n/s
MAR	OLS	383.9	0.06	
	GWR	269.92	0.44	***
Geo	OLS	40.24	0.007	
	GWR	323.3	0.56	n/s
GeoE	OLS	403.8	0.003	
	GWR	323.43	0.59	n/s
MST	OLS	394.92	0.03	
	GWR	282.24	0.49	***
MWT	OLS	390.18	0.04	
	GWR	292.13	0.46	***
RCO	OLS	404.63	<0.001	
	GWR	296.03	0.33	***
H2O stress	OLS	289.32	0.3	
	GWR	276.2	0.47	***
RAS	OLS	404.14	0.001	
	GWR	288.2	0.48	***

Appendix 3. Spatial correlograms for explanatory variables used in GWR model. Dark circles: Moran's I values that remain significant after progressive Bonferroni correction ($P < 0.05$); clear circles represent non-significant values.



Appendix 4. Spearman rank correlations (r_s) for beetle and plant turnover measures correlated against respective environmental, richness, and turnover measures. Correlation analyses restricted to QDS with beetle data from the winter and all year round rainfall regions.

(a) Beetle beta diversity	r_s	P -level	(b) Plant beta diversity	r_s	P -level
TDCV	-0.1547	0.02364	TDCV	-0.3752	0.00000
MAR	0.1466	0.03204	MAR	-0.5655	0.00000
RAR	0.2220	0.00108	RAR	-0.4331	0.00000
RCO	-0.3371	0.00000	RCO	0.3087	0.00000
MST	0.2009	0.00316	MST	0.4366	0.00000
MWT	-0.3149	0.00000	MWT	-0.1932	0.00456
RAS	0.2893	0.00002	RAS	0.3642	0.00000
RWT	0.0210	0.76052	RWT	-0.0954	0.16423
Veg	-0.0773	0.26053	Veg	-0.3624	0.00000
Hetero	-0.0290	0.67261	Hetero	-0.2930	0.00001
VegE	-0.0480	0.48473	VegE	0.0064	0.92544
H ₂ O	0.0750	0.27487	H ₂ O	0.2011	0.00312
Beetle richness ^{Log}	-0.3784	0.00000	Beetle richness	-0.1612	0.01829
ETemp	-0.2177	0.00135	ETemp	0.1204	0.07887
MPLR	-0.1283	0.06097	MPLR	-0.6792	0.00000
P β_{sim}	0.1757	0.01003	H β_{sim}	0.1757	0.01003
P β_g	0.0237	0.73002	H β_g	-0.0628	0.36056
H β_g	0.2328	0.00060	P β_g	0.1389	0.04237

^{Log} beetle richness log₁₀ transformed (see Methods).

4 EXPLAINING PATTERNS OF BETA DIVERSITY FOR SOUTH AFRICAN MONKEY BEETLES USING GENERALISED DISSIMILARITY MODELS

“The first question which may be asked of the data is: How are the populations of foliage insects distributed along gradients and in relation to plant communities?” *R. H. Whittaker (1952)*.

ABSTRACT

The change in species composition (replacement and losses of species) along ecological and geographic gradients (beta diversity or species turnover) is a complex property of species communities and is a key concept to understanding regional diversity patterns. Furthermore, areas of high beta diversity are conservation priorities because of their high evolutionary potential. Studies focussing on beta diversity patterns within South Africa are limited, especially so for insect groups. The lack of knowledge concerning this ecologically important component of biodiversity conservation has been noted, but lack of adequate data thus far has prevented exploration of patterns and associated processes. Here I use generalised dissimilarity models (GDM) to model the spatial turnover in beetle community composition (beta diversity) between pairs of sites as a function of environmental differences (rainfall, temperature, altitude, soil fertility) and plant (host species, vegetation types, and bioregions). To date, most commonly used linear distance matrix approaches to modelling compositional dissimilarities have been limited by two violations of non-linearity (curvilinear relationship between species dissimilarity and geographic distance, and non-stationarity of species turnover rates along ecological gradients). GDM models use a non-linear approach (matrix regression and generalised linear modelling), thus capturing ecological realistic relationships between compositional dissimilarity and ecological gradients. Data sets at two different spatial scales were used: (i) regionally, across biomes using quarter degree grid cells (QDS) (*ca.* 25 km x 25 km) with presence-only data; and (ii) using presence/absence data from field survey sites (*ca.* 100 m x 100 m), focussing specifically on patterns within the beetle rich winter rainfall biomes. Results from both data sets indicated that beetle beta diversity is strongly correlated with environment and plants, but environment appears to be a slightly stronger predictor. Due to the contrasting quality of the data sets, this pattern was strongest at the field survey scale (62.7 % overall deviance explained vs. 24.02% at the QDS scale). Geographic distance between sites explained minimal amounts of species turnover at both QDS and field survey scales. Complete species turnover (100% compositional dissimilarity of beetle communities) is reached within very short distances, and beyond this asymptote, increasing geographical distance has no effect on beta diversity. This finding is explained by the steep ecological and environmental gradients, combined with poor dispersal abilities of some monkey beetles. Individual gradients of high importance were associated with rainfall seasonality and concentration, altitude, vegetation type habitat proportions, and ecological dissimilarities across bioregions. Physiological and morphological adaptations were linked to these gradients highlighting the role of divergence and isolation of populations through ecological specialisations and weak dispersal abilities resulting in high compositional dissimilarities. Overall, the findings here contrast with patterns seen in other Mediterranean and arid systems, and provide interesting contrasts with other biodiversity hotspots, such as tropical rainforests, in that the high richness of local beetle communities (alpha diversity) is matched by high beta diversity. Furthermore, locally co-existing species do not represent a large proportion of the regional species pool.

INTRODUCTION

The change in species composition (replacement and losses of species) along ecological and geographic gradients (beta diversity or species turnover or compositional dissimilarity) has fascinated ecologists for many decades. Robert H. Whittaker in two seminal papers (Whittaker 1960, 1972) first introduced the concept of beta diversity and studied the changes in species composition between communities and the ecological and spatial determinates of these changes. Subsequently, a plethora of beta diversity measurements and approaches have been developed (Wilson and Mohler 1983, Lennon et al. 2001, Koleff et al. 2003, Kiflawi and Spencer 2004, Legendre et al. 2005, Harborne et al. 2006, Tuomisto and Ruokolainen 2006, Ferrier et al. 2007) and some confusion within the ecological literature is noted (see Laiberte 2008, Pelissier et al. 2008, Legendre et al. 2008, and Tuomisto and Ruokolainen 2008). Further, the statistical appropriateness of the mostly linear approaches used when measuring species similarities across sites has been questioned (see Faith and Ferrier 2002, Ferrier et al. 2002, 2007; and see below). Nonetheless, the ecological importance of beta diversity in understanding regional diversity patterns (Whittaker 1972, Cody 1986, Cowling et al. 1989, Cowling 1990, Kerr et al 2001, Veech et al. 2001, Kiflawi and Spencer 2004, Beck and von Khen 2007, McKnight et al. 2007) and its important role in biodiversity assessment and conservation planning (Ferrier et al. 1999, Lombard et al. 1999, Condit et al. 2002, Ferrier 2002, Ferrier et al. 2002, Steinitz et al. 2005, Ferrier et al. 2007) has been commonly stated. A further important, and perhaps more appealing role of beta diversity, has been its use in estimates of terrestrial global species richness (Erwin 1989, Gaston 1991), especially for hyper-diverse tropical rainforests (see Lewinsohn and Roslin 2008).

Hypotheses focussing on explaining beta diversity have most often explored determinants of the dimensions of ecological niches (Gauch 1973, Whittaker 1952, 1956, 1960, Shmida and Wilson 1984, Cody 1993, Legendre et al. 2005, Gaston et al. 2007, Novotny et al. 2002, Brehm et al. 2003) and dispersal abilities (Hubbell 2001, Latimer et al. 2005, Novotny and Weiblen 2005, Novotny et al. 2007). Within South Africa, patterns and determinants of beta diversity have been poorly studied, particularly across regional scales. Those studies that have explored beta diversity have focussed almost exclusively on the role of environmental gradients (Sigfried and Crowe 1983, Cody 1986, Cowling et al. 1989, Cowling 1990, Palmer and Cowling 1994, Samways 1994, Simmons and Cowling 1996, Davis et al. 1999, van Rensburg et al. 1999, Bond et al. 2001, Gaston et al. 2001, Colville et al. 2002, van Rensburg 2004, Botes et al. 2006, 2007). In addition, Latimer et al. (2005), focussing on the plant rich Cape Floristic Region – which shows high beta diversity – highlighted weak migration (dispersal) rates associated with fynbos plant communities (see also Linder 1985). The role of biotic factors such as

competition, predation etc. has, however, not been established. Moreover, the influence of geographic distance on species turnover has been essentially studied only in the context of gamma diversity (see Cody 1986, Cowling et al. 1989, 1992). The largest and perhaps most important gap in our knowledge on beta diversity within South Africa, is the possible sharing of similar spatial beta diversity patterns across disparate taxa (see also Mcknight et al. 2007).

Of recent interest within the beta diversity literature is the partitioning of explained percentage variance for species similarity into its component parts of geographic distance and / or environmental variables (Borcard et al. 1992, Ferrier et al. 1999, Duivenvoorden et al. 2002, Faith and Ferrier 2002, Tuomisto et al. 2003, Steinitz et al. 2005, Chust et al. 2006, Ferrier et al. 2007). Typically, an unexplained component remains, which indicates missing unmeasured abiotic and/or biotic variables (see Faith and Ferrier 2002). A recently developed statistical model – generalised dissimilarity models (GDM) (Ferrier et al. 2002, 2007) – has been shown to be effective in modelling spatial turnover in species composition across sites in relation to geographic distance and the environmental variation between sites, in that explained variance can be easily partitioned into component parts, and the influence on turnover patterns of individual environmental variables can be assessed. GDM models have the further advantage that they use a more ecologically realistic non-linear approach to matrix regression (Ferrier et al. 2002, 2007). To date, however, most commonly used linear distance matrix approaches (see Legendre and Legendre 1998, Legendre et al. 2005) to modelling compositional dissimilarities have been limited by two violations of non-linearity (De'ath 1999, Ferrier et al. 2002): (i) the relationship between species compositional dissimilarity and geographic distance is in fact asymptotic (Gauch 1973, Faith et al. 1987; and see Fig. 13.9 of Cody 1993, and Fig. 2 of Faith and Ferrier 2002); and (ii) the rate of change of species composition across environmental gradients is most often not constant but fluctuates along respective gradients (i.e. shows non-stationarity) (see e.g. Simmons and Cowling 1996). Furthermore, GDM models offer several advantages for biodiversity assessment and planning relative to other dissimilarity techniques (see Faith and Ferrier 2002, and Ferrier et al. 2002, 2007).

Here I use a GDM modelling approach to analyse compositional dissimilarity patterns of South African monkey beetles. Specifically, I investigate the variation in beta diversity explained by: (i) gradients associated with plant (host species, vegetation type habitats, and bioregions) and environmental dissimilarities (topography, altitude, rainfall, temperature, soil fertility) between sites; and (ii) geographic distances between sites. Furthermore, variation in beetle beta diversity is explored at two spatial scales: (i) regionally, across biomes using quarter degree grid cells (QDS) (*ca.* 25 km x 25 km); and (ii) using field survey sites (*ca.* 100 m x 100 m), focussing specifically on patterns within the beetle rich Fynbos and Succulent Karoo biomes.

METHODS

BIOLOGICAL AND ENVIRONMENTAL DATA

Monkey Beetle Species Databases

QDS Scale

A point locality distributional data set was collated from several sources. Monkey beetle distributional data was obtained from an extensive pinned collection housed at the South African Iziko Museum (Cape Town), taxonomic revisions (see Chapter 1), and field collections undertaken during spring flowering seasons (1999-2007). Each point locality was geo-referenced using 1: 50 000 and 1:250 000 topographic cadastral maps of South Africa (sourced from Chief Directorate: Surveys and mapping (CDSM), Mowbray, Cape Town, www.w3sli.wcape.gov.za) and the GeoNet Names Server gazetteer (http://164.214.2.59/gns/htm/cntry_files.html). Only collection records of sufficient accuracy were used. Obscure and/or vague locality records, such as “Cape of Good Hope” were excluded. Highly disjunct records, suggesting misidentification of a species, or incorrect locality label information were further excluded from the data set. In total, 1040 species and 6959 unique locality records were compiled for use in a GIS. Distributional datasets collated from e.g. museum natural history collections are highly useful in biogeographic studies, although limitations of such presence-only data sets are known (Graham et al., 2004).

Monkey beetle point distribution maps were created using Arcmap 9.2 (ESRI 2006) and overlaid onto a Quarter Degree Square (QDS) grid (Edwards and Leistner 1971) of South Africa (including Lesotho and Swaziland). QDS have been commonly used as operational geographic units (Crovello 1981) in studies exploring species diversity patterns within south Africa (van Rensburg et al. 2002, van Rensburg et al. 2004, Richardson et al. 2005, Thuiller et al. 2006). Shortcomings have been noted in the use of QDS due to its geographic coarseness (Williams 2000, Moline and Linder 2006). However, apart from allowing possible comparisons to other studies, using approximately equal area operational units should help reduce the area effect on modelled relationships (Rosenzweig 1995, van Rensburg et al. 2004).

Species occurrence data was calculated for each QDS grid cell creating a site-by-species presence-only table for use in GDM. Longitude/latitude centroid values for each QDS were appended to this table. Within the GDM analyses, a weighting approach was adopted whereby QDS grid cells with low numbers of species achieved a lower weighting in comparison to grid cells with high numbers of species (Ferrier et al. 2007). Such a weighting approach allowed site pair comparisons with low numbers of species to have

less influence on GDM model results. Unlike previous studies (e.g. van Rensburg et al. 2002), QDS grid cells which included both land and sea were retained for analysis. The reasoning for this was (i) only < 4% of QDS showed less than 30% of their area covered by land; (ii) the strength of area effects on comparisons between unequal area sized QDS is mostly likely marginal in comparison to the inherent problem of collector bias (Graham et al. 2004) across the data set ; (iii) the statistical robustness of applying land-area corrections to these QDS are unclear (see Lennon et al., 2001); and (iv) South Africa has an extensive coast line and the exclusion of coastal QDS from analyses would hinder our understanding of processes related to compositional dissimilarities within the important coastal biogeographic areas (see Endrödy-Younga 1978, and Mucina and Rutherford 2006). QDS extending across into neighbouring countries (< 2% of QDS in this study) were assumed to have beetle occurrence data equivalent to that found in the South African area component of the QDS (cf. van Rensburg et al. 2002), and as such, were treated as a full area size QDS.

Field Survey Sites Scale

Monkey beetle species presence/absence data was collected from 22 sites (each approximately 10 000m² in size, except sites located on mountain passes which were smaller – see Table 1) along broad north-south (rainfall) and east-west (vegetation type) gradients from within the winter rainfall Succulent Karoo and Fynbos biomes (see Table 1 for field survey site details). Field survey sites were selected to represent near pristine areas of vegetation types (habitat) to negate the effects of changes in community composition related to disturbance gradients (see Colville et al. 2002). Twelve of these sites were situated within two broad classes of coastal Strandveld vegetation type (Mucina and Rutherford, 2006). The Strandveld classes consisted of “tall” (TS – tall shrubs, deep soils; 7 sites) and “short” (SS - low growing shrubs, shallow soils; 5 sites). The geographic distance between the most northern and southern groups of these sites was approximately 600 km. Four other sites were situated within Heuweltjie Vygiveld (HV) vegetation type (mosaic of low-growing leaf-succulent shrubland communities growing on and between large disk-shaped termite mounds (“heuweltjies”)) (Mucina and Rutherford 2006). These sites were chosen to represent easterly neighbours of respective Strandveld sites, with similar rainfall, but differing floristic components and soil (see Cowling et al. 1989 and Palmer and Cowling 1994). The geographic distance between the most northern and southern groups of HV sites was approximately 320 km. A third set of six sites (Transitional zones-TZ; Fynbos peaks-Fyn) were established along steep altitudinal, rainfall, and soil gradients. These sites provided comparisons along steep ecological gradients over short (<500 m) geographic distances.

Collecting effort at all sites was equal, being comprised of approximately 6-8 hours per site, on days of suitable weather conditions (sunny and warm, when beetle activity was high – see Struck 1992). All sites, except two, were collected over 2-3 consecutive years (spring seasons). Collecting was during the spring months of August and September, coinciding with mass spring flowering displays (Cowling et al. 1999) and peak beetle emergences (Péringuey 1902, Picker and Midgley 1996). Beetles were caught using butterfly nets, coloured pan traps, and hand collected from flowers. Coloured pan trapping followed a similar procedure outlined in Picker and Midgley (1996) and Colville et al. (2002). At each site five sets of coloured pan traps - each set consisting of a yellow, orange, red, blue, pink and white trap -were laid out in a pre-selected pattern of one set of traps at each “corner” of the field site, and one set of traps in the centre of the field survey site. Data from each collecting method and from each collecting year was pooled to give an overall record of species presence/absence data for each site, thereby allowing creation of a second site-by-species table (192 species by 22 sites). Longitude/latitude co-ordinates, calculated with a hand-held GPS (Global Positioning System – Magellan GPS 310) were added to the table for calculation of geographic distance between all site pairs. All beetles collected were identified to species.

Table 1. Climate, size, altitude, vegetation type, and number of sampling seasons for 22 field survey sites. (TS = tall Strandveld, SS = short Strandveld, HV = Heuweltjie Vygie Veld, Fyn – fynbos peak, TZ = transitional zone; MAR = mean annual rainfall).

Field study site (sampling seasons)	Co-ordinates	Vegetation type ^M	Size (m ²)	Altitude ^G (m)	MAR ^S (mm)
Melkbosstrand-TS(2)	-33.7667, 18.4667	Cape Flats Dune Strandveld	10 000	40	408
Yzerfontein-TS(2)	-33.3500, 18.2000	Saldanha Granite Strandveld	10 000	25	398
Rocher Pan-TS(1)	-32.6333, 18.3000	Lamberts Bay Strandveld	10 000	17	208
Doringbaai-SS(2)	-31.8333, 18.2500	Namaqualand Strandveld	10 000	28	175
Groen River-TS(2)	-30.7667, 17.8667	Namaqualand Strandveld	10 000	132	82
Groen River-SS(2)	-30.8381, 17.9061	Namaqualand Coastal Duneveld	10 000	132	82
Vygie Point-TS(2)	-30.5334, 17.4167	Namaqualand Strandveld	10 000	58	102
Vygie Point-SS(2)	-30.4854, 17.3610	Namaqualand Coastal Duneveld	10 000	58	102
Kleinzee-TS(2)	-29.7000, 17.1167	Namaqualand Strandveld	10 000	118	123
Kleinzee-SS(2)	-29.6995, 17.1046	Namaqualand Coastal Duneveld	10 000	118	123
Holgate River-TS(2)	-28.9167, 16.8000	Richtersveld Coastal Duneveld	10 000	125	53
Holgate River-SS(2)	-28.9167, 16.8495	Southern Richtersveld Yellow Duneveld	10 000	125	53
Vyftein Myl se Berg-HV(2)	-29.2333, 17.0833	Vyftein myl se Berg Succulent Shrubland	10 000	244	81
Wilderperde Hoek-HV(2)	-29.9667, 17.6000	Namaqualand Heuweltjieveld	10 000	318	175
Nuwerus-HV(2)	-31.1000, 18.3500	Namaqualand Heuweltjieveld	10 000	362	149
Vanrhynsdorp-HV(3)	-31.8000, 18.6833	Namaqualand Heuweltjieveld	10 000	162	219
Studer's Pass-TZ(2)	-30.4018, 18.0800	Namaqualand Granite Renosterbos	4 800	1104	314
Vanrhyns Pass–top-Fyn(1)	-31.3667, 19.0167	Boekkeveld Sandstone Fynbos	6 400	819	347
Vanrhyns Pass–middle-TZ(1)	-31.4000, 19.0333	Kamiesberg Mountain Shrubland	1 500	701	289
Gifberg Mountain-top-Fyn(2)	-31.8037, 18.6977	Boekkeveld Sandstone Fynbos	10 000	612	336
Gifberg Mountain–middle-TZ(2)	-31.7482, 18.7898	Vanrhynsdorp Shale Renosterveld	5 000	309	263
Gifberg Mountain–base-TZ/HV(2)	-31.7125, 18.7665	Namaqualand Heuweltjieveld	10 000	162	219

^{*}Taken from Mucina and Rutherford (2006), ^GMagellan GPS 310, ^SSchulze (1997)

Predictor Variables

Following procedures outlined below, at each scale (QDS grid cells and field survey sites) an environmental and plant predictors table was created with rows corresponding to QDS or field sites, and columns corresponding to environmental and plant variables (Table 2). Longitude/latitude columns were also added to the tables allowing calculation of geographic distance between sites, and linking the beetle site-by-species tables to the predictor tables.

Environmental

Environmental (Schulze, 1997b) themes were spatially joined in Arcmap 9.2 (ESRI 2006) to the compiled beetle point locality data set and a QDS grid overlay. For each QDS grid cell, average values were calculated for nine selected environmental variables representing measures of rainfall, temperature, and altitude (see Table 2 and Chapter 3). Values for each of the nine variables were extracted from the same GIS themes for the 22 field survey sites.

Table 2. Environmental predictor variables used in GDM models.

Environmental predictor variable	Code	Units
Topographic diversity ^{1,2}	TD-90m	%
Coefficient of variation of annual rainfall ²	RCV	%
Mean summer rainfall (Nov., Dec., Jan., Feb.) ²	SR	mm
Mean winter rainfall (May, June, July, Aug.) ²	WR	mm
Mean annual rainfall ²	MAR	mm
Rainfall concentration ²	RCO	%
Soil fertility ²	SF	score 1-10
Mean of January daily max temperature ²	MST	°C
Mean of July daily min temperature ²	MWT	°C

Source data and/or derivation: ¹Jarvis et al. (2006); ²Schulze 1997

Plant Species and Vegetation- QDS Scale

Four different measures of compositional dissimilarity in plant species and vegetation categories were used as predictor variables within the GDM model (Table 3). These were considered at three ecological scales in order to determine at which floristic level beetles are most responsive in terms of influencing beta diversity. Firstly, a measure of plant taxonomic compositional turnover was created. This was achieved through the following process. A table of plant species, genera, and family occurrence data was firstly created by extracting distributional data for six monkey beetle host plant families (Asteraceae, Iridaceae, Aizoaceae, Haemodoraceae, Hyacinthaceae, and Hypoxidaceae; and see Chapter 3) from the National Herbarium (PRE) Computerised Information (PRECIS) data base (Germishuizen and Meyer 2003, Richardson et al. 2005, Thuiller et al. 2006). This data base comprises data for over 24 000

southern African plant taxa. QDS grid cells across South Africa were used. The table created from the PRECIS data was a “sites by species” matrix, where the “sites” were QDS grid cells, and “species” were plant species, genera, and families (6480 “species” by 1951 “sites”). The approach of using the occurrences of species, genera, and family to measure plant compositional turnover was used in order to obtain better (low stress value – see below) ordination scores, as the number of “outliers” was reduced (Clarke and Gorley 2006), as geographically isolated species were linked to other QDS through higher taxonomic categories. Furthermore, this approach allows compositional turnover to be calculated at deeper plant taxonomic levels (see Proches et al. 2009), and links areas together that are more phylogenetically nested. The final table was then subjected to an ordination analysis (Bray-Curtis distance matrix followed by non-metric multi-dimensional scaling – MDS (Legendre and Legendre 1998, Thessler et al. 2005)) in order to reduce the dimensionality of the data down to a manageable number of ordination axes that explains a high percentage of the variation in the plant data. The ordination approach was considered preferable to using raw inter-site dissimilarities (based on plant data) because it provided the GDM analysis with more information about compositional patterns in the plant data. In order to achieve low stress values – an indication of how realistically the high dimensional relationships among the grid cells are represented in 2-dimensional (2-d) or 3-dimensional space (2-d) – 25 random restarts were used (see Clarke and Gorley 2006). The best dimensional ordination space, either 2-d or 3-d was selected based on the lowest stress value. Ordination axes were then used as predictor variables (*sensu* Gauch, 1973) within the GDM analyses. All ordination analyses were performed within the computer program PRIMER v.6 (Clarke and Gorley 2006).

Secondly, the same approach as above was used on vegetation types (“species”) found within each QDS grid cell, recorded as present or absent. Vegetation types were extracted from the GIS vegetation theme of Mucina and Rutherford (2006). Furthermore, in order to measure compositional dissimilarity in the proportional area size of a vegetation type present in each QDS (see van Rensburg et al. 2002); a similar table as above was created, replacing the presence/absence scores with an area (“abundance”) score. This table was also subjected to an ordination analysis as above, although Bray-Curtis index calculations were set to abundance input data within PRIMER.

