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thesis abstract

Understanding the evolutionary radiation of the mega-diverse Monkey Beetle fauna (Scarabaeidae: Hopliini) of South Africa

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South Africa is the global centre of diversification for monkey beetles (Scarabaeidae: Hopliini). 69 % of the world fauna occur here, with 98% of the 1040 South African species and 80% of the South African genera being national endemics. This thesis was the first analysis of the regional distribution patterns, and the processes underlying the generation of the mega-diverse monkey beetle fauna of South Africa. Specifically, the aims of the thesis were 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.

Methodological procedures followed current and newly-developed analytical techniques used in the fields of biogeography, spatial ecology, and evolutionary biology. A key first methodological step was the compilation of a geo-referenced presence-only dataset from field observations, museum collections, and taxonomic revisions. This comprised 6959 unique point locality records which were analysed within a geographical information system (GIS). This allowed portraying of the spatial variation in richness and endemism across local and regional habitats.

Within South Africa, and particularly within the global hotspots of the Cape Floristic Region and Succulent Karoo, biogeographic congruence of patterns of richness and diversification across faunal and floral groups has not yet been investigated. This was the first study to use modern analytical methods to delimit centres of endemism and diversification (areas of historical biogeographic significance) of a South African insect taxon . Monkey beetle centres of endemism were delimited using an Integrated Weighting technique (a technique which sought consensus from different weighting and clustering algorithms) (Linder 2001, Bradshaw 2009), in conjunction with GIS interrogation, and then spatially matched to other faunal (Carcasson 1964, Endrödy-Younga 1978) and floral biogeographic (van Wyk and Smith 2001, Goldblatt and Manning 2002, Born et al. 2007) centres to search for congruence.

Shifting focus away from historical biogeographic perspectives and towards contemporary ecological variables, localised regression techniques (geographically weighted regression; Fotheringham et al. 2002) were used to relate regional beetle richness patterns to smaller scale environmental explanatory variables (rainfall, temperature, habitat heterogeneity, host plant diversity). Furthermore, generalised dissimilarity models (Ferrier et al. 2007) were used more specifically to explore species compositional dissimilarity (beta diversity) as a function of environmental (rainfall, temperature, altitude, soil fertility) and plant (host species diversity, vegetation habitat categories) variables, at regional (quarter degree grid cells; presence-only data) and field site (presence/absence data from winter-rainfall field survey sites) scales.

Finally, an additional shift in focus was made, away from ecological perspectives, exploring the potential role of sexual selection in influencing rates of speciation of monkey beetles (Ritchie 2007). Leg and colour sexual 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 addition, the proportions of sexually dimorphic species (as based on a point scoring system) were calculated for each genus and related to its species richness.

Key results from this thesis highlighted the exceptional levels of richness and endemism of South African monkey beetles and the importance of the region as a primary centre of diversification for these pollinators. More specifically, hotspots of richness and endemism for South African monkey beetles were concentrated within the winter-rainfall biomes (Fynbos and Succulent Karoo). Based on slope and intercept values from species-area curves (Rosenzweig 1995), the winter-rainfall biomes accumulated species significantly faster per unit area, and showed higher richness per unit habitat area than summer-rainfall biomes, arguing for their evolutionary importance as centres of adaptive radiation. For these biomes, the exceptional diversity of monkey beetles was matched by congruent patterns of insect diversity across a range of disparate taxonomic groups, highlighting the importance of this region as a centre of adaptive radiation (Hesse 1969, Gess 1992, Whitehead and Steiner 2001, Kuhlmann 2005, Barraclough 2006). Furthermore, the patterns of endemism of the beetles showed concordance with phytogeographical centres, suggesting possible co-evolutionary histories between plants and insects, particularly since many of the species-rich insect groups are closely associated with plants and flowers. This congruent pattern was also suggestive of parallel responses of fauna and flora to historical climatic and geological events (Stuckenberg 1998).

Retrieval of a number of well-defined centres of endemism within the winter-rainfall regions allowed historical biogeographic insights into this biodiversity hotspot. In broad congruence with previously delimited zoogeographic zones, such as those delimited intuitively by early historical biogeographers for butterflies (Carcasson 1964) and beetles (Endrödy-Younga 1978), monkey beetle distribution patterns were divided into distinct western and eastern zones, as shown from the primary split of a hierarchical cluster analysis (using presence data of genera) into two distinct clusters at the > 5% similarity (i.e. 95% dissimilarity) level. The western zone showed high monkey beetle species richness, endemism and concentrations of lineage diversifications, conforming to a pattern described for several other insect groups (Tjeder 1967, Mansell 1985, Kuhlmann 2005). 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, Picker and Samways 1996). Of the eighteen centres of endemism that were delimited across South Africa, the largest were located in the winter-rainfall, western regions, and showed the highest levels of endemism and species richness, with species richness strongly correlated with endemism, thus further supporting this region as a centre of diversification. Across this western region, the fairly good spatial congruence with plant and other insect biogeographic centres highlights the presence of possible shared centres of diversification across taxonomic groups. In contrast, the eastern, predominantly summer-rainfall region showed lower richness values, and fewer endemic species. The eastern zone retrieved for monkey beetles was seen to be less zoogeographically distinct compared to the western zone, sharing Afrotropical elements with southern and central African regions (Lawrence 1952). Key historical processes associated with the two distinctive biogeographic patterns were inferred to comprise geographical fragmentation of populations as a result of palaeoclimatic change and geomorphic evolution (Cowling and Proches 2005, Cowling et al. 2009). Such factors are postulated to promoted allopatric speciation through vicariant events and vicariant speciation in the Cape Mountain system has been proposed for various insect and invertebrate taxa (Endrödy-Younga 1988, Wishart and Day 2002, Prendini 2005). Studies have estimated that palaeoclimatic change has isolated various montane insect populations within the Fynbos Biome for at least 4 million years (Wishart and Day 2002). The role of historical processes and their relation 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. The need for phylogenetic data was highlighted in this study, as this would allow a deeper understanding of the evolution of the monkey beetle fauna and provide a means of testing the hypotheses for the observed patterns of cladogenesis and endemism. 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.