Thirdly, ecological dissimilarities between the higher vegetation groupings of bioregion (see Chapter 2) were calculated. This was done firstly by rating, based on local expert opinion (Cowling 2008 pers. com), the ecological similarity between all possible pairs of bioregions on a scale of 0 to 1 (1 = 100% difference, 0 = no difference) (see also Ferrier et al. 2007). This process created a similarity matrix of bioregions (77 by 77). The ecological similarity between each pair of bioregions was based only on the component of the flora that hosts monkey beetles, taking into account the presence of this host flora and

the relative amount of species turnover between all bioregion pairs. Only that component of the flora that hosts monkey beetles was focussed on, as geographic areas may be similar in their overall floristic component, but quite different in their monkey beetle floristic component, and *vice versa*. In order to assist the expert opinion process, an extensive list of monkey beetle host plant families, genera and species was compiled (Colville, unpublished data). Scores were refined using results from similarity clustering of phytogeographic centres based on species occurrence data (Born et al. 2007). The final similarity matrix was then inputted into PRIMER and subjected to an ordination analysis (MDS), with the bioregions as the objects being ordinated. Ordination scores from the best ordination axes (based on stress values) were then assigned to each bioregion. Within Arcmap 9.2 (ESRI 2006), ordination scores for each QDS grid cell were calculated as a weighted average of the scores of the bioregions occurring within that grid cell (i.e. the contribution of each bioregion was weighted according to the proportion of the QDS grid square it covered). These weighted scores were then used as predictor variables within the GDM model.

Table 3. Plant predictor variables used in GDM models at the QDS grid cell scale of analyses.

Plant predictor variable	Code	Best MDS configuration	stress	Source data (Reference)
Plant taxonomic groups (species + genera + family)	Axis	3-d	0.16	PRECIS (Germishuizen and Meyer 2003)
Vegetation types ^L (presence/absence)	veg_categories_axis	2-d	0.02	(Mucina and Rutherford 2006)
Vegetation types ^L (proportion of QDS area covered)	veg_units_area_axis	2-d	0.03	(Mucina and Rutherford 2006)
Higher vegetation categories ^L (host plant ecological similarity)	average_score_axis	3-d	0.08	(Cowling 2008 pers. com, Mucina and Rutherford 2006)

^L Data $\log_{10} + 1$ transformed. Stress values indicate the "best" fit of the data in 2-d or 3-d space (see Clarke and Gorley 2006).

Plant Species and Flower Resource Type – Field Survey Scale

A measure of resource abundance (number of flowers per m² of plant cover) was calculated for each field survey site using five 25 m² quadrates, surveyed at each consecutive season of beetle collecting (average taken across collecting seasons) (see Struck 1992). Quadrates were placed in a pre-selected pattern in each 10 000 m² site – one quadrate at each corner of the site (4 corners), and one quadrate in the centre of the site. Within each quadrate, for each individual plant (only those plant species that were utilised by beetles; all plants identified to species), cover (m²) and total number of flowers were measured. Only flowers that were in anthesis, i.e. still had the ability to open and close and that still offered a viable resource to beetles were counted. Presuming that five 25 m² quadrates adequately represents the monkey beetle host plant resource, in terms of plant species richness and resource abundance (number of plants and flowers) within each site, the total number of monkey beetle flowers per m² of plant cover was calculated by summing measurements across quadrates. The calculation of number of monkey beetle

flowers per m² of plant cover was then divided into monkey beetle plant species categorised into different resource classes based on flower shape and food resource (see Table 4). The percentage cover of total monkey beetle plant cover was calculated for each resource class. The abundance and diversity of floristic resources have been shown to structure pollinator communities (see Potts et al. 2003).

Table 4. Percentage floristic resources offered to monkey beetles at each field survey site. Flower resources classed into categories based on specific resources (pollen, nectar, and floral ovaries) offered by a flower shape (shapes: disk, e.g. Asteraceae; tube, e.g. Lamiaceae; flower-head, e.g. Proteaceae) to beetles. [TS = tall Strandveld, SS = short Strandveld, HV = Heuweltjie Vygie Veld, Fyn – fynbos peak, TZ = transitional zone].

Field study site	Monkey beetle Flowers/m2	Percentage (%) flower resource category						
		disc-ovaries-pollen-nectar	Disc-pollen-nectar	disc-nectar	disc-ovaries-pollen	tube-nectar	flower-head-nectar-pollen	flower-head-nectar
Melkbosstrand-TS	8.33	94.99	5.01	0	0	0	0	0
Yzerfontein-TS	13.54	94.81	0.99	0	4.69	0	0	0
Rocher Pan-TS	24.07	17.18	1.95	0	80.88	0	0	0
Doringbaai-SS	89.39	89.69	0	0	10.31	0	0	0
Groen River-LS	56.38	77.71	2.65	0	20.96	0	0	0
Groen River-SS	64.37	50.63	0	0	49.37	0	0	0
Vygie Point-LS	34.14	86.75	10.28	0	8.11	0	0	0
Vygie Point-SS	26.30	64.73	0	0	35.27	0	0	0
Kleinzee-LS	86.66	92.38	0	0	7.62	0	0	0
Kleinzee-SS	43.19	83.94	0	0	16.06	0	0	0
Holgate River-LS	36.69	51.31	22.64	0	37.37	0	0	0
Holgate River-SS	134.47	69.56	27.68	0	25.94	0	0	0
Vyftein Myl se Berg-HV	85.38	73.26	0	0	26.74	0	0	0
Wilderperde Hoek-HV	93.57	33.08	0	0	66.92	0	0	0
Nuwerus-HV	40.93	73.14	0	0	26.86	0	0	0
Vanrhynsdorp-HV	54.37	38.52	0.19	0	61.38	0	0	0
Studer's Pass	30.98	80.89	6.46	0	0	3.36	9.30	0
Vanrhyns Pass – top-Fyn	52.14	11.36	25.92	14.70	21.98	8.68	0	17.37
Vanrhyns Pass – middle-TZ	115.82	100.0	0	0	0	0	0	0
Gifberg Mountain – top-Fyn	28.35	17.84	28.88	45.91	3.04	26.02	0	7.89
Gifberg Mountain – middle-TZ	27.03	55.51	0.79	13.18	11.40	6.43	0	25.38
Gifberg Mountain – base-TZ/HV	19.67	71.67	15.17	0	0	0	13.16	0

Plant taxonomic compositional turnover was calculated as for the QDS grid square scale, with the creation of an occurrence data table of species, genera, and family for all sites (203 “species” by 22 sites). This table was then analysed using the same ordination techniques as above in the computer programme PRIMER. The best dimensional ordination space was a 3-d solution with a stress value of 0.12.

Geographic Distance

Geographic distance between QDS grid cells and field study sites was included as a predictor variable within the GDM model. Geographic distance was calculated using the geographical co-ordinates (longitude/latitude) for each QDS and field survey site. Co-ordinates were taken from the centre of a field survey site (hand held GPS – MAGELLAN GPS 310), and similarly, the centroid longitude and latitude values were used for QDS grid cells.

MODEL FITTING

GDM models were fitted using the GDM software created by Simon Ferrier and Glenn Manion and following the procedures outlined in Ferrier et al. (2002) and Ferrier et al (2007) (Downloadable software for fitting GDMs in R available at www.biomaps.net.au/gdm/). Using the data from the two tables (beetle and predictor variables) created at the QDS and field survey scale, a basic strategy was followed by fitting a series of GDM models with different combinations of environmental and/or plant composition variables, and then assessing recorded patterns in the proportion of variance (deviance) in beetle turnover explained by each model (see also Borcard et al. 1992). The combinations of predictors used were: (1) environmental predictors; (2) plant predictors (e.g. the ordination axes); and (3) both environmental and plant predictors together (full model). This allowed estimation of the amount of variance in beetle turnover explained by plant composition over and above that explained by environment and vice versa (see Duivenvoorden et al. 2002, and Faith and Ferrier 2002 for similar approach).

Key results examined from the two models fitted (environmental predictors only, and plant predictors only) were the change in proportion of the deviance explained relative to the full model. For the full model, percentage deviance explained, and plots of: (i) observed compositional dissimilarity (Bray-Curtis dissimilarity measure) and predicted ecological distance (i.e. the linear predictor from the fitted model); (ii) observed compositional dissimilarity and predicted compositional dissimilarity; and (iii) fitted non-linear monotonic I-spline functions (three I-splines for all predictors – see Ramsay 1988, and Ferrier et al 2007) for each predictor variable were examined. These latter plots are indicative of the total amount (height of curve– see below) and rate (slope of curve) of beetle turnover along the respective environmental/plant gradient when holding all other predictors constant (Ferrier et al. 2007). Furthermore, the three fitted I-spline coefficients for each predictor were summed (I_c = sum of fitted coefficients; which is equivalent to height reached by curve). This allowed the calculation of the relative influence that different predictor variables were having on beetle turnover (Ferrier et al. 2007).

RESULTS

EXPLAINED DEVIANCE IN OBSERVED BEETLE DISSIMILARITIES

QDS Scale Analyses

At the QDS scale, a GDM model with all environmental and plant variables explained 24.02% of deviance in observed beetle dissimilarity (turnover) between grid cells. Adding geographic distance between grid cells to this model improved the explained deviance by a minimal amount ($< 0.5\%$), and geographic distance was therefore excluded from any further analyses at this scale. The overall deviance explained (Fig. 1a) was partitioned into the following components: (i) 5.9% was explained purely by environmental variables, i.e. this was the increase in deviance explained when the environmental variables were added to a model already containing the plant variables; (ii) 2.6% was explained purely by plant variables, i.e. this was the increase in deviance explained when the plant variables were added to a model already containing the environmental variables; and (iii) 15.6% was explained jointly by environmental and plant variables, i.e. this proportion could not be allocated to either one set of variables or the other, due to correlation between these predictors.

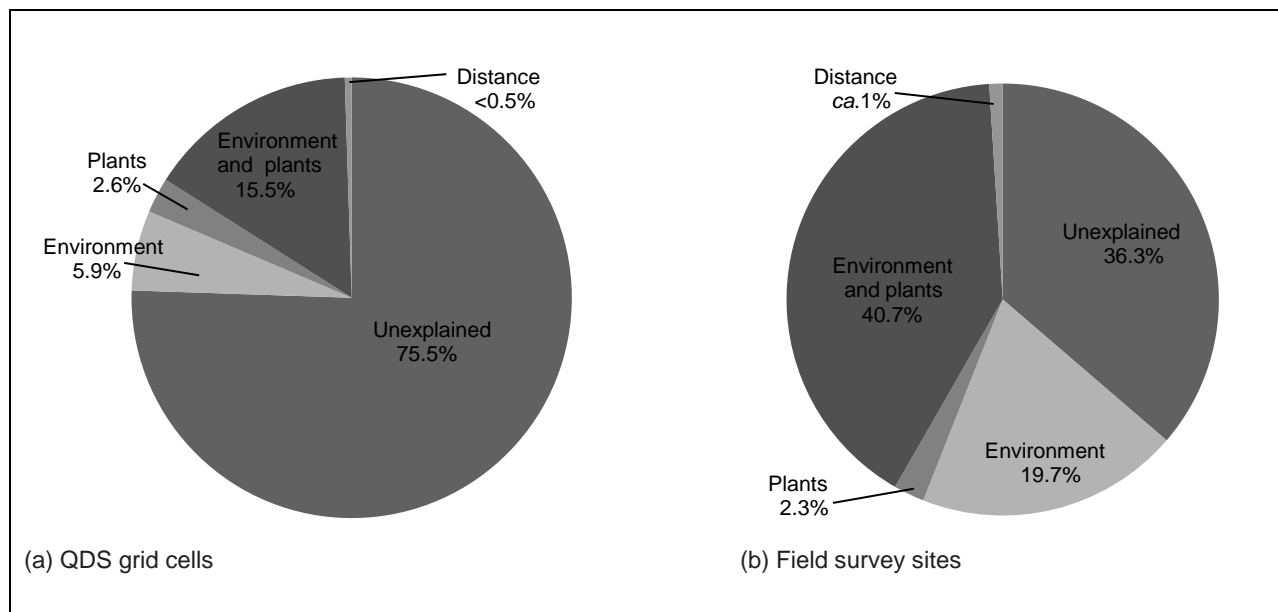
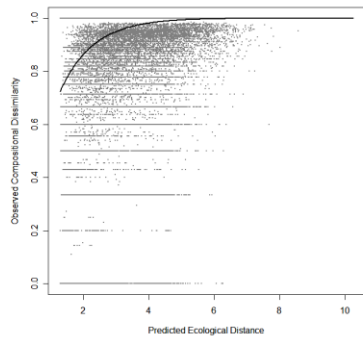


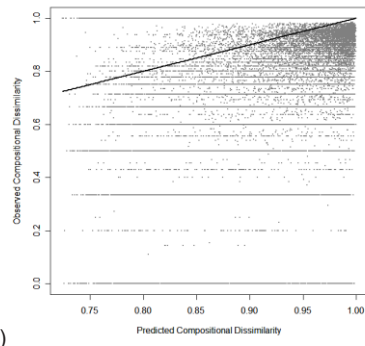
Figure 1. Partitioning of variances in observed dissimilarities explained by the fitted GDM models for (a) QDS grid cells and (b) field survey sites. The full model (environmental and plant predictors) for (a) explains 24.02% of the deviance in observed Bray-Curtis dissimilarity values; whereas, for (b) the full models explains 62.75%. Distance contributed virtually nothing to either model.

The zero readings recorded for all three I-spline function coefficients, for each of the three environmental predictor variables of topographic diversity, rainfall reliability, and soil fertility, suggested that these variables made insignificant contributions to explained patterns of beetle turnover. Of those variables for which monotonic I-spline functions were plotted (Figs. 2c-q), the height of each respective curve indicates the amount of beetle turnover associated with it, when all other predictor variables are held constant. Summer rainfall (SR), rainfall concentration (RCO), proportional area size of vegetation type, and ecological similarity between higher order vegetation categories showed high influence of these variables on beetle turnover (Fig. 2c, f, j, m, and n, respectively). Based on comparisons of the sums of their respective three fitted coefficients (I_c), RCO showed approximately 1.5 times more influence than WR (winter rainfall) and MWT (winter temperature); and 2.5 times more than MAR (annual rainfall) on beetle turnover. SR showed a similar I_c value to RCO. Based on summing all fitted coefficients across ordination scores for plant predictor variables, plant taxonomic composition was seen to be exerting almost three and six times less influence on beetle turnover than proportional area size of a vegetation type and ecological similarity between higher order vegetation categories, respectively. I_c values for individual ordination axes showed ordination axis_3 of ecological similarity between higher order vegetation categories having the largest influence on beetle turnover.

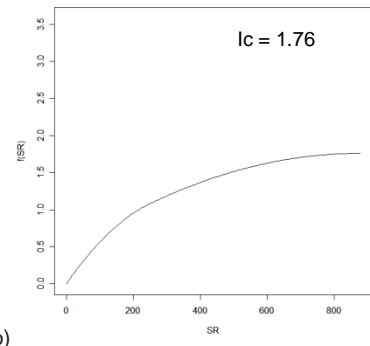
Furthermore, the respective slopes of functions having high influence on beetle turnover showed steep rates of compositional turnover varying along their measured gradients. Steepest compositional turnover was seen along rainfall gradients (SR and WR) of very low to medium rainfall, with a tapering off of turnover along gradients of high rainfall (medium to high). A similar pattern was seen for MAR with almost all turnover associated along the short gradient of low (<50 mm) to medium rainfall (*ca.* 400 mm). For rainfall seasonality, steep turnover rates were mostly seen along the entire RCO gradient. Winter temperature gradients (MWT) showed highest turnover along temperatures from below 0 to > 5⁰C. MWT is strongly correlated to altitude (Chapter 3) and the high turnover rate along this temperature range is most likely reflective of steep altitudinal gradients.



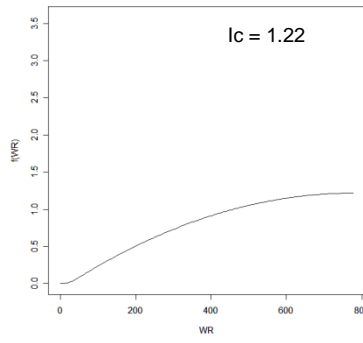
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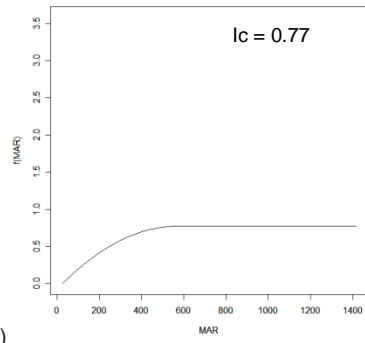
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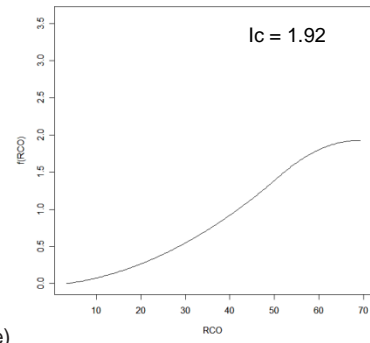
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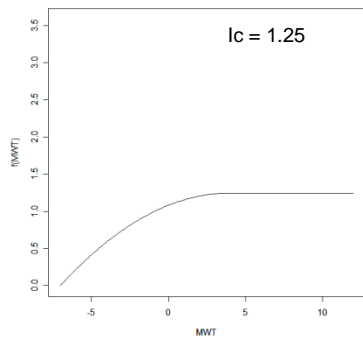
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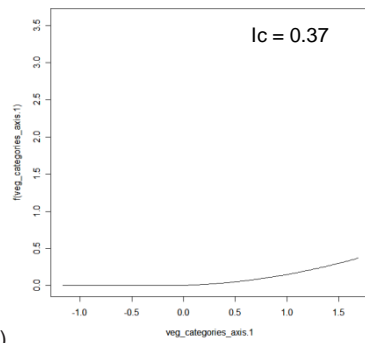
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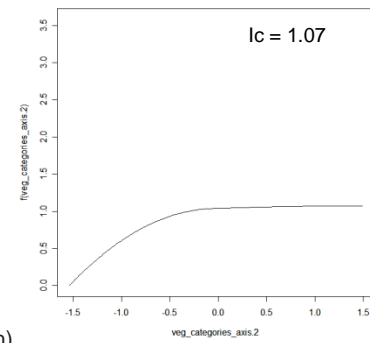
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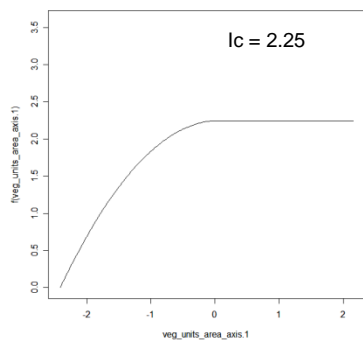
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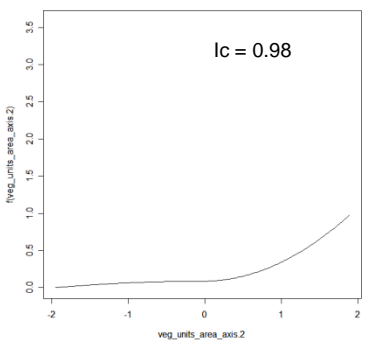
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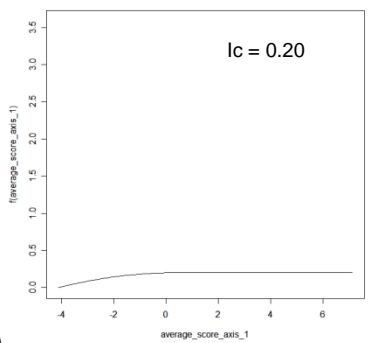
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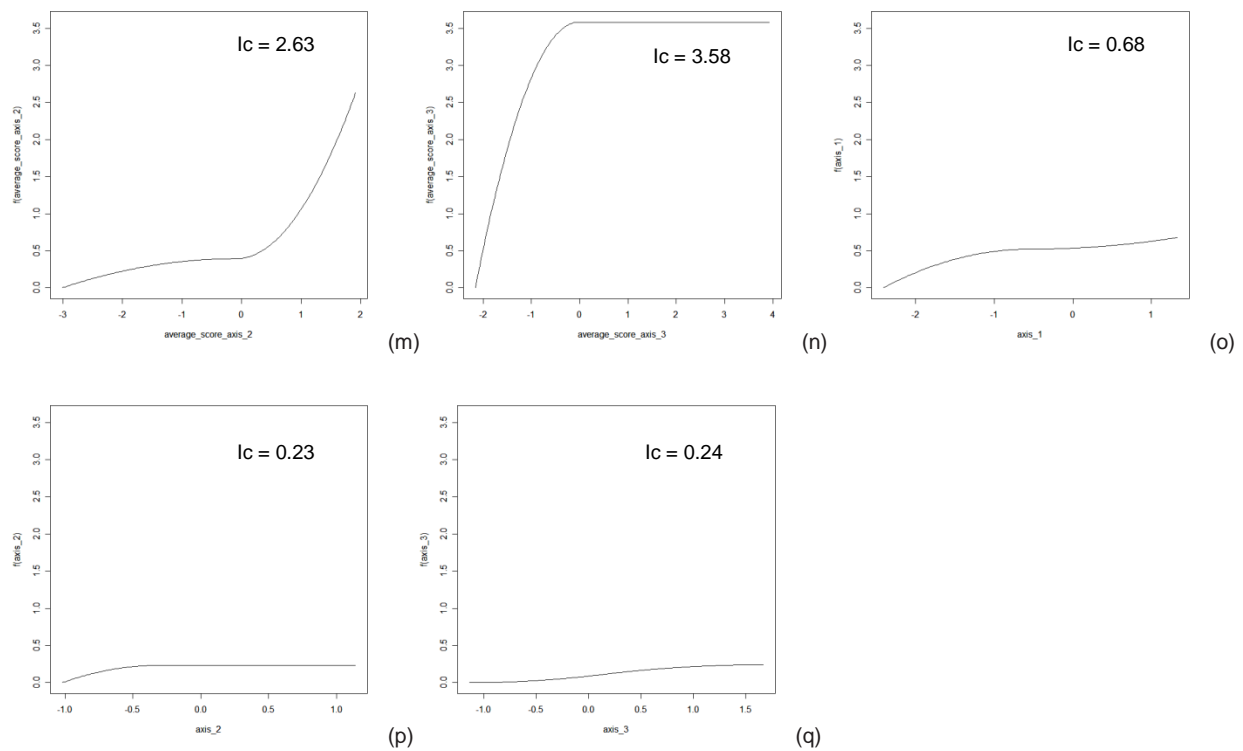
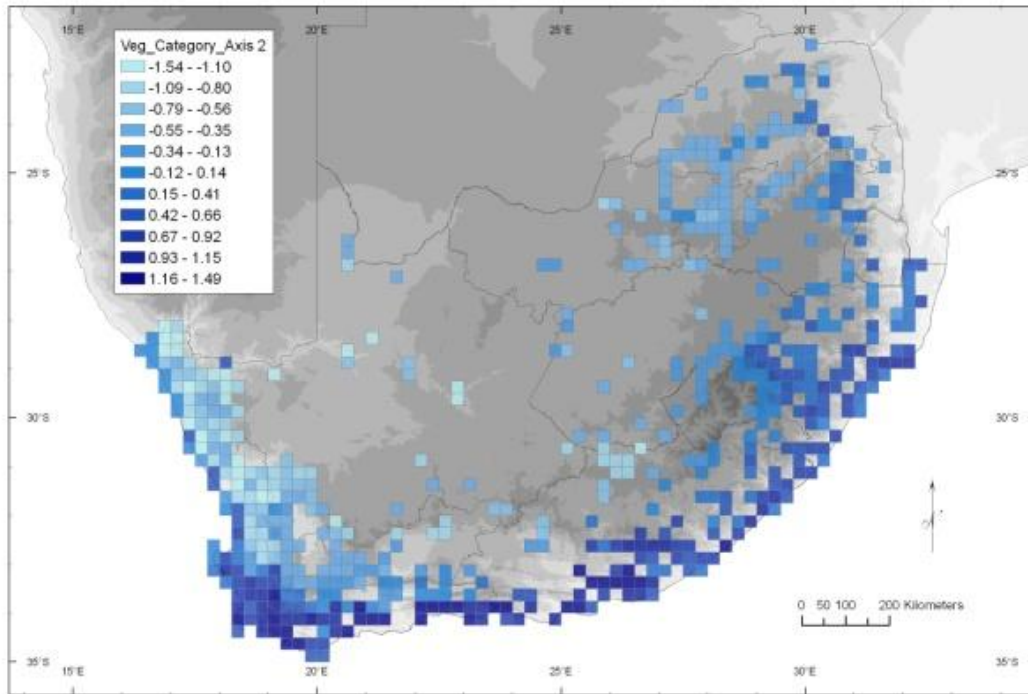


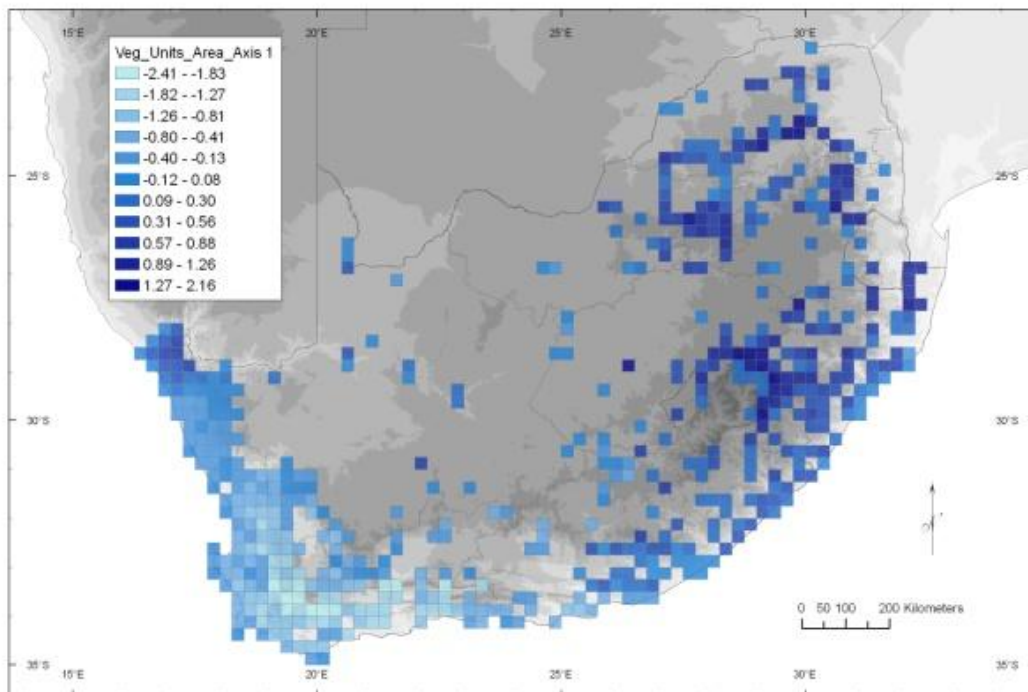
Figure 2. Plots for GDM model fitted to QDS grid cell data. Plot (a) shows an observed vs. predicted scatterplot with predicted ecological distance between QDS grid cells (i.e. the linear predictor from the fitted model) as the x-axis, and observed compositional (beetle) dissimilarity between grid cells as the y-axis. Points represent each possible grid cell pair from data frames used to fit the model. The inverse link function for the model is plotted as a line indicating where “observed equals predicted”. Plot (b) is a second observed vs. predicted scatterplot in which predicted ecological distance is transformed (using the inverse link function) into predicted compositional dissimilarity (i.e. between 0 and 1) and in which “observed equals predicted” is the 45 degree line shown on the plot. Plots (c-q) depict the smooth monotonic I-spline functions. Only those predictor variables with at least one fitted coefficient > 0 are plotted (see Ferrier et al. 2002, 2007 for full computation and statistical details on GDM model fitting). Summed I_c values are shown on plots for each predictor variable (see methods).

For plant predictor variables high rates of turnover were seen along gradients of single ordination axes for the two measures of vegetation types - presence/absence and proportional area size (Fig. 2i, j). Areas corresponding to these steep rates of turnover are seen in the maps of Fig. 3a, b. For vegetation types (presence/absence) composition, steep turnover rates are seen concentrated along gradients captured within the Succulent Karoo Biome (Fig. 3a)). Figure 3b shows steep turnover rates along gradients within the Cape Floristic Region (CFR – Goldblatt and Manning 2002). Ecological similarity between higher order vegetation categories showed two of its three ordination axes with very steep turnover rates varying along their respective gradients (see Fig. 2m, n; and Fig. 3c, d). Figure 3c shows steep turnover rates spatially corresponding to gradients within the western sections of the Succulent Karoo Biome, though incorporating xeric northern areas of the CFR. In contrast, Figure 3d shows steep turnover rates

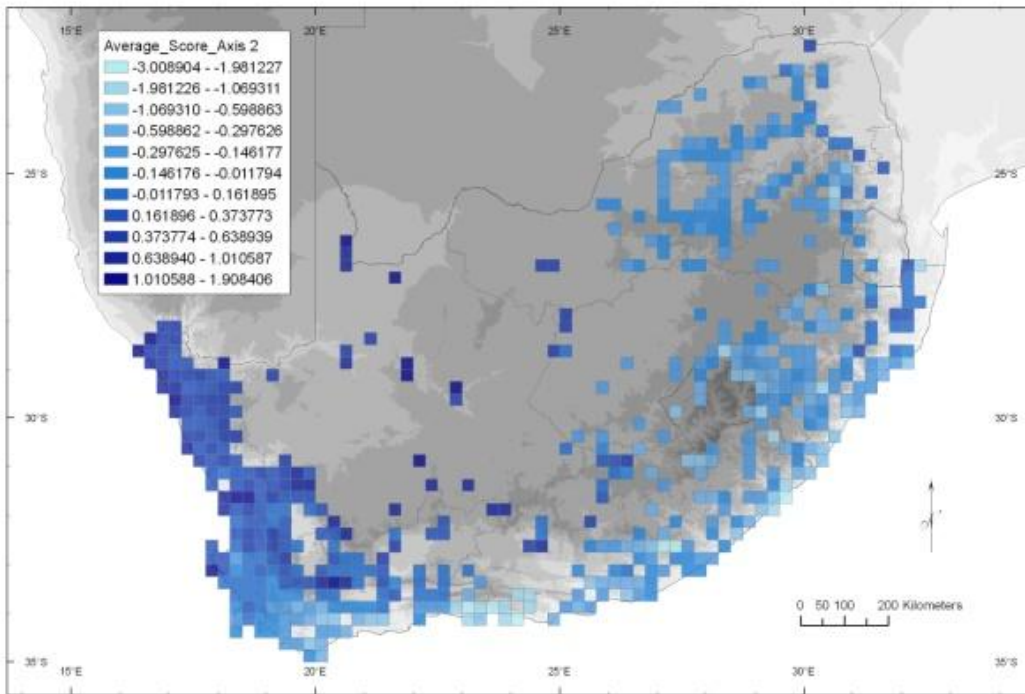
associated with gradients along summer rainfall interior areas (Grassland Biome (Mucina and Rutherford 2006)).



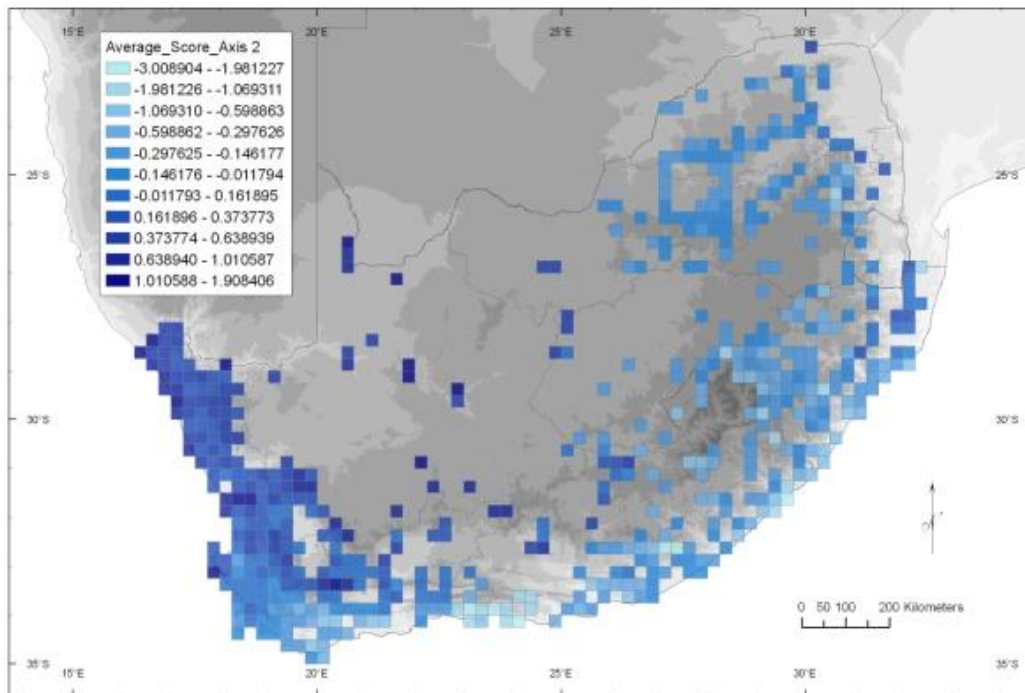
(a)



(b)



(c)



(d)

Figure 3a-d. Maps showing plant ordination scores for QDS grid cells for those plant predictor variables showing steep rates of beetle turnover varying along their respective gradients. From fitted I-spline plots, high rates of turnover were noted along gradients between (a) ordination scores of -1.5 to -0.5 for axis_2 of vegetation type (presence/absent); (b) -2.4 to 0 for axis_1 for vegetation type (area proportion); and (c) 0.5 to 2 for axis_2 and (d) -2 to 0 for axis_3 for ecological similarity of higher order vegetation categories.

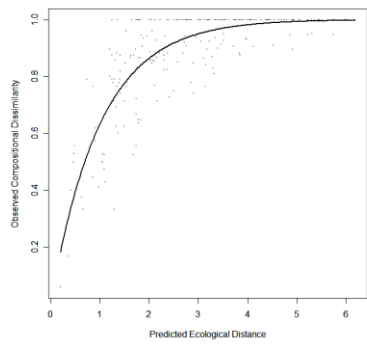
Field Survey Scale Analyses

A far larger percentage deviance in beetle turnover was explained at the field survey scale than at the QDS scale (Fig. 1b). A better model fit was achieved with more accurate presence/absence collated data (see Fig. 4a, b). At this scale, a GDM model with all environmental and plant variables explained 62.7% of deviance observed in beetle dissimilarity between field survey sites. As for the QDS scale, adding geographic distance to the full model improved the amount of explained deviance by only a small amount (approximately 1%). The overall deviance explained was portioned into 19.7% explained purely by environmental variables, 2.3% purely by plant variables, and 40.7% was explained jointly by environmental and plant variables.

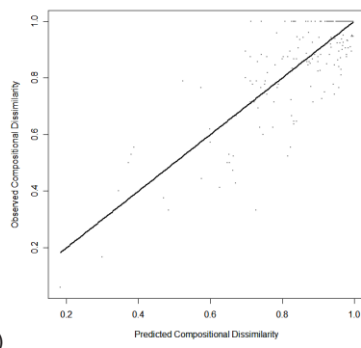
The variables annual rainfall (MAR), summer rainfall (SR), and disc-shaped flowers offering resources of ovaries, pollen and nectar, showed zero reading for all three I-spline coefficients and were thus considered to be making no contribution to the model. Other variables showing weak compositional turnover (low heights achieved by plots and low I_c values) included rainfall reliability (RCV), summer temperatures (MST), plant taxonomic compositional turnover (axes_1 and axes_2), and all remaining flower resource categories (Fig.4d, h, j, k, m-q, respectively).

Large amounts of compositional turnover were seen associated with altitude, rainfall seasonality (RCO), winter rainfall (WR), and winter temperatures (MWT) (Fig. 4 c, e, f, g, respectively). Based on comparisons of the sums of their respective three fitted coefficients (I_c), altitude showed approximately 15 times more influence than RCV, 6.5 times more influence than MST, 2.5 times more influence than soil fertility, and 2 times more influence than RCO and WR on beetle turnover. MWT showed a similar, but slightly lower I_c value to altitude.

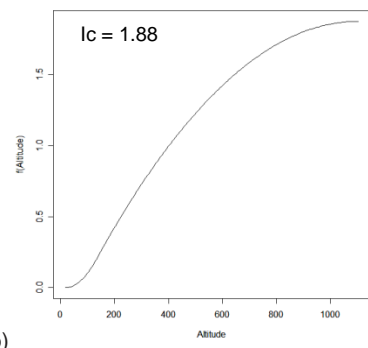
Altitude and MWT further showed the steepest rates of turnover along their respective gradients. As mentioned above, altitude and winter temperatures are strongly co-correlated. Steep turnover rates were also seen along a narrow rainfall seasonality (RCO) gradient (between 50-54%). A similar pattern was seen for winter rainfall (WR) gradients with steep rates of turnover seen across a low rainfall gradient (between 15 mm-80 mm mean winter rainfall). Quite steep beetle turnover was also seen along soil fertility gradients for SF scores > 1.5 . Of the three ordination axes for plant taxonomic compositional turnover, moderately steep turnover rates were seen along axis_3 (Fig. 4l).



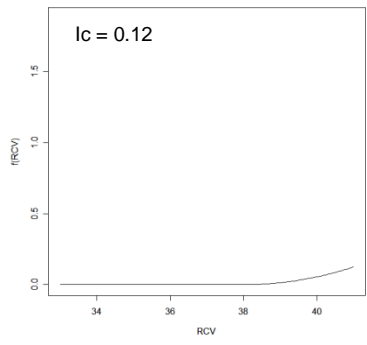
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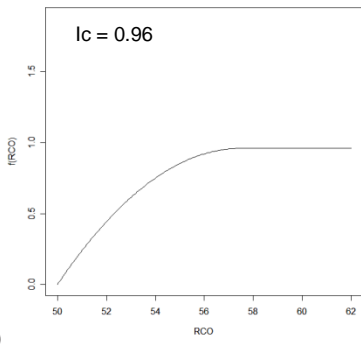
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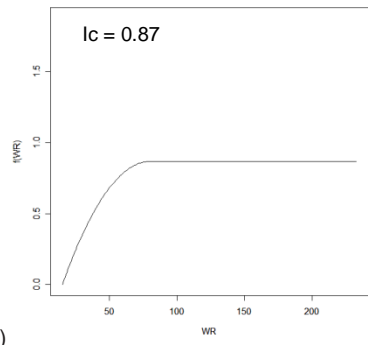
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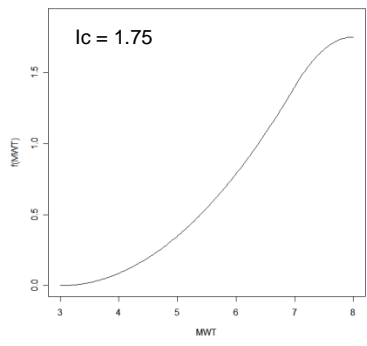
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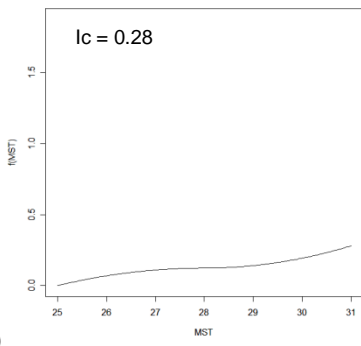
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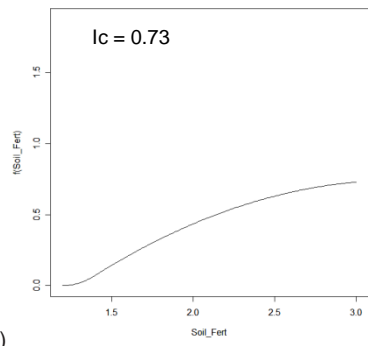
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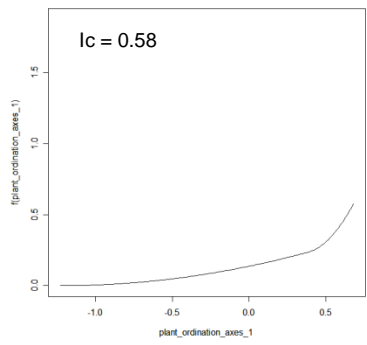
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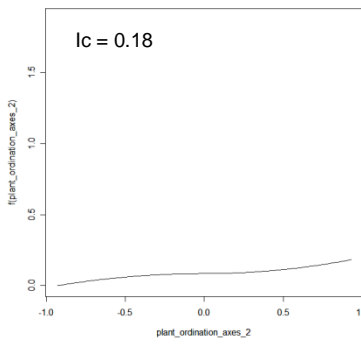
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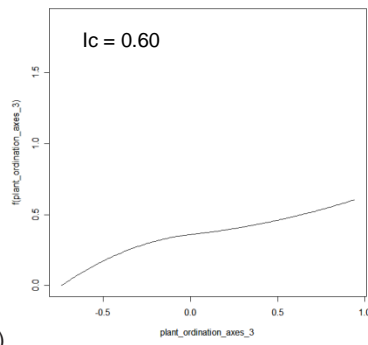
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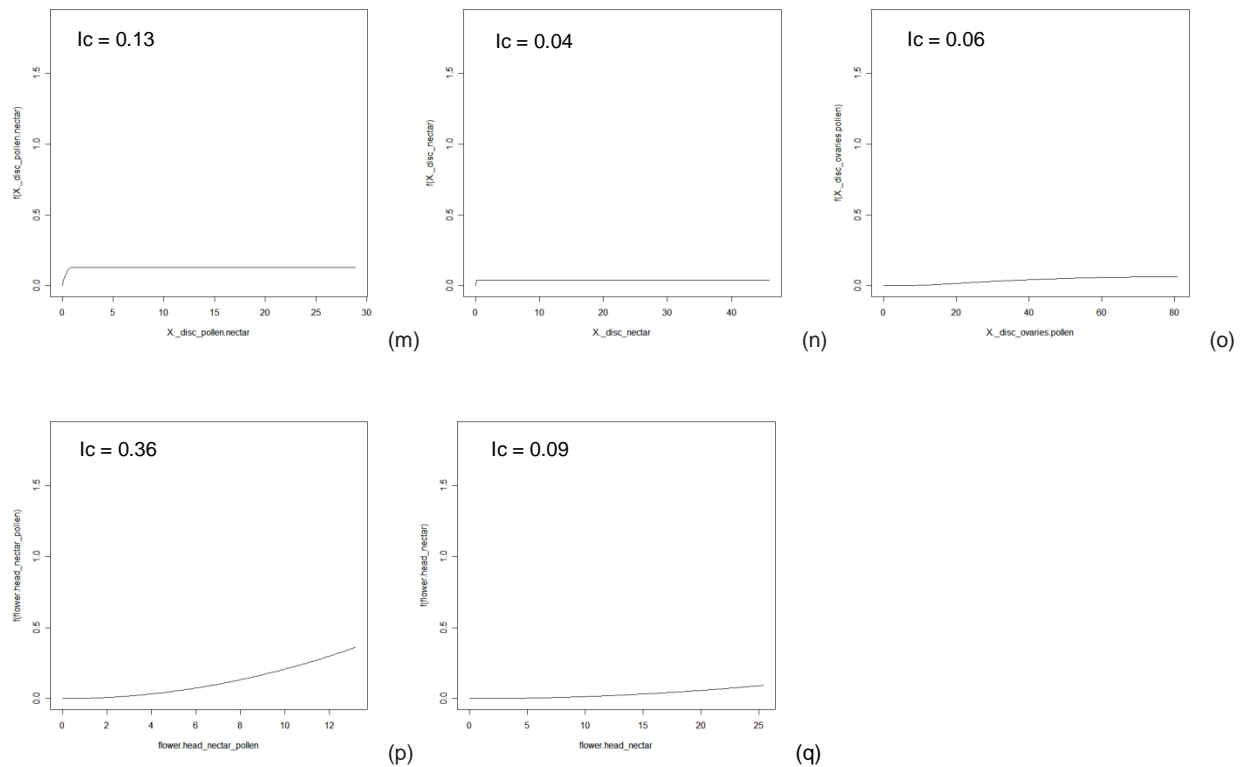


Figure 4. Plots for the GDM fitted model to field survey data. (For methodological details of plots see legend of Fig. 2).

DISCUSSION

PERCENTAGE VARIANCE EXPLAINED

Both GDM models at the two respective scales gave comparative results showing that monkey beetle turnover seems to be strongly correlated with both environment and plants, although driven slightly more by environmental differences than by plant turnover (i.e. higher % pure explanation). Furthermore, geographic distance between sites was seen to explain observed deviance by only negligible amounts for both data sets. The importance of component parts for predictor variables are discussed below.

Environmental Differences

At the QDS grid cell scale 5.9% of deviance in beetle compositional dissimilarity was explained purely by environmental variables (annual rainfall and seasonality, and winter temperature), whereas for the field survey data, 19.7% of deviance was explained (altitude, rainfall reliability and seasonality, temperature,

and soil fertility). Similar patterns were retrieved at both data sets, in terms of the relative importance (or lack thereof) of specific explanatory variables accounting for patterns of beetle species turnover.

Rainfall Gradients

Annual and Seasonal Rainfall

In general, environmental gradients of high importance in explaining beetle turnover were associated with various measures of rainfall. Across South Africa, seasonality of rainfall (summer (SR) and winter (WR)) showed strong influences on beetle turnover, particularly summer rainfall gradients. Mean annual rainfall (MAR) showed a weak influence on turnover (compare result of Steinitz et al. 2005 for Mediterranean terrestrial snails), indicating the greater importance of rainfall season. Interestingly, a steep rate of turnover was seen along a gradient from very low MAR to medium MAR, highlighting sharp turnover between arid and mesic areas. For areas receiving > 500 mm MAR, other factors over and above rainfall are influencing turnover. Varying rates of turnover were seen along summer and winter rainfall gradients, highlighting both the high turnover between areas of differing seasonal rainfall regimes, and within seasonal rainfall regimes. The initial steep slope of the SR curve (Fig. 2d) highlights the steep turnover along a gradient from winter \rightarrow aseasonal \rightarrow summer rainfall.

At the field survey scale, MAR and SR contributed effectively nothing towards the model, even though both SR and MAR showed high differences between field survey sites. Thus, the importance of rainfall season on beetle turnover is again highlighted. However, as seen for the QDS grid square data set, steep turnover along WR gradients are essentially restricted to fine-scaled gradients of very low (> 30 mm) to low (>70 mm) WR. Field survey sites along such gradients were located in the north-western arid Namaqualand, including coastal areas. Beetle turnover at WR > 70 mm is not influenced by winter rainfall, suggesting other predictor variables at play.

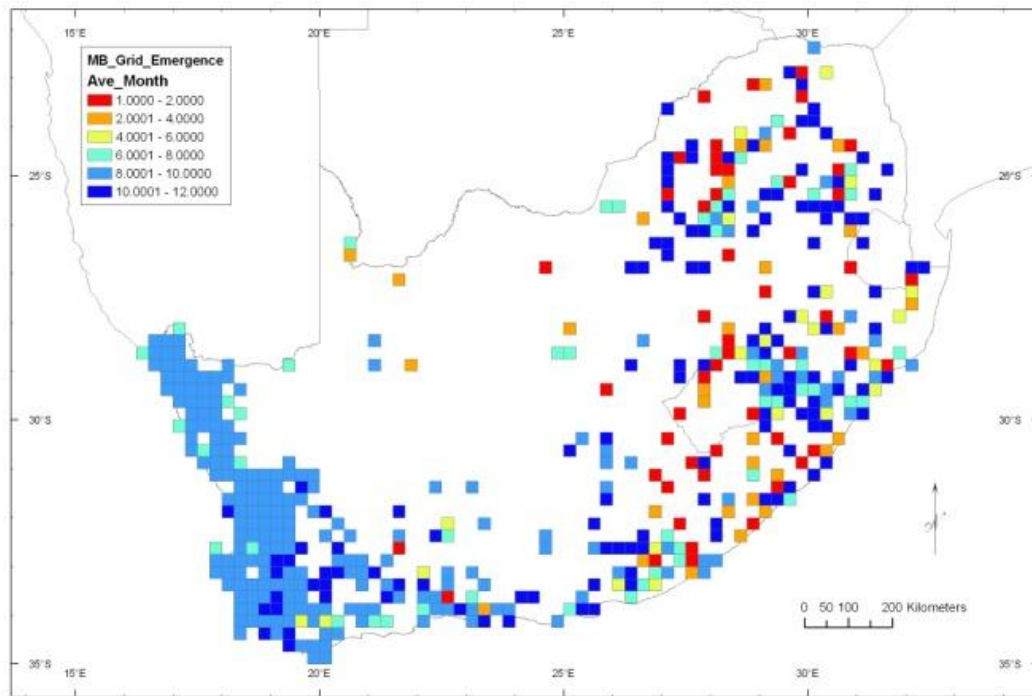
Rainfall Reliability

The weakness of rainfall reliability (RCV) as a predictor variable at both data sets was a surprising result. The use here of annual RCV is most likely obscuring the importance of more fine-grained effects of rainfall reliability. Monthly RCV values may be more appropriate, as used by Cowling et al. (1997) and suggested by Schulze (1997) and Thuiller et al. (2006). However, annual RCV values were used to assess whether consistency in annual rainfall was perhaps influencing beetle turnover, as the two beetle rich winter-rainfall biomes show low annual rainfall consistency (Schulze 1997). The importance of monthly

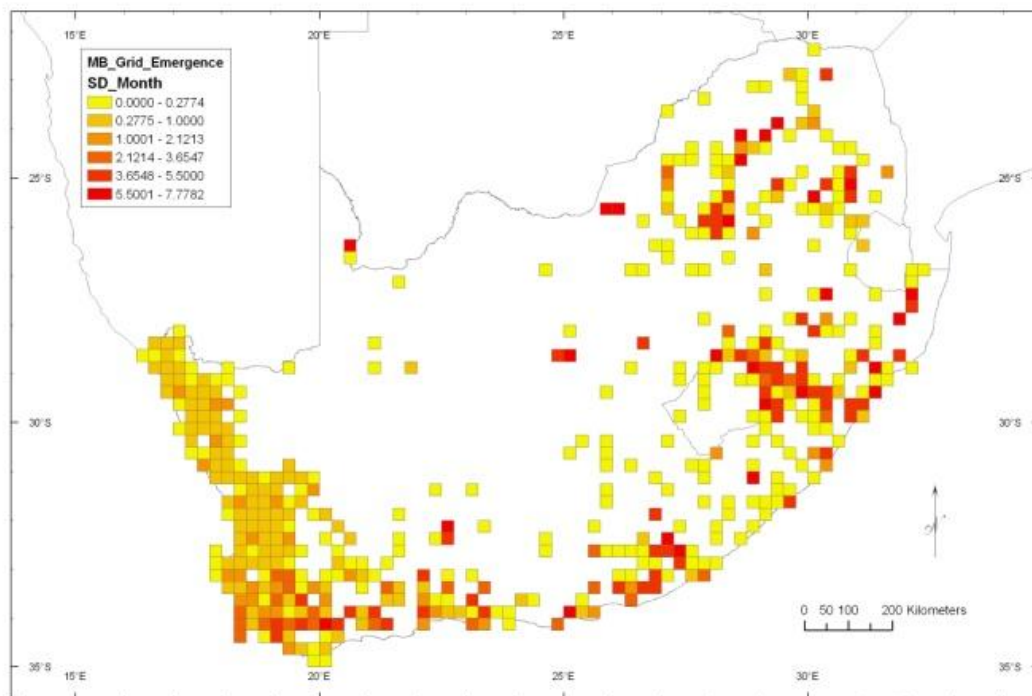
rainfall reliability is, however, most likely retrieved in the rainfall concentration (RCO) and seasonality measure used (see below).