Results from macroecological analyses of beetle distributional and richness data showed host plant richness is generally an important predictor of regional beetle richness; however, the predictive power of explanatory variables (host plant diversity, rainfall, temperature, habitat heterogeneity) varied geographically (strong spatial non-stationarity), and was fundamentally different between areas classed as winter, summer, and non-seasonal-rainfall. The spatial variation of environmental and plant variables as predictors of beetle richness highlighted the necessity of using modelling techniques that can relate regional richness patterns with smaller scale variations in host plant diversity, rainfall, temperature and habitat heterogeneity (see also Foody 2004).

Spatial turnover (beta diversity) at field site and regional scales was strongly correlated with environmental and plant variables, with environment being the stronger predictor. Plant variables recorded contrasting results, with variables associated with habitat heterogeneity of vegetation types being of greater importance, whereas turnover of plant species was seen to be a weak predictor. Plant species were less important because most monkey beetles are generalist feeders and thus do not perceive landscape heterogeneity at the level of plant species occurrence. In contrast, habitat heterogeneity (steep edaphic factors and floristic gradients) provided habitats for a wider range of feeding guilds, and therefore was associated with increased turnover. Interestingly, geographic distance between site pairs explained minimal amounts of species turnover at both data scales (< 1%). Complete species turnover (100%

compositional dissimilarity of beetle communities) was recorded within very short distances, and beyond this asymptote increasing geographical distance had no effect on turnover. This finding was explained by the steep ecological and environmental gradients, combined with poor dispersal abilities (through habitat fidelity) of some monkey beetles. Steep environmental gradients in rainfall seasonality, concentration and annual rainfall, as well as altitude, were all important factors in explaining turnover. 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 (Latimer et al. 2005). Overall, the findings associated with turnover patterns for monkey beetles were in contrast with patterns seen in other Mediterranean and arid systems (e.g. Potts et al. 2003), and are probably related to the unusually steep environmental gradients associated with South Africa's Mediterranean regions. Furthermore, interesting contrasts with other biodiversity hotspots, such as tropical rainforests (see Novotny et al. 2007), were noted in that high 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 also 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. Moreover, 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 geographically weighted models over models that assume static relationships between richness and explanatory variables across the whole region, the ecological models developed here 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, highlighting the need to look beyond ecological determinants of richness patterns. 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. Sexual selection was shown to be an important variable explaining clade richness and diversification. Striking and highly divergent secondary sexual traits (hind leg and colour) were features of a high percentage of species (64.3% were sexually hind leg dimorphic, 84.9% sexually colour dimorphic). 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: 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, colour dimorphism occurred in equally high frequencies across both guilds. Contrasting patterns were seen when relating number of species found within a genus and the proportion of sexually dimorphic species. The proportion of leg dimorphic species within a genus was not related to its species richness. A significant positive relationship was, however, seen between the proportion of colour dimorphic species within a genus and its species richness, with speciose genera showing a myriad of striking colour dimorphic patterns. Thus, the prevalence of sexual dimorphism in monkey beetles suggests that strong sexual selection pressures may be an important driving force of speciation and diversifications.

Tapping the wealth of insect data awaiting collation from natural history collections would greatly improve the understanding of zoogeographic patterns and faunal zones in South Africa. Moreover, 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 of high priority; firstly because monkey beetle richness and levels of endemism were exceptionally high, and secondly because processes relating to the evolution and maintenance of plant and insect richness and turnover patterns can differ, even for insects dependent on plants. Thus, conservation planning needs to be more inclusive in its use of such data.

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 (pollen feeder 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 monkey beetles.

Finally, the role of sexual selection may hold the key to explain elevated levels of speciation, unrelated to host plant diversity. Phylogenetic data being assimilated at present will allow a deeper understanding of the evolution of the group and provide a means of testing the hypothesis that sexual selection has promoted rates of speciation by allowing accurate sister taxa comparisons.

Papers in preparation

Five manuscripts are currently in preparation from the thesis; one manuscript for each of the chapters/key aims of the thesis. Additional analyses undertaken subsequent to the completion of this thesis explore compositional dissimilarities in beetle communities, with plant compositional dissimilarities having also now been modelled, using the same environmental variables used in the beetle model, and using beetle turnover as an explanatory variable. This was done to contrast the varying degrees of influence that dissimilarity in pollinator communities have on host plant communities, and the influence that dissimilarities of host plant communities have on beetle species composition.

Availability of thesis

A print copy of the thesis is available from the University of Cape Town library (www.lib.uct.ac.za); or a PDF copy is available at request from the author.

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