Monthly RCV is high for the beetle rich winter-rainfall biomes (Cowling et al. 1997, Cowling et al. 1999), and is probably an important driver of beetle species richness, particularly for the arid western regions (cf. plants in Namaqualand (Cowling et al. 1998, 2005); and an equivalent finding to that observed for bees in arid ecosystems (Danforth 1999). Predictable rainfall would allow specialisation to occur (Currie 1991, Cody 1993) in that predictable rainfall implies predictable and reliable floristic resources (spring flowering – Struck 1994, Cowling et al. 1999). Thus, specialisation in monkey beetles may be reflected in feeding strategies (guild partitioning - Picker and Midgley 1996) and/or predictable resources would allow specialisation to occur within other life history attributes (e.g. mating strategies) by reducing stresses of, and associated adaptations towards, unpredictable resource availability, e.g. well-developed long-term dormancy strategies associated with physiological adaptations (Danforth 1999; and see Proches et al. (2005) showing lack of specialisation of geophytic organ storage size in reliable winter rainfall areas in contrast to non-reliable rainfall areas which show high specialisations).

This pattern of adaptation towards reliable rainfall was confirmed from extensive field observations (during this study) that indicate spring insect emergence, for pollinating and non-pollinating groups is highly predictable within the winter and spring flowering months of the winter rainfall biomes (see Fig. 5a, b). However, the emergence, at least for several pollinating groups, appears to be irrespective of the extent of that year's winter rainfall, suggesting that the high RCV values for winter-rainfall areas has allowed a decoupling from this variable for some insect groups, including monkey beetles (Fig. 5a, b) (see also Struck 1991 and Mayer and Kuhlmann 2004). Since emergence times appear to be "set" in monkey beetles, the timing of rainfall events (concentration/seasonality) should be of high importance (see discussion below). This is in contrast to other Mediterranean systems where insect emergence is highly temporally (yearly) variable, but flowering times of plants are consistent (Petanidou and Ellis 1993; and see Esler et al. 1999 and Cowling et al. 2005 for high RCV values for South African winter rainfall regions in contrast to other Mediterranean and arid regions). Furthermore, other arid systems with high unpredictable rainfall are geared towards opportunistically timed resource pulses, whereby insects respond to unpredictable environmental cues (e.g. rainfall), as do their respective host plants, having been able to remain dormant for many months or years as a larva, pupa, or egg (Danforth 1999, Danks 2006).



(a)



(b)

Figure 5a-b. Beetle emergence patterns showing (a) mean emergence times per QDS grid cells and (b) the variation (standard deviation) in emergence times. Maps collated from collection record data for 659 species (5546 unique locality records with an average of 8 records per species). Western winter rainfall areas show narrower emergence times with less variation, particularly the more xeric areas, compared to aseasonal and summer rainfall areas. [Months of the year correspond sequentially to numbers on map, i.e. 1 = January, 2 = February, etc.]

Rainfall Concentration

Based on Ic scores, rainfall concentration (RCO) showed strong influence on beetle turnover along gradients of low seasonality to high seasonality across South Africa. Steep gradients of seasonality in rainfall are seen within South Africa (Schulze 1997); with rainfall concentrated within a few winter months (e.g. Namaqualand), or within a few summer months (e.g. savannah and grasslands), or strongly aseasonal (e.g. eastern CFR). RCO values are embedded within the three broad rainfall seasons found within South Africa.

Within the winter-rainfall regions, particularly the arid north western areas, high RCO values are linked with resource-pulsed systems in that short spells of low, but reliable rainfall result in brief periods of mass spring flower displays (Desmet 2007). Monkey beetle eggs hatch in response to winter rainfall, larvae grow during the winter months with adult emergence coinciding with spring flowers (Colville unpublished data). Thus, beetles within such areas have specialised their life history traits towards a brief, but reliable and abundant (see Table 4) floristic resource. Such specialisations would possibly include dormant, drought resistant eggs that are able to withstand the seasonally dry summer, fast larval growth during wet winter months, and with short pupation periods, ending predictably during the spring months with adult emergence (Figs. 5a,b). This brief life history growth pattern is similar to the annual plant component of the winter rainfall biomes (van Rooyen et al. 1991; and see also Danforth (1999) for Mediterranean bee life history traits resembling that of annual host plants).

In contrast to the arid Succulent Karoo, pulsed spring flower displays appear to occur later in the year within the CFR (Pierce 1984, Johnson 1992), and are of longer duration, extending into the summer months. Beetle emergence data reflects this pattern (Fig. 5a, b). Moreover, the CFR receives higher annual rainfall, and lower concentration, i.e. extending over several months. Thus, the selective pressures of a short pulsed system associated with Namaqualand are of possibly less consequence in the south western CFR. The importance of RCO in influencing turnover between areas of differing degrees of seasonality (Succulent Karoo and CFR) is seen for the field survey data with steep turnover along short gradients across short geographic distances from lower seasonality (sites within south western CFR – e.g. Melkbosstrand) to areas of higher seasonality (Namaqualand - Doringbaai). Shifting into the south eastern areas of the CFR, aseasonal rainfall habitats prevail. Here beetle life history traits are possibly more geared towards an unstable climate (Cowling and Lombard 2002) and weaker pulsed resource component, as seen by higher variability in beetle emergence times (Fig. 5b). Abundance and diversity of bulbs and annuals are markedly less within these areas compared to western parts of the CFR (Goldblatt and Manning 2002). Thus, greater demand for foraging specialisations are possibly at play, as seen in the

dominant genus within this area *Eriesthis*, which consists of relatively small-sized, mobile beetles. Similar constraints are possibly also associated with the northern summer rainfall grassland and savanna regions. Although these regions have high seasonality (Schulze 1997), similar to Namaqualand, mass flowering displays such as those seen in the winter-rainfall areas are all but absent. As such, resource availability is possibly limited and more unreliable, as suggested by the presence of non-anthophilic species found here and by the high variability in emergence patterns across these areas (Fig. 5b). It would be interesting to investigate emergence cues and larval biologies between winter rainfall and summer rainfall species, as summer species may show greater adaptability towards, and synchrony with host plant blooms, and better-developed physiological adaptations towards longer dormancy in resting stages and/or longer larval growth periods.

The reliability and abundance of this floristic resource has possibly allowed beetles within these arid north western areas to specialise further in terms of mating strategies and associated development of elaborate secondary sexual traits (colour sexual dimorphisms, exaggerated hind leg morphologies in male beetles). This is evident within the two broadly recognised monkey feeding guilds— Embedders and Non-Embedders (Picker and Midgley 1996). Embedders, which show strong sexual dimorphism in hind leg traits, feed deeply embedded within the flower heads (capitulum/hypanthium) of mainly disk-shaped ‘daisy’ flowers of Asteraceae and Aizoaceae. Males of this feeding guild compete for females in male-male contests using their enlarged hind legs. Non-embedders share a number of host plant with Embedders; however, they are generally associated with non-daisy type flowers, e.g. shallow bowl-shaped petaloid geophytes (Iridaceae) (Picker and Midgley 1996, Goldblatt et al. 1998, Steiner 1998a,b) and flowers occurring in inflorescences, e.g. Rutaceae, Rhamnaceae, Orchidaceae (Steiner 1998b, Chapter 3). Furthermore, they do not embed into flower heads and feed predominantly on pollen and nectar (Johnson and Nicolson 2001). Non-embedders also show low levels of sexual dimorphism in hind leg structure, with male-male contests being far less competitive and aggressive than that seen for Embedders (Chapter 5).

The large, muscular hind legs of male Embedding beetles have most likely been at the cost of compromised flight abilities (and see discussion below on dispersal). Furthermore, secondary sexual traits have been shown to be energetically costly to produce (Anderson 1994, Pomfret and Knell 2006). This implies that selection stresses are rather towards reproduction than traits specialised towards resource foraging and feeding. Within their feeding guilds, beetles are mostly highly generalist feeders, visiting flowers across plant species, genera, and families. However, some specialisation is seen in mouthpart structure for those species feeding on nectar and pollen (Johnson and Nicolson 2001). The concentration of large sized beetles displaying such sexually selected traits within the Succulent Karoo suggest that this

hypothesis is mostly likely correct. Whether selective forces on reproductive specialisations are more conducive to higher divergence and speciation rates than selective forces on physiological and morphological specialisations for e.g. foraging and feeding behaviours is unknown. However, the lack of influence of geographic distance on turnover rates (see discussion below) possibly suggests that high turnover seen over short distances across almost uniform habitats (e.g. across neighbouring Strandveld sites) is a result of divergence within sympatric populations due to sexual selection. There are a number of monkey beetle species complexes within the Succulent Karoo, with sympatric species showing high morphological similarities (colour, shape, size), but strong dissimilarities are seen between male genitalic morphologies (Dombrow pers. comm.), suggesting that sexual selection is possibly causing divergence in populations and therefore, possibly increasing species turnover.

Thus rainfall concentration appears to be associated with both a resource availability/reliability gradient and associated specialisation/emergence/foraging/feeding guild gradients. Furthermore, the narrow emergence times, particularly for the Namaqualand areas, possibly may act as a strong mechanism for disrupting gene flow between populations, as peak beetle emergence between populations of species occurring in contrasting rainfall regimes will be temporally separated. As such, divergence may occur, possibly reflected in high species turnover across these gradients.

Topographic Diversity and Altitude

At the QDS grid cell scale the weakness of topographical heterogeneity (TD90m) as an explanatory variable of beetle compositional dissimilarity was surprising. This variable effectively contributed nothing to the GDM model. It was expected, and based on other studies (Samways 1989, Linder 1991, Simmons and Cowling 1996, Cowling et al. 1989, Cowling et al. 1997, Davis et al. 1999, Kerr et al. 2001, Prendini 2005, Latimer et al. 2005, Botes et al. 2006, Thuiller et al. 2006, Botes et al. 2007) that high differences in topographical diversity should be reflective of extensive ecological gradients (niche width and diversity), which in turn would promote species turnover, either through habitat specialisation or divergence as a result of limited gene flow (cf. plants - Linder 1985). However, adequate measurements of topographic heterogeneity for operational geographic units (e.g. QDS grid cells) are unclear and difficult to select in order to obtain a true representative of actual landscape level topographic diversity (compare measures used by Cowling et al., 1997 with Thuiller et al., 2006; and see also Cowling and Proches 2005). The measure of topographic diversity used herein was strongly correlated (Spearman Rank correlation: $N = 339$; $r_s = 0.83$, $P < 0.0001$) with altitude and the weakness of topographic diversity as an explanatory variable is possibly due to the effect of altitude overriding topographic variation.

The possible crudeness of the measure of topographic heterogeneity used herein is highlighted by the findings and observations at the field study scale, which showed high species turnover along altitudinal gradients (see Fig. 4c). The highest I_c value was recorded for this predictor variable - approximately five times greater than for other environmental predictors. The influence of this variable was perhaps biased by the selection of several field sites along steep altitudinal gradients (see Botes et al. 2007). However, steep turnover rates were also seen across narrower altitudinal gradients extending from coastal sites inland (coastal Strandveld → eastern HV neighbour sites; see Appendix 2). These altitudinal gradients are complex, associated with changing environmental and floristic gradients (see McCoy 1990, Novotny and Weiblen 2005, and references therein). Coastal sites are low altitude areas, low rainfall areas, whose summer temperatures are ameliorated by sea breezes and fog banks. Inland, HV sites are marginally higher lying areas, with approximately double WR rainfall, although summer temperatures are more extreme due to the lack of temperature amelioration by coastal influences (Desmet 2007). Mountainous sites are high altitude, high rainfall, and fynbos montane habitats. Thus, from field survey results, altitudinal gradients represent rapidly changing ecological gradients, acting over remarkably short geographic distances (<1000 m). Altitudinal gradients are also strongly reflective of historical processes in that montane peaks act as refugia (“Pleistocene refugia” – Stuckenberg 1962) for palaeoendemic taxa (see also Colville 2006). Thus, these peaks have long histories of isolation (Wishart and Day 2002) and possibly reflect *in situ* speciation through vicariance on fynbos peaks, with little or no movement off these peaks as they represent islands of favourable climates (Endrödy-Younga 1988).

The importance of altitude influencing beetle turnover at the regional scale is possibly retrieved in the measure of winter temperature (MWT), in that this variable is strongly correlated with average altitude (Spearman Rank correlation: $N = 339$; $r_s = 0.89$, $P < 0.0001$). The third highest I_c value was obtained for this variable at the QDS grid cell scale, with steep beetle turnover recorded between MWT of approximately -5°C to 2°C , concordant with high altitudes (see Schulze 1997). This result is supported by finding for dragonflies (Samways 1989), dung beetles (Davis et al. 1999), ants (Botes et al. 2006), and ground-dwelling beetles (Botes et al. 2007), which show high species turnover associated with steep altitudinal gradients extending from Natal subtropical coastal areas through to high alpine montane peaks of the Drakensberg Mountains.

Temperature and soil Fertility

Summer temperature regimes (MST) across the main distributional ranges of monkey beetles are fairly uniform (Schulze 1997) and it is therefore not surprising that this variable had low explanatory power. Furthermore, for beetle rich areas in the arid western regions of the Succulent Karoo, where MST is

possibly expected to be an important physiological stress for soil dwelling larvae, cool coastal sea breezes and coastal fogs moderate summer temperatures to similar levels experienced in other parts of the region (Desmet 2007).

Similar poor explanatory power was seen for the field survey data, with low species turnover associated with MST. This finding is in contrast to that found for ants and ground-dwelling beetle assemblages within north-western areas of the CFR, and along similar (although more extensive) altitudinal gradients, as used in this study, which showed strong assemblage structuring along temperature gradients (Botes et al. 2006, 2007). However, these three insect groups have strongly contrasting ecological and biological attributes suggesting that differing environmental variables would be of greater ecological importance to each of them. Nonetheless, the importance of these findings is that they highlight the variability across taxonomic groups in environmental variables determining assemblage compositional similarities (see also Chapter 3).

Measurements of Soil fertility gradients used here were most likely inadequate as edaphic measurements for monkey beetles being too unrefined. However, limited soil measurements are available for regional scale analyses within southern Africa (see Schulze, 1997). In addition, for the unrefined SF measure used, large areas of South Africa show similar fertility scores (see Schulze 1997), and ecological differences between site pairs appear to be low. This was also seen for field survey sites, with moderate levels of turnover associated between low fertile coastal soils (Strandveld sites) and higher fertile inland sites. However, this gradient is possibly a surrogate for vegetational changes (see Simmons and Cowling 1996). Furthermore, the influence of this gradient appeared to be overshadowed by rainfall and altitude gradients. Monkey beetle larvae have only very recently been discovered (2003 – Colville unpublished data); with initial observations indicating that beetle larvae are unspecialised in terms of edaphic requirements; with a basic requirement of sufficient soil organic matter the most important. Better measures of edaphic requirements should in future include percentage soil organic matter and possibly a soil moisture and temperature measurement as well (cf. Botes et al. 2006).

Plant Variables

Lower explained percentages of deviance were seen for plant variables than for environmental variables, with 2.6% at the QDS grid cell scale and 2.3% at the field survey scale explained purely by plants. Reasonably high percentages of explained deviance in beetle turnover were linked with that component of deviance explained jointly by environmental and plant variables, i.e. this proportion could not be allocated to either variable, due to correlation between them. Nonetheless, plant variables, particularly

those measuring compositional similarities between higher order vegetation units, showed high beetle turnover associated with their respective gradients.

Compositional Dissimilarities

Taxonomic compositional dissimilarities were the weakest of the three plant predictor variables used. Only a handful of beetle species appear to be specialised on specific host plants, with most beetle species feeding off a wide range of plants, across familial and generic levels. Thus, this plant taxonomic variable is possibly too fine-grained to influence beetle turnover (Novotny et al. 2002, Proches et al. 2009). This pattern was also seen at the field survey scale with only limited levels of turnover associated with taxonomic compositional dissimilarities between study sites. Furthermore, several of the host plant taxa recorded from field sites were commonly encountered across sites; however, very few beetle taxa tracked these host plants. Therefore, beetles appeared to be associated with habitats and not individual host plants. This possibly emphasises the poor dispersal abilities of some beetle species and/or other factors preventing host plant tracking. This finding is in contrast to herbivorous insects in tropical forest (see Novotny and Weiblen 2005, Novotny et al. 2007). Furthermore, the prediction of low beta diversities of insects associated with wide-spread plant taxa (Novotny and Weiblen 2005) is also not supported by the findings here, as wide-spread monkey host plants show strong dissimilarities in beetle visitors across their distributional ranges.

Proportional Area of Vegetation Types and Ecological Dissimilarities Between Bioregions

Stronger influence was seen for plant variables reflecting more three-dimensional ecological differences in terms of habitat complexities (vegetation structure and floristic composition of vegetation types and bioregions - see Mucina and Rutherford, 2006). At the QDS data scale, vegetation variables of particularly high influence on beetle turnover were associated with compositional differences in proportional size of vegetation type within QDS grid cells; possibly an indication of vegetation habitat heterogeneity (i.e. small proportional sizes of large number of vegetation types) and/or proportional differences in size of vegetation types which support high or low numbers of beetle species. Particularly steep rates of beetle turnover were seen along gradients for this plant variable within core areas of the CFR (Fig. 3b), mostly centered on mountainous areas of complex topography, thus highlighting the importance of vegetation habitat heterogeneity in explaining turnover patterns.

Ecological dissimilarities between the higher vegetation groupings of bioregions showed the highest influence on beetle turnover amongst the plant variables used (approximately on average four times more

influence). Steep beetle turnover rates were seen across gradients within the Succulent Karoo and northern interior summer-rainfall areas (Fig 4 c, d). This vegetation variable highlights the importance of compositional dissimilarities in host plants across higher vegetation units, i.e. the differences between vegetation types, especially those that are floristically similar or contiguous, may not be of importance to beetles, due to their vagility and/or generalist feeding behaviours. However, bioregions encompass greater vegetational complexities (a suite of vegetation types and floristic diversities) more reflective of the scale that some beetle species possibly perceive differences across landscapes. Gradients spanning higher order vegetation categories can occur frequently over short geographic distances (e.g. transitional areas –see van Rensburg et al. 2004), particularly within the winter rainfall biomes, highlighting the high habitat heterogeneity of these areas.

Flower Resource Abundance

Measures of resource abundance at the field survey scale (number of flowers per m² of plant cover) showed poor predictive influence on beetle turnover. Two of the variables (disk shaped flowers with ovaries, pollen and nectar as resources, and tubular flowers offering nectar as a resource) made no contribution to the GDM model. These two flower resource categories represent the most generalist and specialist of feeding categories. Disk shaped flowers offering the full range of resources are the most common of resource offered and utilised by beetles across their distributional ranges. Thus, the most wide-spread and most generalist of beetle feeding guilds are found associated with this resource, and most likely show the least dissimilarities between beetle assemblages. On the other extreme, beetles feeding on tubular flowers are highly specialised, rare, and locally restricted, and thus also possibly contribute minimally to differences in beetle assemblages. However, the flexibility in feeding strategies of beetles can be high, as seen during poor flowering seasons, when beetles utilise almost all, and any available flower resource. Therefore, categorising flower resources into specific categories may not be necessary, and instead a total measure of floristic resource, encompassing broad-scale floristic categories utilised by beetles, may possibly be more reflective in predicting beetle turnover. Such broad-scale categories could be divided on flower shape, as in addition to flowers providing food, they are also important as mating platforms for beetles; most notably, disk-shaped flowers. Additionally, the relationship between quantity and quality of pollen (energy: protein ratios), and/or energy content of nectar may reveal better explanatory relationships (see Petanidou and Vokou 1990, Potts et al. 2003).

Geographic Distance

One of the most interesting and surprising findings of this study was the very minor proportion explained in beetle turnover by geographic distance (Fig. 1a, b). It is expected that with increasing distance (space)

between sites pairs, less and less species are shared between respective sites (Gauch 1973, Cody 1993). With increasing distance, differences in ecological gradients increase (Rosenzweig 1995, Kerr et al 2001), as do evolutionary differences (phylogenetic relatedness – see Ribera and Balke 2007). However, strong differences in beetle composition between both geographically near (lack of spatial autocorrelation –see Tuomisto et al. 2003, Beck and von Khen 2007) and distant sites were noted (see similarity matrix of Appendix 2), i.e. the curvilinear relationship associated with compositional dissimilarity and geographic separation reaches the asymptotic value of 1 (100% dissimilarity) relatively quickly. On average, across all site pair comparisons, sites only shared 12.03% (± 17.36) of species with each other (see Appendix 2). This is in sharp contrast to other winter rainfall systems which show high percentages (27-59%) of shared insect pollinators between sites (Petanidou and Ellis 1993, Potts et al. 2003). The pattern retrieved here suggests weak dispersal abilities of species and/or high fidelity to floristic habitats (habitat specialists and rare local endemics – see Latimer et al 2005, Cowling and Proches 2005) and/or physical characteristics of the landscape limiting dispersal, i.e. steep environmental gradients (see Condit et al. 2002, Tuomisto et al. 2003). Furthermore, this observed pattern further suggests that local communities are not representative of a large proportion of the regional species pool. This pattern is in contrast to that recorded for some herbivorous insects in tropical forests, which show low beta diversity (local species represent a high proportion of the regional species pool) associated with lack of dispersal limitations allowing tracking of plant resources across large geographic distances (Novotny and Weiblen 2005, Novotny et al. 2007; but see Beck and von Khen 2007 for contrasting pattern).

Dispersal abilities appear to be most limited in the embedding monkey beetle feeding guild. Species within this guild are generally clumsy fliers more typical of large scarab beetles. Females remain embedded in flowers for extended periods. Furthermore, males of most Embedders have highly exaggerated hind leg morphologies and have possibly compromised flight abilities by increased size and musculature of hind legs for male-male combat. Thus, lack of dispersal will cause limited gene flow between populations; most notably across ecological gradients, resulting in divergence. However, limited dispersal abilities have also been seen to increase differences between communities within a homogenous habitat matrix (Hubbell 2001, and see Beck and von Khen 2007), e.g. as seen between the ecologically similar and geographically close HV sites of Vanrhynsdorp and Nuwerus (see Table 1). In contrast to Embedders, Non-embedding species are highly accomplished fliers, suggesting that they have the ability to fly long distances. However, high species turnover is also noted in this guild indicating other constraints limiting distribution. Such limitations may include the steep ecological gradients (see e.g. Samways 1989) associated with complex topographies (e.g. the Fold mountains of the south western Cape) and high habitat heterogeneity (Linder 1985). Several studies have highlighted geographic

speciation in association with strong vicariant barriers (Stuckenberg 1962, Endrödy-Younga 1988, Wishart and Hughes. 2001, Latimer et al. 2005, Prendini 2001, 2005). Moreover, the speciose non-embedding genus *Anisonyx* contains a high proportion of palaeoendemic species confined to montane relictual habitats highlighting the narrow habitat requirements for this genus.

Unexplained Variation Component

Of further interest in this study was the unexplained component of variation in beetle dissimilarity seen for both data sets, although particularly at the regional QDS grid scale (see Duivenvoorden et al. 2002, Faith and Ferrier 2002, Steinitz et al. 2005, Chust et al. 2006 for comparison). No doubt, the poorer quality of the data at the QDS scale is influencing the result to some extent. The QDS scale consisted of presence-only (“false” absences) beetle records, whereas the field survey data was collated by a systematic approach, and reflected well-surveyed presence/absence data. Although of importance for biogeographical and biodiversity studies, presence-only data may contain taxonomic errors of identification, collector biases (inadequate sampling of rare species – see Erwin 1991, Gaston 1991), and possibly large numbers of “false” absences (see Graham et al. 2004, Elith et al. 2006). Such “noise” in presence only data sets could influence the predictive capabilities of models and underscore the influences of plant and environmental variables. This is most likely of high relevance for insect data sets due to the exceptionally high numbers of insect species (difficulty in collecting all species from a site) and relatively poor taxonomic knowledge for many groups (difficulty in separation into discrete taxa) (see Novotny and Weiblen 2005, Novotny et al. 2007). An alternative approach to account for the weaker predictive capabilities of presence only data models would be to use the finer-scaled survey data as a surrogate data set to predict or “fine-tune” broader scaled models (Ferrier 2002, Elith et al. 2006). This approach appears to be particularly useful for applied conservation planning processes (Faith and Ferrier 2002, Ferrier 2002, Ferrier 2007).

The GDM model at the more systematic presence-absence field survey data provided a good explanation of beetle beta diversity, based on plant and environmental variables; however, still some variation was left unexplained indicating unexplored variables and/or other factors besides plant and environmental variables influencing beta diversity (see Chust et al. 2006, Beck and van Khen 2007). Missing variables could be those associated with the fossorial larvae, e.g. edaphic gradients, soil water concentration or physical properties. Additional factors explaining beta diversity could possibly include historical processes associated with speciation rates. Such a possibility may exist in the Fynbos Biome, as seen in differing speciation rates between eastern and western regions. In contrast to eastern fynbos regions, elevated rates of speciation are seen for western regions, linked to long term climatic stability (Cowling

and Lombard 2002, Cowling and Proches 2005). As such, contrasting speciation between regions may negate the role of contemporary environmental variables when explaining beta diversity patterns (see also Qian and Ricklefs 2000). Finally, the role of sexual selection may also be an important variable in explaining beta diversity. The development of exaggerated hind leg traits in male Embedders may be influencing the dispersal abilities of species, thus preventing gene flow between communities and possibly resulting in reproductive isolation. In addition, sexual selection appears to be a strong selective force driving divergence in sexually selected traits within and between populations (Gavrilets and Waxman 2002, Parker 2006, Ritchie 2008). Thus, the formation of reproductively isolated populations of species either through weak dispersal as a result of compromised flight abilities due to exaggerated trait development, or strong selection pressures on trait divergence may well help explain beta diversity patterns. This may be particularly applicable for the high beta diversity patterns seen across similar ecological habitats along short geographic distances. Considering the ecological importance of beta diversity, seeking such “missing” variables is of high importance for our understanding of regional diversity patterns and for effective conservation planning.

CONCLUSION

GDM modelling was effective in identifying the most important explanatory variables in beetle species turnover. At both QDS and field survey scales, GDM models showed that environmental factors explained more of the variation in beta diversity than plant variables, though both were important.

Steep environmental gradients in rainfall seasonality, concentration and annual rainfall, as well as altitude, were all important factors in explaining beta diversity. These factors reflect extensive ecological gradients (niche width and diversity), which promote species turnover, either through habitat specialisation or divergence as a result of limited gene flow. Vegetation type and bioregion (habitat heterogeneity) explained turnover better than plant species distribution. Plant species were less important because most monkey beetles are generalist feeders and they do not perceive landscape heterogeneity at the level of species. In contrast, habitat heterogeneity, in terms of steep edaphic factors and floristic gradients, provided habitats for a wider range of feeding guilds, and therefore was associated with increased beta diversity.

Geographic distance between sites explained minimal amounts of species turnover at both QDS and field survey scales. This finding is easily explained by the steep ecological and environmental gradients, mentioned above, combined with poor dispersal abilities of some monkey beetles. Complete species

turnover (100% compositional dissimilarity of beetle communities) is reached within very short distances, and beyond this asymptote, increasing geographical distance has no effect on beta diversity.

The patterns observed across the beetle and plant rich winter rainfall biomes provide interesting contrasts to other Mediterranean and arid ecosystems, and to other species rich regions, such as tropical forests, where geographic distance is more important in explaining beta diversity. In these tropical areas, environmental and ecological gradients are less steep, and herbivorous insects appear not to be restricted by dispersal limitations, so complete turnover is reached over much greater geographical distances. The results described here highlight the importance of adopting a non-linear modelling approach in the winter rainfall region, where there are steep environmental and plant gradients, and assumption of a constant rate of turnover along gradients and increasing turnover with geographic distance is violated. Furthermore, the GDM approach identifies those areas along an environmental or plant gradient where beetle species turnover is particularly high. In such areas, the high degree of local adaptation reflects evolutionary and ecological processes that can be prioritised for conservation.

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APPENDIX

Appendix 1. Host plant species compositional similarity matrix for field survey sites measured using the Bray-Curtis similarity measure (Clarke and Gorley 2006). [On average, across all site pair comparisons, sites shared 28.34 % (± 16.62) of host plant species].

	M	Y	RP	G1	G3	G4	GN	V1	VT	N	D	GTS	GSS	KS	WH	VTS	VSS	KTS	KSS	VMB	HTS	
Y	54.1																					
RP	40.0	52.4																				
G1	13.8	18.5	15.9																			
G3	10.3	13.0	13.6	38.8																		
G4	43.9	29.2	43.5	20.3	28.0																	
GN	20.7	27.7	28.6	16.3	11.9	34.8																
V1	17.6	14.6	20.5	19.4	18.6	35.6	25.8															
VT	3.8	16.9	24.6	35.0	36.1	12.7	22.5	21.4														
N	27.8	23.3	19.5	12.5	8.9	29.8	28.1	45.0	10.3													
D	23.5	24.4	30.8	12.9	9.3	22.2	25.8	26.3	14.3	40.0												
GTS	23.8	36.7	25.5	11.4	11.8	15.1	25.7	30.4	12.5	41.7	47.8											
GSS	21.6	27.3	19.0	9.2	13.0	16.7	18.5	24.4	13.6	32.6	58.5	61.2										
KS	15.1	20.0	27.6	34.6	12.9	21.9	17.3	10.5	26.7	16.9	17.5	12.3	10.0									
WH	25.0	14.5	26.4	5.3	14.0	27.1	39.5	30.8	11.4	37.0	23.1	33.3	21.8	16.9								
VTS	41.2	48.8	35.9	12.9	14.0	31.1	16.1	26.3	7.1	35.0	47.4	60.9	53.7	24.6	38.5							
VSS	28.6	33.3	25.0	9.5	13.6	17.4	19.0	15.4	10.5	34.1	56.4	55.3	76.2	10.3	22.6	51.3						
KTS	30.3	30.0	21.1	9.8	14.3	22.7	23.0	27.0	10.9	41.0	59.5	66.7	65.0	10.7	35.3	59.5	73.7					
KSS	30.3	30.0	21.1	9.8	14.3	22.7	19.7	27.0	10.9	41.0	59.5	66.7	65.0	10.7	31.4	59.5	78.9	94.4				
VMB	16.2	27.3	33.3	9.2	8.7	8.3	24.6	9.8	16.9	23.3	39.0	28.6	36.4	16.7	25.5	29.3	42.9	35.0	35.0			
HTS	35.0	25.5	40.0	17.6	12.2	31.4	20.6	22.7	9.7	34.8	50.0	57.7	55.3	19.0	41.4	63.6	57.8	65.1	65.1	34.0		
HSS	13.3	16.2	11.4	6.9	10.3	4.9	13.8	17.6	11.5	27.8	41.2	38.1	43.2	7.5	25.0	41.2	45.7	42.4	48.5	43.2	45.0	

M=Melbostrand; Y=Yzerfontein; G1 = Gifberg Mountain base-TZ/HV; G3 = Gifberg Mountain middle-TZ; G4 = Gifberg Mountain-top-Fyn; GN = Vanrhyns Pass-top-Fyn; V1 Vanrhyns Pass-middle-TZ =; VT Vanrhyns Pass-top-Fyn =; N=Nuwerus; D=Doringbaai; GTS=Groen River Tall Strandveld; GSS=Groen River Short Strandveld; KS=Studers Pass Tranzitional; WH=Wilderperde Hoek; VTS=Vygie Point Tall Strandveld; VSS=Vygie Point Short Strandveld; VMB=Vyftein Myl se Berg; HTS=Holgat River Tall Strandveld; HSS=Holgat River Short Strandveld

Appendix 2. Monkey beetle species compositional similarity matrix for field survey sites measured using the Bray-Curtis similarity measure (Clarke and Gorley 2006). [On average, across all site pair comparisons, sites shared 12.03 % (± 17.36) of beetle species].

	M	Y	RP	G1	G3	G4	GN	V1	VT	N	D	GTS	GSS	KS	WH	VTS	VSS	KTS	KSS	VMB	HTS	
Y	42.9																					
RP	28.6	55.6																				
G1	0.0	0.0	0.0																			
G3	0.0	0.0	0.0	27.8																		
G4	0.0	0.0	0.0	23.5	23.1																	
GN	0.0	0.0	0.0	13.6	5.6	23.5																
V1	0.0	0.0	0.0	5.7	14.8	16.0	5.7															
VT	0.0	0.0	0.0	38.1	17.6	12.5	9.5	36.4														
N	0.0	0.0	0.0	15.0	12.5	13.3	20.0	6.5	10.5													
D	13.3	10.5	21.1	6.3	0.0	0.0	0.0	0.0	6.7	0.0												
GTS	11.8	28.6	47.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.2											
GSS	15.4	11.8	35.3	0.0	0.0	0.0	0.0	0.0	0.0	7.7	22.2	60.0										
KS	0.0	5.3	5.3	3.9	9.3	4.9	11.8	9.5	4.1	17.0	0.0	4.9	0.0									
WH	0.0	0.0	0.0	5.7	7.4	8.0	11.4	7.7	6.1	25.8	17.4	0.0	0.0	9.5								
VTS	16.7	12.5	37.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	23.5	52.6	66.7	0.0	0.0							
VSS	14.3	22.2	44.4	0.0	0.0	0.0	0.0	0.0	0.0	7.4	21.1	57.1	58.8	5.3	0.0	50.0						
KTS	15.4	23.5	35.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	22.2	50.0	50.0	0.0	0.0	66.7	47.1					
KSS	14.3	22.2	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.1	47.6	47.1	0.0	0.0	62.5	44.4	94.1				
VMB	0.0	0.0	0.0	12.9	8.7	19.0	25.8	9.1	6.9	22.2	10.5	0.0	0.0	10.5	27.3	0.0	0.0	0.0	0.0			
HTS	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.3	11.8	15.4	0.0	0.0	33.3	14.3	30.8	28.6	0.0		
HSS	0.0	12.5	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.8	21.1	13.3	0.0	10.0	28.6	12.5	40.0	37.5	12.5	83.3	

M=Melbostrand; Y=Yzerfontein; G1 = Gifberg Mountain base-TZ/HV; G3 = Gifberg Mountain middle-TZ; G4 = Gifberg Mountain-top-Fyn; GN = Vanrhyns Pass-top-Fyn; V1 Vanrhyns Pass-middle-TZ =; VT Vanrhyns Pass-top-Fyn =; N=Nuwerus; D=Doringbaai; GTS=Groen River Tall Strandveld; GSS=Groen River Short Strandveld; KS=Studers Pass Tranzitional; WH=Wilderperde Hoek; VTS=Vygie Point Tall Strandveld; VSS=Vygie Point Short Strandveld; VMB=Vyftein Myl se Berg; HTS=Holgat River Tall Strandveld; HSS=Holgat River Short Strandveld

PART 3

SEXUAL DIMORPHISM AND SEXUAL SELECTION

5 SEXUAL DIMORPHISM, SEXUAL SELECTION, AND SPECIATION OF SOUTH AFRICAN MONKEY BEETLES

“There is nothing more ridiculous than to see half a dozen males with their long legs emerging from the pistils of a composite flower where they are mobbing a female which is almost entirely buried head foremost in the pistils, the sub-horizontal pygidium alone being exposed to view.” — *Louis Péringuey, 1902*

Abstract

Though important, ecological models do not fully account for variation in species richness of monkey beetle assemblages. Strong sexual selection pressure may prove to be an additional explanatory factor, as this is recognised as a strong driving force of speciation. This is the first description and evaluation of the forms of sexual dimorphism and putative sexually selected traits in monkey beetles. This was achieved by first measuring sexual dimorphism using a point scoring system for hind leg and colour dimorphism of species across two ecological feeding guilds (Embedders and Non-embedders). Second, stability of hind leg traits (coefficients of variation) and allometric scaling relationships were used to identify traits undergoing directional sexual selection, and third, using a comparative approach, the proportions of sexually dimorphic species were calculated for each genus and related to its species richness. This was done by regressing the number of dimorphic species against the number of monomorphic species. Standardised residuals from these regressions provided an estimate of the relative abundance of dimorphic species, while accounting for overall species richness. High positive residuals indicate genera that have disproportionately high numbers of dimorphic species - a possible indication of sexual selection influencing speciation. Results for hind leg dimorphism showed a contrasting pattern between Embedders and Non-embedders—Embedders showing high dimorphism scores and Non-embedders showing low dimorphism scores. Male Embedders further showed lower coefficients of variation for strongly dimorphic traits than female Embedders and male Non-embedders. In contrast, Non-embedder males showed similar coefficients of variation in hind leg traits to Non-embedding females. Embedder males also showed high proportions (*ca.* 76%) of species with positive linear allometric slopes for almost all hind leg traits. For male Non-embedders, only *ca.* 38% of species showed positive scaling relationships. In contrast to patterns for hind leg dimorphism, colour dimorphism was equally represented across the two feeding guilds. The proportion of leg dimorphic species appeared not to be related to the species richness of a genus. High and low species richness was noted for both leg dimorphic and monomorphic genera. Thus, for species rich monomorphic Non-embedding genera, richness appears to be influenced by factors other than sexual selection. Hypothesised factors include the possible adaptive shift into an alternative floristic niche that is less conducive for Embedder guild mating and feeding strategies. In addition, the role of colour as a visual display to other males appears to be a strong selective force for both guilds. Based on standardised residuals from regressions of numbers of colour dimorphic species against numbers of monomorphic species, species rich genera were disproportionately rich in colour dimorphic species. These data, with the combined evidence of clear sexual dimorphism, plus positive allometry of hind leg traits suggests that monkey beetles are under strong sexual selection forces.

INTRODUCTION

The exaggerated morphology of many male insects (Thornhill and Alcock 1983, Emlen and Nijhout 2000, Emlen 2008) was explained originally by Darwin (1871) through his theory of sexual selection (competition for mates involving male-male combat or female choice). Fisher (1930) in his seminal study built on Darwin's theory of sexual selection and through his "runaway process" was able to explain the evolution of secondary sexual traits through mate choice. Lande (1981) used genetic models to show that male secondary sexual traits and female preferences can evolve in a Fisherian runaway process. An important finding of this study was the ability of sexual selection to promote speciation through reproductive isolation as a result of diversification of secondary sexual traits.

Sexual selection has subsequently been shown in empirical and theoretical studies to be a strong driving force in speciation (West-Eberhard 1983, Barraclough et al. 1995, Møller and Cuervo 1998, Higashi et al. 1999, Seehausen and van Alphen 1999, Arnqvist et al. 2000, Gray and Cade 2000, Boughman 2001, Panhuis et al. 2001, Kirkpatrick and Ravigne 2002, Martin and Hosken 2003, Knight and Turner 2004, Seehausen and Schluter 2004, Grey and McKinnon 2006, Ritchie 2007). In addition, strong correlative support for a role of sexual selection in promoting rates of speciation comes from studies relating species richness between sister taxa with various surrogates of sexual selection (Barraclough et al. 1995, Møller and Cuervo 1998, Arnqvist et al. 2000). However, some debate exists about the direct role of sexual selection in speciation, with arguments suggesting that it rather occurs either in conjunction with ecological selection or that natural selection is an overriding force, better able to explain speciation (Gage et al. 2002, Ritchie 2007).

A related process of sexual selection, sexual conflict ("differing evolutionary interests of the two sexes" – Parker and Partridge 1998) has recently been recognised as a common occurrence in numerous animal groups (reviewed in Chapman et al. 2003 and Parker 2006). Furthermore, it is recognised as a strong evolutionary force inducing antagonistic co-evolution between males and females, which in turn has the ability to generate rapid divergence in traits involved in reproduction, with subsequent speciation through reproductive isolation (Holland and Rice 1998, Parker 1998, Parker and Partridge 1998, Arnqvist et al. 2000, Arnqvist and Rowe 2002, Gavrilets 2000, Gavrilets and Waxman 2002, Martin and Hosken 2003, Parker 2006). Sexual conflict in insects is particularly well developed with conflict seen pre- and post-copulation (Thornhill and Alcock 1983). The influence of inter-specific sexual conflict has also been shown to be a strong driving force causing trait divergence (colour polymorphism – Johnson 1975).

Most studies focussing on speciation through sexual selection have concentrated on using the model of female choice (Fisher 1930, Anderson 1994, Arnqvist et al. 2000, Anderson and Simmons 2006, Emlen et al. 2005, Emlen 2008). However, the role of male-male combat in competition over females and resources required for procuring females (e.g. feeding and oviposition sites), is seen as a powerful selective force in explaining the huge diversification recorded in the array of weaponry used in male contests (Darwin 1871, Anderson 1994, Moczek 2005, Emlen 2008). Beetles, bugs, bees, wasps, ants, flies, and earwigs all have representatives showing exaggerated and often highly diverse weaponry (reviewed in Emlen 2008). Scarab (Scarabaeoidea) beetles, due to their extreme and bizarre array of horn development have attracted the most interest and are a particularly well studied group (Emlen et al. 2005, Hosoya and Araya 2005, Moczek 2005). Here I use the South African Hopliini (monkey beetles) to explore the unusual and unique occurrence within the Scarabaeoidea of dimorphic hind legs, structures that appear to mirror the diversification and complexity of horns of other scarabs and that serve the same function in sexual selection.

The 1000-odd species of South African Monkey beetles (for more information about diversity of the South African fauna see Chapter 1) show extreme sexual dimorphism and a diversity of potentially adaptive secondary sexual traits (exaggerated hind leg morphologies, and colour of body parts. Their global centre of adaptive radiation falls within the floristically diverse winter rainfall regions of South Africa (cf. Greater Cape Floristic Region (Born et al. 2007)). Male-male combat is a common feature of many species of monkey beetle (Louw 1987, Midgley 1992, Picker and Midgley 1994). Males, using their enlarged hind legs as weapons, will aggressively fight with rival males over females, and have also been observed to guard females post-copulation for extended periods of time (Midgley 1992, Lewis 2007). Females are polyandrous mating with multiple males (Lewis 2007). Furthermore, the ratio of males to females within populations appears to be strongly male biased (Louw 1987, Midgley 1992). Thus, competition between males appears to be high. Moreover, due to the lengthy periods of male guarding there exist extended opportunities for male-male combat (see also Thornhill and Alcock 1983, Saeki et al. 2005), and the possibility of antagonistic sexual conflict.

Mating and feeding for most species of monkey beetle takes place on disc-shaped flowers (Asteraceae, Aizoaceae) and bowl-shaped geophytic flowers, which are large, and offer an ideal platform for feeding, mating and male-male combat (Picker and Midgley 1996, Steiner 1998a). Several geophytic plant families pollinated by monkey beetles show strong convergent evolution towards bowl shaped flowers (Goldblatt et al. 1998). Flowers are thus focal points of monkey beetle activity (Péringuey 1902). Furthermore, within their centre of adaptive radiation, host flowers emerge in mass spring flowering displays (Cowling et al 1999). Monkey beetle emergence is timed to coincide with this huge but

ephemeral floristic resource during the spring months. Péringuey (1902) describing one of his (successful) spring collecting trips wrote: "...so plentiful indeed that they [monkey beetles] had to be scooped by the hand from the flower into the killing bottle..."). Beetles only live for approximately 5-7 days (Colville, unpublished data), so the temporal pressures for reproduction are seemingly also high, generating elevated competition between males for securing females in a limited period of time.

Within this environment, three broad monkey beetle feeding guilds occur: Embedding and Non-Embedding flower guilds (Picker and Midgley 1996), and a poorly known and studied assemblage of non-anthophilic species. Female Embedders feed partially or wholly embedded inside the capitulum (in Asteraceae) or hypanthium (in Aizoaceae) of the flower, with the pygidium being the only body part exposed. During this period they are inactive, remaining embedded in the same flower for up to a few days (Lewis 2007). Male Embedders are more active, searching for females. Non-Embedding species are fast-flying, active pollinators (Picker and Midgley 1996, Goldblatt et al. 1998, Steiner 1998a, van Klunen et al. 2007), visiting many flowers and feeding more superficially on pollen and nectar.



Figure 1. Typical feeding posture of Embedding species of monkey beetle (*Scelophysa scheffoldi*) - female (right) partially embedded, with mate guarding male (left).

The three feeding guilds differ in species richness, diversity of secondary sexual traits and degree of sexual dimorphism. They thus provide a framework for testing the intensity of sexual selection (as measured by sexual dimorphism and degree of development of secondary sexual traits) against guild species richness. Ecological models do not adequately explain gradients in monkey beetle species

diversity (Chapters 3 & 4). Since strong sexual selection pressures have the potential to promote speciation and thus species richness, I investigated several components of sexual selection within monkey beetles and attempted to relate these findings to species richness patterns.

The approach used to evaluate the potential contribution of sexual selection to species richness of the different feeding guilds was as follows: (1) Highly dimorphic traits in insects are usually associated with strong sexual selection and thus, dimorphism scores should indicate which species and guilds are being influenced by sexual selection. Dimorphism scores based on hind legs and colour were thus quantified for monkey beetles identified within two feeding guilds; (2) Measures of trait size stability (coefficients of variation) and allometric scaling relationships were used to indicate directional sexual selection on hind leg traits and to identify intensities of sexual selection on specific hind leg traits; and (3) A comparative approach, similar to Barraclough et al. (1995) and Møller and Cuervo (1998), was used to test for correlations between the species richness of genera and the proportions of sexually dimorphic species (a proxy measure for sexual selection).

MATERIALS AND METHODS

All beetle species and genera were classed into one of two defined feeding guilds (Embedders and Non-embedders – see Picker and Midgley 1996) based on field observations (Chapter 4) and published host plant records and pollination studies. A species-depauparate group of non-anthophilic species are known however; these species have been poorly collected and studied, and as such, were ignored in this study. The Embedder and Non-embedder guilds were examined for taxonomic composition, and correlates were made with levels of sexual dimorphism.

QUANTIFYING HIND LEG AND COLOUR DIMORPHISM

The degree of sexual dimorphism in leg morphology and body colouration between males and females was quantified on a point scoring system using 5700 male-female comparisons from 837 unique localities, representing over 370 species. Specimens used were from a well-represented museum collection (Iziko Museum, Cape Town, South Africa) and field-collected material. Male and female pairs were selected randomly (sequentially in museum collection drawers), from a series collected by a collector or collection expedition, from a stated locality and date. Where possible, all collection series for a species were used. The number of pairs compared from each series was limited by the sex with the fewest individuals.

Hind leg dimorphism scores were based on a three point scale for each hind leg segment save the small coxa (viz. femur, tibia, and tarsus – Fig. 1). A score of 1 was assigned if the trait was exaggerated in the male compared to the female, and a score of 0 indicated no difference between the sexes; broadness/thickness of segment and segment length were evaluated on this score. In addition, scores of 1 or 0 indicated the presence or absence of femoral/tibial spines, and the presence or absence of an enlarged tarsal claw. The scores for each hind leg segment were then summed to give a total hind leg score out of a maximum of nine. For hind leg segment lengths and widths (thicknesses), a score of 1 was indicated for differences of at least 25%. All body measurements were taken with electronic digital callipers (accurate to ± 0.01 mm). From the above; mean total hind leg and colour scores were compared between the two guilds using the Mann-Whitney U-test (Sokal and Rohlf 1995).

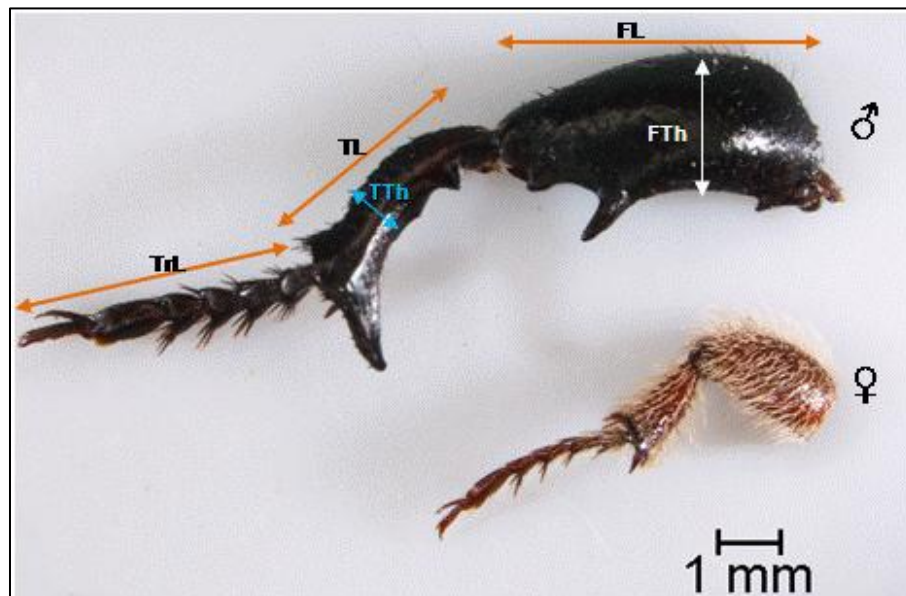


Figure 2. Male (top) and female (bottom) hind legs of *Heterochelus chiragricus* showing strong dimorphism (score of 6 = 1 (femur longer) + 1 (femur thicker) + 1 (femur with spine) + 1 (tibia longer) + 1 (tibia thicker) + 1 (tibia with spine) + 0 (tarsi not longer) + 0 (no tarsal claw). (Male body length for individual from which hind leg was removed = 10.14 mm; female body length = 9.96 mm)[FL = femur length, TL = tibial length, TrL – tarsal length, FTh = femoral thickness, TTh = tibial thickness].

In addition to the above measurements, an independent set of 37 species (23 embedders, 14 Non-embedders; $n \geq 20$ per species) representing a range of body lengths and leg dimorphism was used for quantifying hind leg dimorphism for use in the analysis of coefficients of variation (V^*) and allometric scaling. Hind femoral and tibial thicknesses (broadest section of respective leg part –Fig. 2) were measured (± 0.01 mm) with a dissecting microscope fitted with an ocular micrometer. Widths were considered a good measure of both the “thickness” (musculature) and enlargement in male legs (from

here on referred to as thickness). All leg length and thickness measurements were restricted to either the left or right hind leg, depending on which hind leg was the easiest to measure in terms of accessibility of measurement of all leg segments, and completeness – some individuals had missing and broken leg parts. Of all monkey beetle species and individuals examined none showed obvious or exaggerated levels of asymmetry in left and right hind leg lengths, thicknesses, or in the case of males, size of weaponry (femoral and tibial spines, and tarsal claws). However, within some populations for some species, variations in body lengths were seen. This is a common phenomenon in beetles whereby the quantity and quality of available nutrients during larval growth can determine body size attained and trait size in sexually dimorphic male beetles (Emlen 1994).

Colour sexual dimorphism was measured on a scale from zero (monomorphic) to four (complete dimorphism). Colour dimorphism scores were based on the sum of scores from four body parts (pronotum, elytra, abdomen, and pygidium) where a 0 was assigned to cases where males and females had the same colour of a part, and a 1 where they differed. Only different colours as opposed to hue variations scored a 1. For most monkey beetle species, colour patterns covering the full spectrum (including iridescent colours) are produced by scales. However, some species show cuticular colour production. Colour polymorphism was also noted in some species. As such, if a collection series (population) showed colour polymorphism, then a mean colour score was taken for that collection series.

STABILITY OF HIND LEG TRAITS

Coefficients of variation (V) (Yablokov 1974, Lande 1977, Sokal and Braumann 1980) were used to examine the differences in the amounts by which hind leg traits varied. Coefficients of variation allow comparisons in variation of traits, between and within populations and species, independent of the magnitude of their means (Sokal and Braumann, 1980). I used coefficients of variation to examine (i) intra-guild comparisons of leg traits variance between sexes and (ii) intra-guild; between leg trait comparisons in embedder males (see Table 3). Haldane's (1955) V^* estimate was used to correct for population biases in V (Sokal and Rohlf 1995). As suggested by Lande (1977), comparisons were restricted to coefficients of variation of ratio data (i.e. hind leg traits divided by body length) and differences were compared using paired *t*-tests.

HIND LEG ALLOMETRY

Static allometry (Shingleton et al. 2007) for hind leg lengths and widths for males from 37 species were described based on allometric slopes estimated from polynomial regression or Major Axis (MA) Model II

regression (Legendre and Legendre 1998, Warton and Weber 2002, Warton et al. 2006). For many insects, the shape of the relationship between body size and trait size can deviate from linearity; this is especially evident for exaggerated traits such as those associated with sexually selected weaponry used in male-male combat as well as for ornaments (Eberhard and Gutierrez 1991, Emlen and Nijhout 2000, Pomfret and Knell 2006, Kodric-Brown et al. 2006). Furthermore, allometric slopes in insects are strongly influenced by (i) environmental factors that determine larval growth and final adult body size attained (Emlen 1994), and subsequently expressed as different phenotypes (Emlen and Nijhout 2000) (ii) the extent of intra-sexual selection (Kodric-Brown et al. 2006, Bonduriansky 2007) and (iii) functional (allometric) constraints on body parts (Fairbairn 1997) imposed by habitat and diet. Monkey beetle species and genera selected here for allometric studies vary in both habitat and diet, feeding guild membership, and in the extent of reproductive competition between males (sexual selection). To test for non-linear relationships between body length and trait size, partial F tests (Quinn and Keough 2002) were firstly used in fitting higher order terms to the linear model:

$$y = \beta_0 + \beta_1 x_i + \beta_2 x_i^2 + \varepsilon_i \quad (1)$$

where y is \log_{10} body length, x_i \log_{10} of the selected trait (leg lengths or thickness), β_2 the regression coefficient, and ε_i the random or unexplained error with assumed normality, homogeneity of variances and independence (Quinn and Keough 2002). Slopes of the polynomial curves were calculated as the derivative of the best fit higher order equation calculated at y_i . If there was no significant deviation from linearity, then MA regression was used to calculate allometric slopes (b_{MA}) for only those traits showing a significant relationship between body length and trait size (Legendre and Legendre 1998). Major axis slopes were calculated from estimates of the slope of OLS regression lines (b_{OLS}), and the correlation coefficient (r_{xy}) (Legendre and Legendre 1998). In general, allometric slopes of $b=1$ reflect isometry, while slopes of $b>1$ and $b<1$ reflect positive (hypermetric) and negative (hypometric) allometry, respectively (Shingleton et al. 2007). Positive and negative (linear) allometry indicates relative increases, or decreases, in trait size with increasing body size.

Mean slope values were compared between Embedders and Non-embedders to test for significance. The non-parametric Mann-Whitney U-tests were used, as slopes were not normally distributed amongst traits.

SPECIES RICHNESS AND PROPORTIONS OF SEXUALLY DIMORPHIC SPECIES

Species richness values of South African Hopliini were obtained from an extensive data set which has been compiled as part of a larger project studying the richness and distributional patterns of the South African Hopliini (Chapter 1). Sexual dimorphism of hind leg dimensions and body colour were used as an indirect measure of sexual selection, to test whether sexual selection and species richness of monkey beetles are correlated. The approach followed that used for passerine birds to correlate the proportions of sexually dimorphic species within a taxon with the species richness of that taxon (Barraclough et al. 1995, Møller and Cuervo 1998).

Genera with ≤ 3 species, and genera where less than 30% of currently known species were seen, were excluded. Two exceptions (*Amblymelanoplia* Dombrow and *Lepitrichula* Schein) to this rule occurred, where adequate taxonomic information was obtained from published taxonomic revisions (Dombrow 1997b, Dombrow 2002) as opposed to museum material. Species were classed as being sexually dimorphic if a hind leg score of three (33.33%) or greater was achieved. This minimum score was chosen to adequately reflect sexual hind leg dimorphism in that a score of three reflects strong dimorphism of one leg component (e.g. femur: longer, thicker, and with spine), or dimorphism of two leg components (e.g. femur: longer and thicker; and tibia: longer), or dimorphism of all three leg components (e.g. femur: longer; tibia: longer; and tarsus: longer). Species were classed as colour dimorphic if they achieved a score of one (25%) or greater. A score of one reflects colour dimorphism in one of the four body parts chosen for scoring. Since each of the four body parts chosen are mostly of relatively large size compared to overall body size, and these chosen body parts are mostly prominent and brightly coloured, a score of 25% dimorphism was considered an adequate minimum measure for sexual colour dimorphism. Furthermore, species were classed as sexually dimorphic for both hind leg and colour if they achieved scores greater than 33.33% for hind legs and 25% for colour. Using the “quantitative” technique of Barraclough et al. (1995), genera were labelled as hind leg dimorphic or colour dimorphic or hind leg and colour dimorphic if 40% or more of their species were classed sexually dimorphic for each respective feature, or combination of features. Species richness comparisons were then made across these dimorphic classes.

From the above, firstly the proportions of sexually dimorphic species (based on hind leg and body colour) were compared across the two feeding guilds using Chi-square analysis to test whether or not dimorphism was related to guild membership, i.e. with a null hypothesis of dimorphism being independent of feeding guild. Secondly, the proportions of sexually dimorphic species (for both hind leg and body colour) within a genus were related to its species richness (statistical approach cf. Møller and Cuervo 1998; however,

currently no phylogenetic hypothesis exists for the Hopliini, thus the identification of, and comparisons across sister genera was not possible, as seen in Barraclough et al. (1995), and Møller and Cuervo (1998)). To overcome this, the number of dimorphic species was regressed on the number of monomorphic species for those genera with at least one dimorphic species. This was done for species labelled leg dimorphic, colour dimorphic, and leg and colour dimorphic. The standardized residuals from significant regressions should provide an estimate of the relative abundance of dimorphic species, while controlling for species richness. Positive residuals should indicate genera that have disproportionately high values of dimorphic taxa, whereas negative values will indicate genera depauperate in dimorphic taxa. These residuals were then used as a variable to regress against the species richness of a genus, i.e. if species richness of a genus is related to the proportion of dimorphic species, one would predict that the most speciose genera would be those containing the highest proportion of dimorphic species (i.e. higher positive standardized residuals).

RESULTS

PATTERNS OF SEXUAL DIMORPHISM

Hind Legs

Over 5700 male-female pairs, representing almost 400 monkey beetle species and 52 genera were scored. On average 69.58% ($\pm 26.44\%$) of all known species per genus and 65.75% of all known genera were examined. In terms of membership to the two feeding guilds, on average 71.9% ($\pm 26\%$) of all known embedders and 72.1% ($\pm 25\%$) of all known Non-Embedders were scored. Hind leg dimorphism scores ranged from zero to nine across guilds (Fig. 3a) with Embedders showing high leg scores (> 7), whereas most Non-embedders showed scores of ≤ 3 , i.e. weak dimorphism.

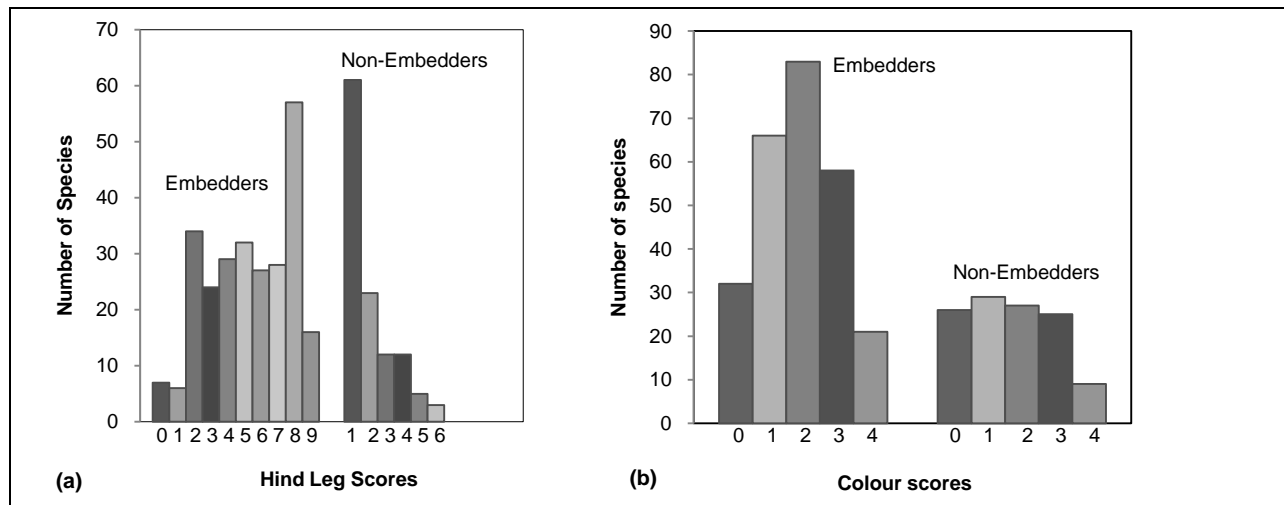


Figure 3. Numbers of Embedders and Non-embedders showing respective dimorphism scores for (a) leg and (b) colour. High scores represent strongly sexually dimorphic species.

Hind leg dimorphism was mostly reflected in thicknesses and particularly lengths of the femur, tibia, and tarsus (Table 1). Tarsal length was a particularly dimorphic hind leg feature in a large number of species (72% of all species scored). Tibial and femoral spines, and modified tarsal claws were less common, generally only noted in species with high hind leg dimorphism scores. Within the Embedding guild, high proportions of species showed dimorphism in all leg components, especially in femoral, tibial, and tarsal lengths. Embedding species had significantly higher mean hind leg scores than Non-embedders (Mann-Whitney U-test: $z = 13.15$; $P < 0.0001$; Embedders: $\bar{x} = 5.31 (\pm 2.47)$; $n = 265$; Non-Embedders: $\bar{x} = 1.12 (\pm 0.51)$, $n = 110$). Species associated with the Non-Embedding guild mostly showed weak hind leg dimorphism, however, as with Embedders, dimorphism in femoral, tibial, and tarsal lengths were the most common forms of dimorphism. In sharp contrast to Embedders, only a single Non-Embedder showed femoral thickness dimorphism, however, 18.20% of Non-Embedders showed dimorphism in tibial thickness. As observed in Embedders, the tibia appears to be the most dimorphic of hind leg segments (Table 1). Tibial and femoral spines, and modified tarsal claws were almost exclusively features of the Embedders with only a single Non-Embedder showing tarsal claw dimorphism.

Table 1. Numbers of species within each guild (% of total number of species found within respective guild) showing dimorphism in hind leg traits and body part colour. [Dashes indicate zero values].

(a) Hind Leg Dimorphism	Femur thicker (%)	Femur longer (%)	Femur spine (%)	Tibia thicker (%)	Tibia longer (%)	Tibia spine (%)	Tarsus thicker (%)	Tarsus longer (%)	Tarsus claw (%)
No. of Embedders with:	149 (56.23)	203 (76.60)	83 (31.32)	161 (60.75)	224 (84.53)	99 (37.36)	163 (61.51)	237 (89.43)	62 (23.40)
No. of Non-Embedders with:	1 (0.91)	23 (20.91)	-	20 (18.18)	30 (27.27)	-	5 (4.55)	38 (34.55)	1 (0.91)
(b) Colour Dimorphism	<u>Pronotum</u> (%)	<u>Elytra</u> (%)	<u>Pygidium</u> (%)	<u>Abdomen</u> (%)					
No. of Embedders with:	37 (13.96)	132 (49.81)	202 (76.23)	119 (44.91)					
No. of Non-Embedders with:	14 (12.72)	57 (51.82)	80 (72.73)	43 (39.09)					

As expected, male Embedders showed larger hind leg traits (in relation to body length) in comparison to male non-Embedders. All hind leg traits and showed significantly larger mean values in Embedder males (Table 2.).

Table 2. Mean male hind leg trait sizes, as a ratio of body length (BL) compared between Embedders and Non-embedders using the Mann-Whitney U-test (*Z*). (All comparisons significant at $P < 0.001$; $n = 654$, and $n = 403$ for Embedders and Non-embedders, respectively). [SE = standard error, LL = leg length, FL = femur length, TL = tibial length, Tr = tarsal length, TTh = tibial thickness, FTh = femoral thickness].

Trait	Embedders mean (SE)	Non-Embedders mean (SE)	<i>Z</i>
BL	8.24 (0.076)	7.54 (0.049)	7.88
LL:BL	1.48 (0.007)	1.29 (0.007)	15.96
FL:BL	0.48 (0.003)	0.41 (0.002)	15.34
TL:BL	0.43 (0.003)	0.36 (0.003)	14.65
Tr:BL	0.57 (0.004)	0.52 (0.004)	9.31
FTh:BL	0.20 (0.002)	0.12 (0.001)	25.45
TTh:BL	0.17 (0.002)	0.09 (0.001)	24.33

Colour

Colour dimorphism was widespread across the two guilds with a high proportion of species (82.7%) showing colour dimorphism in at least one of the selected scored body parts (Fig. 3b). Many species showed striking colour dimorphism (Fig. 4). The most common dimorphic body part was the pygidium (73.62% of species), followed by the elytra (48.24 % of species) (Table 1). Interestingly, in contrast to leg scores, proportions of species showing colour dimorphism for each scored body part were very similar for Embedders and Non-Embedders. Mean colour scores for Embedders were similar to Non-Embedders

(Mann-Whitney U-test: $z = 1.57$, $P = 0.12$; Embedders: $\bar{x} = 1.49$ (± 0.025), $n = 265$; Non-Embedders: $\bar{x} = 1.40$ (± 0.043), $n = 110$).

Colour polymorphism was noted between populations for 45% of species scored (*ca.* 38% Embedders; *ca.* 57% Non-embedders). Colour polymorphisms appeared to be mostly associated with females (*ca.* 81% of populations showing female colour polymorphisms; Fig. 4). However, five Non-embedders species showed polymorphisms within populations for both male and females. Most species, and their respective populations, only displayed a maximum of two female (68% of populations showing female polymorphism) or male (88% of populations showing male polymorphism) colour morphs. *Lepisia braunsi* (Non-embedder) displayed five different male colour morphs within one population, while the sympatric species *Scelophysa trimeni* and *S. pruinosa* (Embedders) displayed impressive variety in female colour polymorphisms, both within and between populations; the former species displaying 11 different female colour morphs found within a single population. Female colour morphs of *S. trimeni* ranged in colour from bright blue (same as males), through green, yellow, orange, dark brown, tan, dirty white, to a combination of these colours; for example: blue elytra; green pronotum; yellow pygidium (males pygidium is always bright white); and orange abdomen.



Figure 4. Colour polymorphism seen within females of *Amblymelanoplia* sp. nov. Two strikingly dichromatic female colour morphs are noted: one resembling the colour patterns of males (middle; body not covered in scales) and one resembling the orange/yellow colour of host plant flowers (far right; body densely covered in scales). [Note also strong dimorphism in hind legs between male and female beetles; males have highly elongated hind legs with thickened femora with a large spine].

Stability in Hind Leg Traits

Comparisons of coefficient of variation between measured hind leg traits showed a general pattern of less variation within male hind leg traits compared to females (Table 3). This was most evident within the Embedding guild.

1. Intra-Guild Comparisons of Leg Trait Variance Between Sexes

For Embedders, females showed significantly larger amounts of variation of hind leg traits than males (for five of seven trait comparisons with $P < 0.05$). In contrast variances of leg parts were the same in males and females of Non-embedders.

2. Intra-guild, Between Leg Trait Comparisons In Embedder Males

In embedders, some of the leg traits showed significantly greater variance than other (seven of the 12 variance contrasts), with a general pattern of less variability associated with those hind leg traits which are strongly dimorphic (Table 3). Total hind leg length, and particularly tibial lengths and thicknesses, were the least variable of hind leg traits, showing significantly ($P < 0.01$) less variability than most other measured hind leg traits. Femoral length and thickness generally showed the highest amounts of variability when compared to other leg traits.

3. Inter-guild Comparisons of Leg trait Variance

For the contrast of the variance of males Embedders vs. Non-embedders, variances were generally similar, apart from tibial contrasts where Non-embedders had greater variance.

Table 3. Intra-guild comparisons of levels of stability of hind leg traits measured as coefficients of variation (V^*). Stability in hind leg traits was compared between males and females for both guilds, and between individual leg traits for male Embedders. [BL = body length, LL = leg length, FL = femur length, TL = tibial length, Tr = tarsal length, TTh = tibial thickness, FTh = femoral thickness].

Sex/Guild	Trait Comparison	Mean V^* (\pm sd.)	Mean V^* (\pm sd.)	t-value (<i>df</i>)	<i>P</i>
Female vs. Male Embedders		<u>Female</u>	<u>Male</u>		
	BL	5.72 (1.27)	5.84 (1.47)	-0.44	0.6626
	LL:BL	6.39 (1.56)	5.47 (1.49)	3.72	0.0012
	FL:BL	9.31 (1.71)	7.96 (2.23)	4.91	<0.0001
	TL:BL	9.03 (2.71)	6.89 (1.93)	5.77	<0.0001
	Tr:BL	9.13 (2.34)	7.77 (1.74)	3.83	0.0009
	FTh:BL	7.97 (1.79)	8.99 (2.22)	2.24	0.0356
TTh:BL	8.97 (2.67)	7.57 (1.96)	2.54	0.0188	
Female vs. Male Non-Embedders		<u>Female</u>	<u>Male</u>		
	BL	4.74 (0.93)	5.18 (0.68)	-1.61	0.1314
	LL:BL	5.86 (0.01)	5.75 (0.01)	0.23	0.8190
	FL:BL	8.34 (0.02)	8.29 (0.01)	0.09	0.9320
	TL:BL	8.78 (0.02)	8.02 (0.01)	1.12	0.2847
	Tr:BL	7.67 (0.01)	7.64 (0.02)	0.06	0.9509
	FTh:BL	8.08 (0.02)	8.06 (0.01)	0.04	0.9721
TTh:BL	8.79 (0.02)	9.27 (0.02)	-1.24	0.2360	
Male Embedders vs. Male Non-Embedders		<u>Embedder</u>	<u>Non-Embedders</u>		
	BL	5.84 (1.47)	5.18 (0.68)	1.85	0.0729
	LL:BL	5.47 (1.49)	5.75 (1.20)	-0.62	0.5402
	FL:BL	7.96 (2.23)	8.29 (1.32)	-0.56	0.5817
	TL:BL	6.89 (1.93)	8.02 (1.26)	-2.15	0.0385
	Tr:BL	7.77 (1.74)	7.64 (1.86)	0.22	0.8255
	FTh:BL	8.99 (2.22)	8.06 (0.82)	1.83	0.0773
TTh:BL	7.57 (1.96)	9.27 (1.98)	-2.55	0.0169	
Male Embedders vs. Male Embedders	LL:BL vs. FTh:BL	5.47 (1.49)	8.99 (2.22)	-7.95	<0.0001**
	LL:BL vs. TTh:BL	5.47 (1.49)	7.57 (1.96)	-6.69	<0.0001**
	FL:BL vs. TL:BL	7.96 (2.23)	6.89 (1.93)	3.33	0.0031**
	FL:BL vs. Tr:BL	7.96 (2.23)	7.77 (1.74)	0.63	0.5375
	TL:BL vs. Tr:BL	6.89 (1.93)	7.77 (1.74)	-3.05	0.0058
	TTh:BL:bl vs. FL:BL	7.57(1.96)	7.96 (2.23)	-0.98	0.3363
	TTh:BL vs. TL:BL	7.57(1.96)	6.89 (1.93)	1.54	0.1387
	FTh:BL vs. TTh:BL	8.99 (2.22)	7.57 (1.96)	2.89	0.0085
	FTh:BL vs. Tr:BL	8.99 (2.23)	7.77 (1.74)	2.74	0.0120
	TTh:BL:bl vs. Tr:BL	7.57 (1.96)	7.77 (1.74)	-0.56	0.5827
	FL:BL vs. FTh:BL	7.96 (2.23)	8.99 (2.22)	-1.57	0.1231
	FTh:BL vs. TL:BL	8.99 (2.22)	6.89 (1.93)	3.23	0.0025**

**Significant at Bonferroni-corrected level of $P < 0.004$ (Sokal and Rohlf 1995).

HIND LEG ALLOMETRY

General Patterns

Approximately 76 % of male Embedders and 38% of male Non-Embedders showed significant ($P < 0.05$) scaling relationships between body length and hind leg trait sizes (average taken across all six hind leg traits) (Table 4). Linear allometric relationships between body length and hind leg trait size were recorded

for the vast majority of species. For two Embedders and one Non-Embedder a second-order polynomial gave a significantly better fit to one hind leg trait for each of these three species (see below).

Embedders generally showed steeper allometric slopes across traits compared to Non-embedders, however; only femoral thickness and tarsal length had significantly larger slope values in embedders (Table 5).

Table 4. Percentages of Embedders and Non-embedders showing positive ($b_{MA} > 1$), negative ($b_{MA} < 1$), and non-linear allometric relationships between hind leg trait size and body length. Slopes were calculated using Major Axes Model II regressions (both variables \log_{10} transformed). (Note: trait percentages do not add up to 100%; remaining percentage is reflective of those species showing a non-significant relationship). [E = Embedder, NE = Non-embedder; LL = leg length, FL = femur length, TL = tibial length, Tr = tarsal length, TTh = tibial thickness, FTh = femoral thickness].

Percentage (%)	FL	FTh	LL	TrL	TL	TTh	Average (\pm sd.)
E: $b_{MA} > 1$	82.61	91.30	65.22	69.57	73.91	73.91	76.09 (9.43)
$b_{MA} < 1$	-	-	26.09	4.35	4.35	4.35	6.52 (9.82)
Non-Linear	-	-	-	-	4.35	4.00	1.39 (2.16)
NE: $b_{MA} > 1$	57.14	42.86	28.57	29.00	35.71	36.00	38.21 (10.67)
$b_{MA} < 1$	-	-	21.43	7.14	-	-	4.79 (8.65)
Non-Linear	-	-	7.14	-	-	-	1.19 (2.92)

Table 5. Mann-Whitney U-test (Z) comparing mean slope values between Embedders (E) and Non-embedders (NE) for those hind leg traits showing positive significant relationships with body length. Mean (and standard error (SE)) slope values also shown. (** $P < 0.01$, * $P < 0.05$, ns = non-significant). [LL = leg length, FL = femur length, TL = tibial length, Tr = tarsal length, TTh = tibial thickness, FTh = femoral thickness].

Guild	Trait	Mean b_{MA} (SE)	Z (n - Embedder, n - Non-embedder)	P
E	FL	1.96 (0.27)	0.25 (19,8)	ns
NE		1.68 (0.43)		
E	FTh	2.48 (0.23)	2.53 (19,8)	**
NE		1.15 (0.39)		
E	LL	1.17 (0.11)	1.83 (16,6)	ns
NE		0.73 (0.19)		
E	TrL	1.40 (0.2)	2.07 (17,4)	*
NE		0.66 (0.29)		
E	TL	1.44 (0.19)	1.44 (18,5)	ns
NE		0.88 (0.35)		
E	TTh	1.76 (0.27)	1.51 (19,5)	ns
NE		1.17 (0.48)		

Embedding species

A high percentage (>70%) of embedders showed positive allometry for femoral length, femoral thickness, tarsal length, tibial length, and tibial thickness (Table 4), whereas, somewhat fewer embedders showed positive leg length allometries (*ca.* 65%). Negative allometry was the exception, occurring only for leg length (*ca.* 26% of species with slopes $b_{MA} < 1$). However, for several species, leg length slopes were close to one ($b_{MA} \approx 1$) suggesting a possible isometric relationship.

For two Embedder species a second-order polynomial gave a significantly better fit to one hind leg trait in each, respectively. Hind leg traits showing a non-linear scaling relationship were tibial length (*Pachycnema crassipes*: partial *F*-test: $F_{1, 27} = 4.61$, $P < 0.05$); and tibial thickness (*Gymnoloma femorata*: partial *F*-test: $F_{1, 27} = 13.0$, $P < 0.01$).

Allometric slopes between $b_{MA} = 1.50 - 1.70$ were most common for males (Table 4). Male Embedders showed steepest allometric slopes ($b_{MA} > 2.5$) for femoral thickness (14 species) and femoral length (eight species). Highest recorded slopes were seen for femoral thickness in the two embedders *Gymnoloma femorata* ($b_{MA} = 4.61$) and *Pachycnema crassipes* (and $b_{MA} = 4.22$), respectively.

Non-embedding species

Only approximately 38% (averaged across all species and leg traits) of male Non-embedders showed significant scaling relationships between body length and leg traits. Femoral length showed the highest percentage (*ca.* 57%) of Non-embedders displaying slopes of $b_{MA} > 1$. The remaining leg traits showed low percentages (*ca.* < 40%) of Non-embedders showing positive allometric slopes. Similarly as for Embedders, leg lengths generally recovered negative allometric slopes (*ca.* 23% of Non-embedders). For a single Non-Embedder, a second-order polynomial gave a significantly better fit (*Anisochelus inornatus*: leg length; partial *F*-test: $F_{1, 27} = 4.40$, $P < 0.05$).

Allometric slopes between $b_{MA} = 1.2 - 1.8$ were the most common for male non-Embedders (Table 4), with steep allometric slopes ($b_{MA} > 1.2$) for femoral length and femoral thickness. The two Non-Embedders, *Lepithrix longitarsus* and *Lepisia gifensis* sp. nov., displayed very steep allometric slopes for tibial thickness ($b_{MA} = 4.89$ and $b_{MA} = 4.36$, respectively), while *Peritrichia hessei*, showed an equally steep allometric slope for femoral thickness ($b_{MA} = 4.47$). These latter slope values were unusually steep for Non-embedders.

SPECIES RICHNESS AND PROPORTIONS OF SEXUALLY DIMORPHIC SPECIES

64.34% of species sampled had sexually dimorphic hind legs, 84.96% of species were sexually colour dimorphic, while 56.25% of species were labelled sexually dimorphic for the combination of hind leg and colour. The majority of monkey beetle species fall within the Embedding feeding guild (*ca.* 66%), and this guild had by far the greatest concentration of sexually dimorphic species. Of the species labelled sexually dimorphic for hind legs, 87.30% were Embedders, and 12.70% non-Embedders (Fig. 3a). This result is highly significant, with disproportionately more sexually hind leg dimorphic species found within the Embedding guild ($\chi^2 = 143.41$, $df = 2$, $P < 0.0001$). For sexually colour dimorphic species, 68.94% fall within the Embedding guild and 31.06% within the non-Embedding guild (Fig. 3b). As for sexual hind leg dimorphism, the Embedding guild contains significantly more sexually colour dimorphic species ($\chi^2 = 15.63$, $df = 2$, $P < 0.0005$).

Highly dimorphic species (when classed sexually dimorphic on both hind leg and colour) were not surprisingly largely comprised of Embedders (86.92%), followed by Non-Embedders (13.08%) ($\chi^2 = 100.6$, $df = 2$, $P < 0.0001$). Of genera labelled sexually dimorphic: 55.77% were labelled hind leg dimorphic, 78.85% sexually colour dimorphic, and 51.92% of genera had 40% or more of their species labelled sexually dimorphic for both hind leg and colour.

The proportion of leg dimorphic species within a genus was not related to its species richness ($F_{(1,14)} = 0.22$, $r^2 = 0.02$, $P = 0.644$) between the number of leg dimorphic and monomorphic species across those genera containing at least one dimorphic species. A similar non-significant relationship was seen between the number species labelled as leg and colour dimorphic and those labelled monomorphic ($F_{(1,20)} = 2.89$, $r^2 = 0.13$, $P = 0.105$). As such, the relationship between species richness and number of dimorphic species was not explored further for these two latter dimorphic classes. A significant positive relationship ($F_{(1,23)} = 10.72$, $r^2 = 0.32$, $P = 0.003$) was, however, seen between the proportion of colour dimorphic species within a genus and its species richness. Furthermore, the residuals from this regression – positive values being indicative of genera that are disproportionately rich in colour dimorphic species - showed a significant positive relationship ($F_{(1,23)} = 38.84$, $r^2 = 0.61$, $P < 0.001$) with speciose genera generally showing higher standardized residual values.

DISCUSSION

PATTERNS OF SEXUAL DIMORPHISM

Hind Legs

Clear patterns of sexual dimorphism occurred within the South African Hopliini, with the vast majority of species labelled hind leg dimorphic (*ca.* 87%) being part of the Embedder guild. This guild exhibited hind leg dimorphism in all hind leg traits examined (length and thickness of the femur, tibia, and tarsus; but most evident in the tibia and tarsi). Exaggerated musculature of the femur and tibia was also a common dimorphic feature of Embedders, with many species showing hugely thickened and swollen femora and tibia in males. Furthermore, additional dimorphic features included the presence of varying numbers and combinations of spines on the femur and tibia, and the presence of large, well-developed tarsal claws, e.g. *Heterochelus bivittatus* Burmeister shows extreme elongation of the last two tarsal segments, which account for *ca.* 74% of the length of the body, and are *ca.* 170% larger than those of females. In addition, at least a third of embedders displayed spines on both femur and tibia, often with elaborate three-dimensional complexities of combinations of spines, recurved teeth, and spurs. These exaggerated hind leg structures and weaponry function as a single unit for use in male contests over, and mate guarding of females (Louw 1987, Midgley 1992, Lewis 2007). Thus, the high levels of dimorphism and role of hind legs in male combat strongly suggests that hind leg size and morphology of male embedders has been directly influenced by sexual selection through frequency-dependant competition for females.

A similar pattern of exaggerated traits in male insects under the influence of sexual selection has been recorded for a range of insect groups (Emlen 2008). The scarab beetles (Scarabaeoidea) are particularly well known for their exaggerated horn and mandible morphologies (Moczek 2005, Hosoya and Araya 2005). However, the results from this study showing high percentages of hind leg dimorphism within a tribe of the Scarabaeoidea appears to be highly unusual and mostly unique to the South African Hopliini. In two recent and extensive reviews of exaggerated traits in male insects (Emlen and Nijhout 2000, Emlen 2008), no mention of hind leg dimorphism within the Scarabaeoidea was mentioned. Hind leg dimorphism of monkey beetles apparently is analogous to the form of leg dimorphism recorded for some chrysomelid (Chrysomelidae) leaf beetles (Eberhard and Marin 1996, Emlen and Nijhout 2000) and coreid bugs (Coreidae) (Miyatake 1997, Eberhard 1998). Males of these insects use their hind legs as weapons in male-male combat over females and the hind legs are subject to sexual selection (Eberhard and Marin 1996, Miyatake 1997, Eberhard 1998).

In contrast to Embedders, Non-Embedders mostly showed weak hind leg dimorphism (ca. 70% of species) with only ca. 8% of Non-embedders classed as truly hind leg dimorphic. Moreover, the array of extraordinary hind leg weaponry (excessive musculature, spines, rachets and extreme elongations) associated with Embedders was all but absent in Non-Embedders. However, a handful of species from the latter guild (across several genera) showed notable elongation of the tibia and tarsus, accompanied in several species by extensive pilosity, forming tarsal or tibial “socks” and creating an impression of “thickened” leg traits. Amongst the Non-embedding genera, the speciose genus *Peritrichia* Burmeister displayed the highest number (35%) of species classed as hind leg dimorphic. Species of this genus show pronounced elongation of the tibia and tarsi, tibial and tarsal “socks”, and in a few species, moderately swollen tibia. Non-Embedding males in general also engage in male-male combat, however, these battles are far less combative, and involve brief tussling and wrestling. Thus, for some Non-embedders, hind leg traits also appear to be influenced by sexual selection; however, this selection appears to be less intensive, and therefore, results in lower levels of dimorphism of hind leg size and morphology.

Both Embedders and Non-embedders are found within the same habitats, at the same time, and utilize a shared suite of host plant species (Picker and Midgley 1996). Moczek (2005) stresses the need to relate biology to observed patterns in the intra- and inter-specific variability (shape, size and presence/absence) of sexually dimorphic traits (see also Slatkin 1994). What then is the driving forces explaining these disparate patterns in Embedders and Non-embedders? Much of their sexual dimorphism seen is best interpreted in the light of the feeding biologies of Embedders and Non-embedders. Midgley (1992), based on observational data from a single dimorphic and single monomorphic species, first hypothesised a role of differing feeding biologies in explaining contrasting level of dimorphism. This study, based on observational data from several hundred species, supports this hypothesis. Furthermore, the hypothesis of Péringuey (1902) that the large hind legs of male beetles have evolved as an adaptation that enable them to extract themselves out of host plant flowers is refuted. Female beetles of the Embedding guild are generally embedded deeper within a flower’s capitulum than males, but have small, unmodified hind legs.

Based on field observations, the feeding biologies of Embedders and Non-embedders contrast strongly, particularly between females. Female Embedders, feeding predominantly on disk-shaped (“daisy flowers”) of Asteraceae and Aizoaceae (Picker and Midgley 1996), burrow deep into the flower head (Fig. 6), feeding on pollen and/or ovules, and will remain embedded for extended periods of time. These (often large) flowers provide abundant resources (pollen and ovules) and an ideal platform for mating and male contests. Quite frequently females are buried so deeply that only a fraction of the pygidium is exposed. This crypsism by females will reduce the number of females readily visible to males, thus skewing the apparent sex ratio in favour of males, and resulting in more intense competition for the

limited resource. Male embedders, using their enlarged hind legs, engage in male-male combat and mate guarding. Levels of aggression can result in amputation of an opponent's hind leg (see Thornhill and Alcock 1983, for other examples of physical costs of male-male combat). Male monkey beetles will remain *in copula* with females for extended periods of time, during which time females continue to feed. Furthermore, post copulation, males will continue to remain attached to the female ("contact mate guarding" *sensu* Thornhill and Alcock 1983); riding in tandem, either clasped to her back by means of his fore and mid-legs while she feeds superficially near the surface of the flower's capitulum, or embedded deep within the flowers capitulum with her, but still remaining clasped to her, and thus, guarding her from other males (Fig. 6).



Figure 6. Male of *Denticnema striata* (left) mate guarding female (right; male removed and flower head broken open to reveal female) who is embedded deeply below him within the flower's capitulum. [Note colour and hind leg dimorphism between male and female; male body length = 11.84 mm; female body length = 11.59 mm].

Although Non-embedders share a number of host plant with Embedders, they are generally associated with non-daisy type flowers, e.g. shallow bowl-shaped petaloid geophytes (Iridaceae) (Picker and Midgley 1996, Goldblatt et al. 1998, Steiner 1998b) and flowers occurring in inflorescences, e.g. Rutaceae, Rhamnaceae, Orchidaceae (Steiner 1998b) (Fig. 7). Furthermore, females feed predominantly on pollen and nectar (Johnson and Nicolson 2001), and generally visit flowers for only short periods. Many Non-embedders are highly pilose and very active fliers, resembling pollinating bees and wasps in their foraging behaviour far more closely than beetles. Convergent feeding behaviour and morphologies are seen in closely related tribes whose member species are flower visitors (e.g. Lichnini (Hawkins

2006), Macroductylini (Katovich 2008), and the bumble bee scarabs (Glaphyridae) (Smith et al. 2006)). These later tribes appear to show minimal hind leg dimorphism.



Figure 7. *Anisonyx* sp. nov., a Non-embedding species feeding on the inflorescences of a species of Rhamnaceae. [Female left; male right. Note lack of hind leg or colour dimorphism].

In addition to differences in feeding biology, male-male contests in Non-embedders are markedly different to those of Embedders. From field observations, it was seen that in the former, male combat involves relatively brief tussles, whereby males will grapple using fore, mid and hind legs. Several males may grapple with each other simultaneously over a female. Mate guarding was mostly observed within the genus *Peritrichia*, particularly for those species whose males show some degree of leg dimorphism. Copulation can extend for a period of time, although couples will rapidly detach and fly off when disturbed, unlike the situation seen in Embedders – with males doggedly guard females, and remaining clasped to females even when removed from the flower head.

From the above discussion, several factors can be seen to be promoting more intensive sexual selection in Embedders compared to Non-embedders. These include the long-term fidelity of females to disk-shaped flower heads which provide a large, stable platform for male combat, thus allowing males to attain large hind legs, which are generally cumbersome, and difficult to utilize when walking on non-flat surfaces, as observed when male Embedders try mate and feed on non-disk-shaped flowers. In addition, the almost sessile nature of females has possibly allowed males to compromise their flight abilities by having larger, heavier hind legs (since they do not need to actively follow females beetles from flower to flower as is the

case for Non-embedders). Male Embedders are slow, cumbersome fliers, more reminiscent of large scarab beetles, e.g. fruit chafers (Cetoniidae). The extended copulation and mate guarding of virtually sessile females further suggests that the potential for male-male combat would be both predictable and prolonged, hence the evolution of formidable weaponry. In addition, the two brief studies investigating male contests in monkey beetles (Louw 1987, Midgley 1992) both note the dominance of males within populations of embedders, suggesting that competition between males for females is high (see also Wang 2002, Saeki et al. 2005).

In contrast, Non-embedder males need to be equally good fliers as are the females, and requiring leg structures capable of hanging onto females and negotiating the uneven surfaces of host inflorescences. Male combat appears to occur less frequently, is of shorter duration, and involves less aggression and use of the hind legs in contests. Moreover, mate guarding was rarely observed, further reducing the role of the hind legs as weapons. Thus, it is not unexpected that male Non-embedders do not possess large powerful hind legs fortified with spines and spurs. In addition, Non-Embedding species are active, rapid flyers, visiting numerous flowers in search of food and mates and would be hindered by having large hind legs

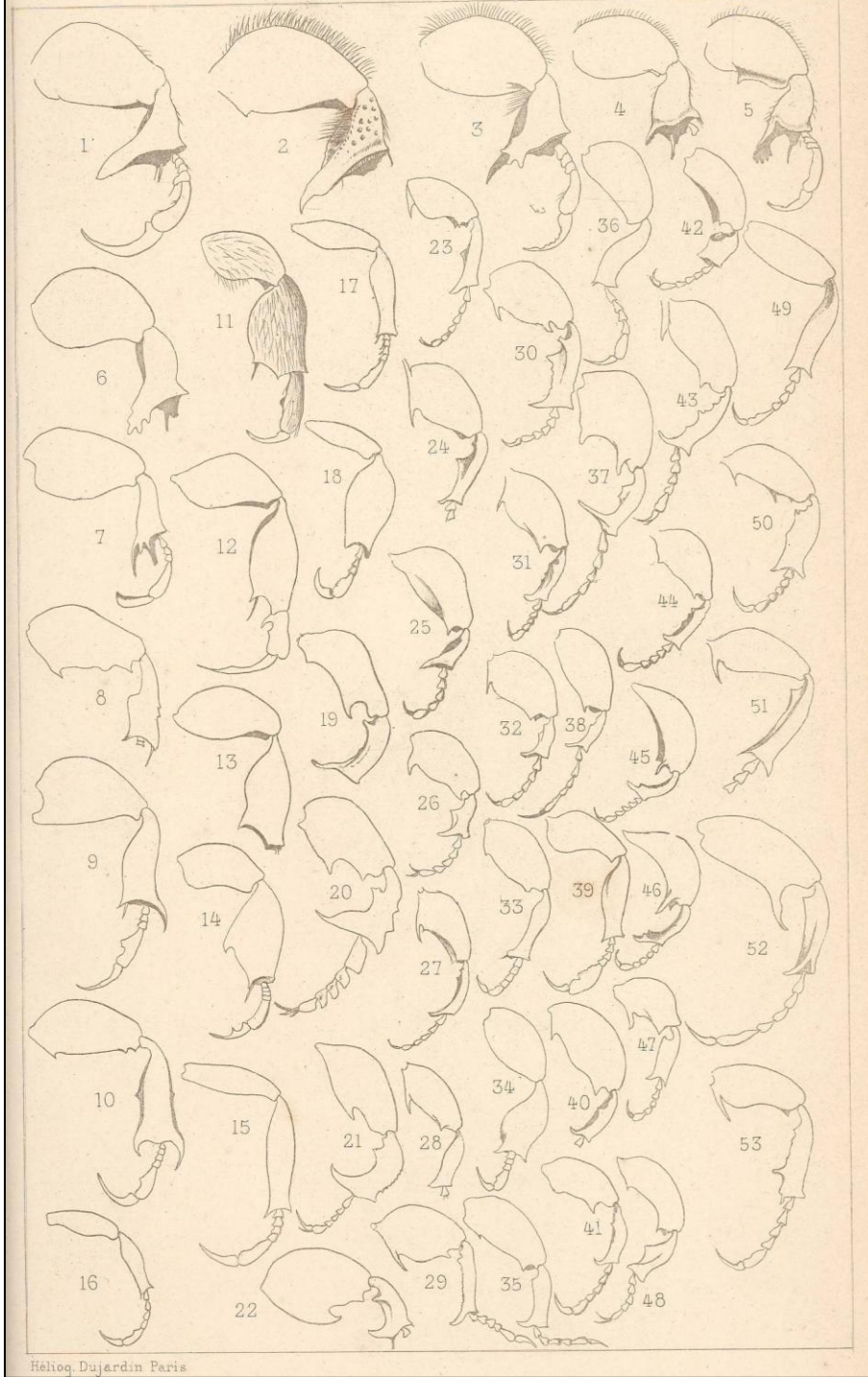


Figure 8. Adaptive diversity of male hind leg traits for 53 Embedding species (five genera). High interspecific diversity of hind leg traits is seen for the speciose genus *Heterochelus* (Numbers 19-22, 29, 31, and 33-50). [Diagram taken from Péringuey (1902)].

Colour

Both Embedders and Non-Embedders showed striking colour dimorphism ranging from complete colour dichromatism in all body parts, to males and females resembling each other chromatically (Figs. 4, 6, 7). A large majority of species showed colour dimorphism in at least one body part (*ca.* 80%). However, species classified as colour dimorphic were still dominated by Embedders (*ca.* 68%). Colour dimorphisms were elaborate; most often due to complex patterns of different coloured scales, or patterns of scales and dense pilosity. Very seldom were colour differences the result of non-scale, cuticular colouration (see Dombrow 1997a, b, c; 1998; 2000; 2001; 2002, for descriptions of colour patterns).

The most common dimorphic body parts were the pygidium and elytra, with the former showing dimorphism in *ca.* > 70% of species. The pygidium was often uniquely coloured compared to the rest of the body, and showed both morphological and colour dimorphism in a large number of species, especially amongst Embedders. Male pygidia are noticeably larger in males than those of females, distinctly triangular in shape (declivous), and reflexed sharply anteriorly. Male pygidia are also brightly, and in some species, intricately patterned with different coloured scales and hairs (Fig. 9). Furthermore, the pygidium consists of colour patterns possibly indicating ultra violet (uv) reflection (see Brunton and Majerus 1995). A number of Embedders have pygidium colour patterns showing sharp contrasts between bright colours (white, yellow, and orange) and black (Fig. 9). The patterns consist of symmetrically placed black “eye-spots”, white or black horizontal lines and/or a central, vertical white or black line. Several species have all-black pygidia. This blackness, which is dull and velvety, is created by densely black scales. The “eye-spots” and horizontal and vertical lines are also often the result of black scale bands rather than cuticular colouration. Further evidence for the visual importance of the pygidium can be seen in the presence of a large propygidium in conjunction with shortened elytra, characteristic of many species of monkey beetle. The propygidium is made up of the last adjacent tergite preceding the pygidial tergite, and matches the colour of the pygidium and not the other abdominal tergites, nor the elytra. This “extension” of the pygidium is seen in both Embedders and non-Embedders. The pygidium and propygidium are the most prominent exposed body parts of embedders when they feed head down while burrowed within the capitulum of the flower. Males guarding females also adopt this position of head down - pygidium up (guarding male beetles remain mounted on females as the latter feed; see also Thornhill and Alcock 1983).



Figure. 9. Male Embedder beetle (*Heterochelus* sp.) showing typically large pygidium with complex coloration of light and dark scale patterns. [Note highly thickened femora with large basal spine].

The widespread occurrence and intricate colour dimorphism associated with several body parts suggests sexual selection may be influencing these colour dimorphism patterns (Anderson 1994). Many monkey beetle species have “brightly” coloured males, with duller, often cryptic females, suggesting a possible role for intra-sexual “warning” displays to other males intent on take-over bids during mating or mate-guarding, pre-empting costly physical combat; alternatively or additionally these colours may signal genetic quality to females (Thornhill and Alcock 1983, Anderson 1994, True 2003, Gray and Mckinnon 2006). Retaining the possession of a female during mate guarding might also be reinforced through visual display (such as through pygidial signals). However, the role of colour in mating signals and the selective advantage of brightly coloured males in monkey beetles remains to be examined. In addition, colour polymorphism may be the result of environmental factors such as diet (Ojala et al. 2007), or a particular colour morph may offer a physiological advantage such as more efficient thermoregulation (Gray and McKinnon 2006, Punzalan et al. 2008). Such functions seem unlikely in monkey beetles. Nonetheless, colour and visual signalling in monkey beetles appears to be of considerable importance. Beetles employ their acute vision for flower selection, and they have been shown to be able to differentiate between different reflectance spectra, patterns, and hue (Picker and Midgley 1996, Steiner 1998a, van Kleunen et al. 2007). Other possible evidence indicating the importance of colour in monkey beetles comes from the presence of conspicuous coloured patches on certain host plants (their resemblance to monkey beetles has resulted in them being termed “beetle markings”(Hutchinson 1946, Midgley 1993); they occur on a

number of species of monkey beetle host flowers (Goldblatt et al. 1998, van Kleunen et al. 2007). These beetle marks have been recorded as visual attractants which increase the frequency of visitation by monkey beetles (van Kleunen et al. 2007). In contrast Hutchinson (1946) suggested that such beetle ‘mimics’ may act as a deterrent to beetles who feed destructively on floral parts. The marks possibly indicate the occupation of a flower by another (male) beetle, and thus beetles will not land. Although untested, the visually dimorphic and very conspicuous pygidia of many embedding males may deter other males, and the plant disc florets may be manipulating this system to reduce ovule predation.

Further evidence suggesting the importance of colour and visual signals is seen in the number of dramatic cases of colour polymorphism within and between populations of beetle species. Colour polymorphism, recorded in several insect groups has been linked to the influences of sexual selection (mate choice and intra-specific sexual mimicry, including sexual conflict) (Anderson 1994, True 2003, Gray and Mckinnon 2006, Parker 2006, Svensson et al. 2007). Multiple colour morphs in males may reflect the adaptation towards a brightly coloured morph indicative of a male’s vigour (hind leg size) which in turn would deter other male beetles (Anderson 1994, Knight and Turner 2004, Seehausen and Schultze 2004). In insects, males mimicking female morphs have been well documented (Forsyth and Alcock 1990, Field and Keller 1993, Gosden and Svensson 2007). Several reasons for this have been suggested, which include mimicking females to gain access to mates and resources, and increased paternity through post-copulation mate guarding. For monkey beetles, males resemble females most likely to avoid physically damaging battles with other males (see section below on leg allometry).

The adaptive significance of female sexual polymorphism is less clear and has been somewhat neglected in sexual selection studies (Svensson et al. 2007, Cothram 2008). However, the majority of colour polymorphism seen within monkey beetle populations was associated with females. The presence of male coloured females (andromorphs) was recorded for at least 10 monkey beetle genera (across guilds), and is strongly suggestive that sexual conflict is at play (Johnson 1975, Chapman et al. 2003, Gosden and Svensson 2007). This is further supported by the observation of both female Embedders and Non-embedders resisting copulation by attempting to fight-off ‘interested’ males. Sexual conflict results when the characteristics that enhance the reproductive success of one sex negatively affect the fitness of the other sex (Chapman et al. 2003), e.g. excessive harassment by males may impact on her non-reproductive activities such as feeding (Johnson 1975, Jormalainen et al. 2001). Thus, matching a male’s colouration may be a female’s strategy of avoiding sexual conflict. However, this needs to be balanced with the advantages of repeated matings by a number of males.

In populations showing multiple colour polymorphisms for females, sexual conflict may also be the influencing factor. Female colour morphs, other than the one matching male beetles, appear to “match” the host flower’s colour (Fig. 4), and thus, these females may be using a form of crypsis in avoiding males, or possible predators. This pattern is seen in *Scelophysa trimeni* where multiple (up to 10) female colour morphs were recorded within populations, with the majority of female morphs showing cryptic colours matching the spectrum of host flower colour. *Scelophysa trimeni* feed on a range of different host plants, with differing coloured flowers, possibly explaining the diversity of colour morphs seen in female beetles. Of course, females would have to match their own colour with only a few host plants, so this strategy is unlikely. An alternative hypothesis explaining why some populations show much female polymorphism, may relate to inter-specific sexual conflict, whereby, within communities of closely related sympatric species, females may face additional harassment from sympatric males (Johnson 1975). Thus females may evolve towards colouration that minimises (additional) harassment from sympatric species, i.e. colours which clearly distinguish them from sympatric females. However, the disadvantages of mimicking males, especially brightly coloured males needs to be balanced with the predation risks. In damselflies, male mimicking females have been seen to incur greater losses due to predation (Robertson 1985). Specialised monkey beetle predators, such as the robberfly *Gonioscelis*, do take their toll (Picker et al. 1991). These active predators hunt by sight, capturing beetles on the wing, and thus, brightly coloured beetles may be more susceptible to attack.

The colouration of male hind legs suggests a further role for visual signalling. Brightly coloured hind legs may serve as a possible deterrent to other males - *Pachycnema alternans* has bright red and hugely swollen tibia (Fig. 10). The red/orange tibia are in stark visual contrast to the black femora and tarsi. A similar dramatic contrast is observed in *P. calcarata* which has hugely swollen black tibia with a broad, red dorsal-lateral band and large, bright red sickle-like tarsal claws. Furthermore, the tibial and tarsal “socks” mentioned above possibly act as visual displays by males during mate guarding, when the ‘socks’ are displayed in an upward and extended posture. The “socks” may also give the impression of much thickened (musculature) hind legs, deterring rival males. This secondary function of hind leg traits is also found within highly dimorphic Embedders, e.g. males of *Heterochelus detritus* have highly dorso-ventrally flattened tarsal segments, forming feathery fan-like structures, which play no role in male combat due to their delicate structure. *Heterochelus detritus* have massive femora and tibia, each segment armed with a large spine, and forming a ratchet. Guarding and *in copula* males will hold their tarsi prominently upwards, possibly as a visual discouragement to other males. Thus, hind legs may have dual functions; that of weaponry and as visual deterrents to other males of the presence of weaponry (see Rosenberg 2002, Emlen 2008).



Figure 10. *Pachycnema alternans* males grappling over a female (male on right is holding female with mid and forelegs). [Note large, red swollen tibia and large tarsal claws].

STABILITY IN HIND LEG TRAITS – DIRECTIONAL SELECTION AND POSITIVE SCALING RELATIONSHIPS

In general, intra-specific variation in hind leg trait sizes was seen to be mostly low - leg traits were phenotypically conservative in the sense that all males examined either had enlarged hind legs with their associated armaments of spines, or not, as was the case for most Non-embedders) (see discussion below on leg allometry). Furthermore, the conservative mating strategies of Embedders, i.e. no alternative mating strategy such as sneak males (cf. dung beetles – Moczek 2005) or small-legged, mobile males, stresses the high importance of hind legs in securing and defending a female. Thus, although smaller males may lose battles to larger sized males (with larger legs) they still retain and require large hind legs to compete against other males of equal size. In addition, no asymmetry was seen, with hind legs showing similar size, shape, and armaments (see Hunt and Simmons 1997). This lack of intra-specific variability is in contrast to that recorded for a range of other insect groups whose males also show exaggerated weaponry (Moczek 2005, Emlen 2008). The extent of the variation that was seen (as measured by coefficient of variation) was, however, less in males than females of Embedders. This pattern was in contrast to that found for other insects (Zeh et al. 1992, Tseng and Rowe 1999). However, these studies did not adequately account for the influence of variations in body size and its related influence on trait size (see Cotton et al. 2004). Interestingly, the difference in coefficients of variation was not apparent in

Non-Embedders. When the same dimorphism traits were compared between males of Embedders and Non-embedders, the coefficient of variation scores were found to be lower in the Embedders for their highly dimorphic tibia. Stabilising sexual selection on the legs of male non-Embedders is therefore presumed to be less extreme. The greater variation of leg size in Non-embedders may be influenced by other factors overriding the importance of hind leg trait size for male contests, e.g. greater selection towards traits enhancing scramble competition (mobility, sensory capabilities (Thornhill and Alcock 1983)). For Embedders, the high competition for females and the essential role of hind legs in securing and guarding a female is most likely inducing stabilising selection on hind leg traits (Fisher 1930, Anderson 1994), and therefore resulting in reduced variation in hind legs. Furthermore, sexual selection in Embedders may override the influence of environmental variables that could influence trait size (Zeh et al. 1992), as size stability in exaggerated traits were observed in beetles of the same species collected from several environmentally contrasting habitats. This would suggest that sexual selection alone may influence trait size.

Certain hind leg traits appear to be of greater importance than others, as specific hind leg traits showed less variation than other legs, possibly indicating more intense directional selection on certain hind leg components within species. This pattern is additionally reflected in the steeper allometric slopes seen for some traits (see below), e.g. tibial thickness –which displayed low variation and high allometric slopes. However, leg traits may be inter-correlated such that the stability (minimum size requirement) of one leg trait is a prerequisite for another leg trait, i.e. leg traits function as a unit, with adequate femoral musculature a requirement to support a large, swollen tibia, which in turn is needed to control a large tarsal claw (see Tseng and Rowe 1999).

POSITIVE HIND LEG ALLOMETRY – INDICATIONS OF SEXUAL SELECTION

Exaggerated traits used in male combat which display positive allometric slopes ($b_{MA} > 1$) are mostly indicative of directional sexual selection (Anderson, 1994, Emlen and Nijhout 2000, Bonduriansky and Day 2003, Kodric-Brown et al. 2006; but see Emlen and Nijhout 2000 and Bonduriansky 2007 for exceptions). Theoretical models of sexual selection predict such a pattern (Petrie 1988, Kodric-Brown et al 2006). The advantages for larger males to have proportionately larger trait sizes are reflected in increased reproductive success and survivorship (Thornhill and Alcock 1983, Anderson 1994, Jennions et al 2001). The intensity of sexual selection is further reflected in its correlation with the steepness of the allometric slopes for traits such as those used in male contests (Simmons and Tomkins 1996). This pattern is seen here for monkey beetles with highly dimorphic traits (reflective of strong sexual selection) showing slopes ranging from 1.2-2.5, and comparable to slopes recorded for other insect groups

undergoing strong sexual selection on male traits (Kodric-Brown et al 2006). In contrast, Non-embedders which appear to experience less intense sexual selection (at least sexual selection on hind leg traits) generally showed less steep slopes for hind leg traits.

Only a very small percentage of Embedders and Non-embedders displayed non-linear allometric relationships (see Emlen and Nijhout 2000 for list of insects groups showing non-linear scaling relationships). Non-linear or sigmoid allometric relationships have been shown to be reflective of alternative mating strategies in contrasting morphological morphs, i.e. within a species large males with large traits (e.g. horns) aggressively defend females, whereas small males with absence of traits are non-aggressive and rather use sneak mating strategies (Thornhill and Alcock 1983, Emlen and Nijhout 2000, Moczek 2005). The general pattern observed for monkey beetles supports the notion that hind leg morphology within monkey beetles is conservative, with hind leg traits expressed in both large and small sized males. In addition, the presence of alternative male morphs or mating strategies, e.g. scrambling mate competition, appears not to have been developed. However, the presence of female-mimicking male colour morphs (see above) may suggest that alternative strategies, involving colour deception, have possibly been developed. Whether or not these female mimicking colour morphs are associated with males with disproportionately smaller leg traits (shallow allometric slopes) still requires investigation. Establishing such alternative strategies is important in understanding possible selective forces generating divergence in morphology, i.e. loss of traits in smaller males and associated behavioural adaptations (Emlen and Nijhout 2000). Such morphological divergences may eventually result in reproductive isolation, highlighting the potential role of sexual selection in promoting speciation.

GAINING INSIGHTS INTO SPECIES RICHNESS PATTERNS FROM PATTERNS OF SEXUAL DIMORPHISM

Speciose genera of monkey beetles did not necessarily show greater proportions of hind leg dimorphic species. Richness patterns were also not related to proportions of species that were dimorphic for both hind leg and colour. However, these patterns were most likely obscured by the lack of phylogenetic data allowing sister taxon comparisons. Using comparisons of sister clades controls for lineage age and richness, thus limiting these and other confounding factors (Barraclough et al. 1995).

A bimodal pattern was seen for the relationship of richness and degree of leg dimorphism: genera, irrespective of species richness, mostly either showed very high or very low proportions of hind leg dimorphic species. This contrast was especially notable in two of the most speciose genera: Embedder *Heterochelus* (77 species; 98.7% hind leg dimorphic); and Non-embedder *Peritrichia* (40 species; 12.5%

hind leg dimorphic). Such a pattern is difficult to explain and may relate to recently diverged lineages yet to build up a species flock, or taxonomic inaccuracies, whereby genera may be para- or polyphyletic . However, data from several recently revised speciose genera of monkey beetle (Dombrow 1997a, 1998b, 2000a) suggest that hind leg dimorphism is not a prerequisite for obtaining high species richness, as seen in the high levels of richness of some hind leg monomorphic, Non-embedding genera such as *Lepithrix*. For these Non-embedder genera, other parameters affecting cladogenesis may be of greater influence on richness values.

Phylogenetic distributions of leg and colour dimorphism are not yet known, thus the ancestral condition and evolution of dimorphism within the Hopliini must remain speculative. Placing such dimorphism patterns within a phylogenetic context is a necessary step in interpreting the evolution of host choice and mating systems of the Hopliini (see Emlen et al. 2005, Hosoya and Araya 2005). The initial stimulus for the formation of a Non-embedding guild may have been related to divergence away from hind leg dimorphism - possibly due to the expense of developing exaggerated hind leg traits (Kotiaho 2003, Kodric-Brown et al. 2006). The subsequent high speciation rate achieved by certain non-embedding genera may also be related to a shift towards the rich floristic resource evident in the core area of Non-embedder richness (western winter rainfall areas of the Fynbos and Succulent Karoo Biomes).

Approximately 45% and 37% of all Non-embedders are found within the Fynbos and Succulent Karoo biomes, respectively. The Biome housing the next highest number of Non-embedders is the Savanna Biome with approximately 7%. The Fynbos and Succulent Karoo are well known for their rich diversity and abundance of plants, especially bulbs (Iridaceae) (Goldblatt and Manning 2002, Proches 2005), which are much favoured host plants of Non-embedders (Picker and Midgley 1996, Goldblatt et al. 1998, Steiner 1998a). Furthermore, the ratio of Embedders to Non-embedders is lowest for the Fynbos and Succulent Karoo (ca. 2.5), whereas, other biomes, which show lower plant diversity (Cowling et al. 1989), show populations dominated more by Embedders (ratios of 4.0-7.0 Embedders per Non-embedder). Thus, high species richness of Non-embedders may be due to an adaptive shift into an alternative floristic niche, i.e. flower shapes favouring Non-embedding feeding species, which would in turn impact on the kind of mating strategy.

In contrast to patterns seen above for hind legs, the most speciose genera did, however, show the highest proportions of colour dimorphic species (cf. birds – Barraclough et al. 1995). Furthermore, unlike for hind legs, this pattern was seen across feeding guilds. Generally, the role of colour in sexual selection is well established, either through female choice and/or acting as an indication of strength to rival males (Anderson 1994, True 2003, Gray and Mckinnon 2006). For monkey beetles, the latter role is most likely, as the mate choice by female monkey beetles does not appear to be operational. The physical cost of male

contests in monkey beetles can be very high, due to physical injury. Embedder males have the ability to amputate another male's leg during combat. I have observed "winning" males of several species retaining an opponent's severed hind leg, trapped between the femora and tibia. Thus colour in males (especially of a weapon) would be an expected parallel adaptation to the weapons themselves, allowing males the option of avoiding other males in copula or guarding females in their search for mates. For Non-embedders, avoiding male contests is equally important as females of many species are highly "skittish" and will often fly off while males are tussling. For most Non-embedders, hind leg trait size was not found to be selected for, i.e. weak allometric slopes and dimorphism, and therefore, male colouration is considered most likely a signal advertising presence to other males. Thus males that can easily distinguish other males based on colour patterns will not waste time and energy by landing on a flower occupied by a male and/or occupied by a male *in copula* with a female, but rather only target flowers occupied by females.

As stressed above, without adequate phylogenetic data it is difficult to conclusively link proportions of dimorphic species with species richness of a genus, and to generalize this trend across the tribe to explain the megadiverse monkey beetle fauna of South Africa. Nonetheless, inter-specific variation in hind leg traits and colour was observed to be extremely diverse for South African monkey beetles (see Emlen 2008 for review on variety of forms of sexually selected weapons across taxonomic groups). This suggests that they represent a case of adaptive radiation as well in terms of diversity in body form, colour, feeding ecology and mating systems. For species showing hind leg dimorphism, the range of shapes, lengths, breadths, thicknesses, and armaments for each hind leg segment, with many different combinations of these, was impressively high both within a genus and across genera (see Fig. 8). The number of adaptations seen also appeared to be higher in those traits that show higher dimorphism scores (legs - tibia, colour - pygidium). In contrast, general morphologies and dimensions of other structures (pronotum, elytra, mid legs, pygidium) remain fairly uniform between species, although the colour adaptation of these body parts is highly variable. Furthermore, other ecological and behavioural attributes are commonly shared across species (e.g. habitat (niche space), host plants, feeding strategies). Thus, this myriad of forms seen for monkey beetle hind legs and colour may be explained by sexual selection favouring more competitively successful traits (Andersson 1994). Divergence in these traits would possibly result in speciation as a result of reproductive isolation (West-Eberhard 1983) that accrues from positive assortative mating associated with a variant of a sexually selected trait. These strong selective forces may help explain the high numbers of congeneric species occurring in sympatry which show high differentiation of secondary selected traits but similar feeding and host plant strategies. The high species turnover seen along environmental gradients (see Chapter 4) may thus be influenced not only by ecological factors but also by sexual selection and associated mating strategies. Across these gradients

floristic changes are also high, e.g. along altitudinal gradients plant communities can change from dominance of large disk shaped Asteraceae and Aizoaceae favouring Embedders through to montane fynbos dominated more by plants associated with Non-embedders (see Chapter 3). Thus the role of sexual selection needs to be incorporated into ecological models describing richness and diversity patterns.

CONCLUSION

Ecological and environmental variables only partially explain beetle richness. In order to explore the possible evolutionary role of sexual selection influencing rates of speciation, leg and colour dimorphism was measured across two beetle feeding guilds, Embedders and Non-embedders. Striking and highly divergent secondary sexual traits (hind leg and colour) were seen for a high percentage of species. Dimorphism patterns were strongly linked to feeding guild and mating strategies. Leg dimorphism was almost exclusively associated with Embedders, in which males use their hind legs as weapons in male-male combat over females. The evidence of clear sexual hind leg dimorphism, plus positive allometry of hind leg traits suggests that the hind legs of Embedder species are under strong sexual selection forces. In contrast to hind leg dimorphism, colour dimorphism occurred in equally high frequencies across both guilds. Furthermore, speciose genera showed higher proportions of colour dimorphic species. Thus, the prevalence of sexual dimorphism suggests that strong sexual selection pressures may be an important driving force of speciation and an explanatory factor in species diversity of monkey beetles.

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SUMMARY

For over a century, biogeographers have grappled with the fundamental problem of diversity and distribution. Understanding why species occur where they do, and why some areas have more species than others, is a much debated but still poorly understood field. This is especially so for the megadiverse and ecologically pivotal insects. Insects have an exceptionally long and successful evolutionary history, and have radiated into a bewildering number of diverse taxa.

South Africa is well known for its remarkably species rich and highly endemic fauna and flora, and hosts two global biodiversity hotspots. However, there is a distinct study bias towards vertebrates and plants when highlighting this exceptional diversity and its ecological and evolutionary origins. In contrast, the insect fauna of these biomes have not been profiled or well-studied, although displaying equally high, if not higher levels of richness and endemism than for example, plants. Extensive adaptive radiation and associated endemism have been recorded for many invertebrate groups, and South Africa has a well represented Gondwanan relictual fauna. Many pollinator groups in the western winter rainfall biomes display remarkable levels of co-adaptation and unique guild associations with host plants. The lack of distributional databases for invertebrates is a well-recognised gap in conservation planning, but the group is so speciose, taxonomically complex, and unequally sampled that conservation efforts have prioritised vertebrates and plants.

In this context, the central aim of this thesis was to explore the diversity patterns of a megadiverse group of pollinating beetles, the Hopliini (monkey beetles). Globally, the centre of diversification for monkey beetles is clearly South Africa with high proportions of the world's species found within (*ca.* 63%) and endemic (*ca.* 98%) to this country. The overall aim of this thesis was to investigate and explain monkey beetle diversity and distribution in South Africa. The key findings can be summarised under 4 main headings.

The relationship between area and richness in Hotspots of richness and endemism (Chapters 1 and 2)

In order to identify areas of species richness and endemism, a geo-referenced presence-only dataset, comprising 6959 unique point locality records for the 1040 monkey beetles species currently recognised in South Africa, was compiled from field observations and museum collections and analysed with a

geographical information system (GIS) in terms of spatial variations in richness and endemism. Centres of endemism were delimited using an Integrated Weighting technique in conjunction with GIS interrogation and then spatially matched to other faunal and floral biogeographic centres to search for congruence.

The Fynbos Biome showed the highest beetle richness, accumulated species significantly faster and showed higher richness per unit habitat area. The Succulent Karoo Biome was the next most diverse biome with many endemics and morphologically unique species. Across biomes, habitat heterogeneity was indicated as more important than area in explaining species richness

18 centres of endemism were delimited. Hotspots of richness and endemism in South Africa were concentrated within the winter rainfall biomes (Fynbos and Succulent Karoo). Endemism was found to be strongly associated with monkey beetle species richness. Moreover, congruence was observed between centres of monkey beetle endemism and those of other taxa, including plants. This gradient of species richness having concentrations of species in the winter rainfall regions shows congruence with other faunal and floral groups and for some taxa indicates a coevolved response to, and with, the evolution of the flora of the winter rainfall biomes.

Role of local environmental factors as explanatory variables of regional beetle richness (Chapter 3)

In this chapter, Geographically Weighted Regression (GWR) techniques were used to relate regional beetle richness patterns to smaller scale environmental (rainfall, temperature, habitat heterogeneity, host plant diversity) explanatory variables and diversity measures (beta diversity measures of monkey beetles and associated host plants).

Plant richness was an important predictor of regional beetle richness, but the predictive power of explanatory variables (rainfall, temperature, habitat heterogeneity, host plant diversity) varied geographically (strong spatial non-stationarity), and are fundamentally different between the winter rainfall and summer rainfall areas. This spatial non-stationarity in the importance of plant richness as a predictor of beetle richness highlights the merit of using a modelling approach that can relate regional richness patterns with smaller scale variations in host plant diversity, rainfall, temperature, and habitat heterogeneity.

Spatial turnover (beta diversity) in beetle community composition as a function of environmental and plant variables (Chapter 4)

Generalised dissimilarity models (GDM) were used to explore compositional dissimilarity (beta diversity) as a function of geographic distance, environmental (rainfall, temperature, altitude, soil fertility), and plant (host species, vegetation types, and bioregions) variables, at regional (quarter degree grid cells; presence-only data) and field survey (presence/absence data from winter rainfall field sites) scales.

At both regional and field survey scales, beetle compositional dissimilarity was strongly correlated with environment and plants, but environment appeared to be a slightly stronger predictor. Geographic distance between sites added virtually nothing to the explanatory power of the model, because of steep environmental gradients and poor dispersal abilities of Embedder species.

Compositional dissimilarities at the regional scale were most strongly correlated with environmental factors (rainfall seasonality and concentration) though plant variables (vegetation type habitat proportions, and ecological dissimilarities across bioregions) were also important. At the field site scale compositional dissimilarities are most strongly correlated with altitude and rainfall (concentration). Plant variables (host compositional turnover and flower abundance) were weakly correlated with beetle compositional dissimilarities between sites.

The role of sexual selection as an explanatory factor in species diversity (Chapter 5)

Leg and colour dimorphism was measured across two beetle feeding guilds, Embedders (relatively sessile beetles feeding embedded in the capitulum of disk-shaped flowers) and Non-embedders (highly mobile beetles feeding on a wider range of flower shapes). This was done in order to explore the possible evolutionary role of sexual selection influencing rates of speciation.

Striking and highly divergent secondary sexual traits (hind leg and colour) was noted for a high percentage of species. Dimorphism patterns were strongly linked to feeding guild and mating system. Leg dimorphism was almost exclusively associated with Embedders. In contrast, colour dimorphism occurred in equally high frequencies across both guilds.

Ecological models incorporating environmental and plant variables, however, do not fully account for variation in beetle species diversity. The prevalence of pronounced sexual dimorphism suggests that strong sexual selection pressures may be an important driving force of speciation and thus an explanatory factor in species diversity

Significance of the study

The exceptional levels of richness and endemism of South African monkey beetles highlights the importance of the region as a primary centre of diversification for these pollinators. More specifically, by far the highest levels of diversity were found to be concentrated within the winter rainfall biomes which contain two floristic global biodiversity hotspots (Cape Floristic Region and Succulent Karoo). This study has identified centres of endemism for monkey beetles based on weighted clustering techniques, and matched them with those for other insects and flora. In spite of their relatively small size, the Fynbos and Succulent Karoo biomes recorded the highest levels of endemism and species richness per unit area, arguing for their evolutionary importance as centres of adaptive radiation.

This is the first study to use modern analytical methods to delimit centres of endemism of an insect group in South Africa, and has sought congruence between the biogeography of beetles and that of other plant and insect groups. Results from this are significant because they emphasize congruence with richness patterns of other faunal and floral groups and suggest a possible coevolved response to the plant radiation in the winter rainfall biomes of South Africa.

Notably, in this study plants were used as an explanatory variable for insects across all of South Africa's biomes. In addition, the spatial variation (non-stationarity) of environmental and plant variables as predictors of beetle richness highlights the necessity of using modelling techniques like geographically weighted regression (GWR) that can relate regional richness patterns with smaller scale variations in host plant diversity, rainfall, temperature and habitat heterogeneity. With regards to beta diversity, at both regional and field survey scales, beetle turnover was strongly correlated with environment and plants, but environment (rainfall, temperature, altitude, soil fertility) appears to be a slightly stronger predictor. Interestingly, geographic distance between sites explained minimal amounts of species turnover at both data scales. This finding is in contrast with patterns seen in other Mediterranean and arid systems, and is probably related to steep environmental gradients. Furthermore, interesting contrasts with other biodiversity hotspots, such as tropical rainforests were noted in that high beetle alpha diversity was matched by high beta diversity indicating that locally co-existing beetle species do not represent a large proportion of the regional species pool.

The study showed that the processes explaining richness in beetles are not necessarily the same as those for plants, even when plant and beetle taxa are closely linked, through, for example, pollination. However, cladogenesis in monkey beetles may be independent and separate from processes driving

diversification in individual host plants, because their generalist feeding habits and vagility allow them to perceive the landscape not at a plant species level but at a coarser grain such as vegetation types.

Despite the increased power of models used here over global models that assume static relationships between richness and explanatory variables, the ecological models developed did not fully account for variation in species diversity. A key finding was that sexual selection may be an important driver of diversification and speciation in monkey beetles.

The use of insect data in conservation planning has been hampered by a lack of available data, but the results of this study suggest that obtaining such data is a high priority; firstly because monkey beetle richness and levels of endemism were exceptionally high, particularly within the two global hotspots of the Cape Floristic Region and Succulent Karoo, and secondly because processes relating to the evolution and maintenance of plant and insect richness and turnover patterns can differ, even for insects tightly tied with plants, e.g. pollinators. Thus, conservation planning needs to look beyond the use of plants as key drivers of conservation initiatives.

FUTURE RESEARCH

Further research may improve the sampling resolution of insects across South Africa. Furthermore, the huge wealth of data awaiting collation from natural history collections would greatly improve the understanding of zoogeographic patterns and faunal zones.

There is currently little knowledge of the physiological requirements of adult monkey beetles, and even less about their larvae, which may have entirely different ecological requirements because of the contrast in feeding habits between the two stages of the life cycle (viz. pollinator vs. detritivore, respectively) and mobility. These requirements, together with ecophysiological parameters of adults (e.g. temperate montane vs. arid-adapted species) could be used profitably to further investigate fine scale distributions within the Hopliini.

Phylogenetic data would allow a deeper understanding of the evolution of the group and a means of testing the hypothesis, raised here, that sexual selection has promoted rates of speciation, by allowing accurate sister taxa comparisons. The role of sexual selection may hold the key to explaining perceived processes related to elevated levels of speciation, disconnected from host plants diversity. Furthermore, the possibility of dating lineage diversifications would allow cladogenetic events to be related to the geological and climatic evolutionary history of the winter vs. summer rainfall regions of South Africa.

Finally, the inclusion of insect data into conservation planning and biodiversity assessments would allow identification of additional areas of high conservation importance and establishment of a more comprehensive network of protective areas. Endemism was found to be strongly associated with monkey beetle species richness. Moreover, congruence was observed between centres of monkey beetle endemism and those of other taxa, including plants. In addition, the status of South Africa's two global hotspots would further be enhanced, in that insect diversifications within these areas appears to match, if not supersede, that seen for plants.

"Finally: It was stated at the onset, that this system would not be here at once perfected. You can but plainly see that I have kept my word. But know I leave my Cetological System standing thus unfinished, even as the great Cathedral of Cologne was left, with the crane still standing upon the top of the uncompleted tower. For small erections may be finished by their first architects; grand ones, true ones, ever leave the copestone to posterity. God keep me from ever completing anything. This whole book is but a draught – nay, but the draught of a draught. Oh, Time, Strength, Cash, and Patience!" – **Herman Melville, *Moby Dick***