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RESEARCH  
PAPER



# Insect diversity in Cape fynbos and neighbouring South African vegetation

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## ABSTRACT

**Aim** It has often been suggested that South Africa's Cape fynbos shrublands, although extremely rich in plant species, are poor in insects, thus representing a notable exception from the broad plant–insect diversity relationship. The aims of this study were to compare the diversity patterns of plant-inhabiting insects in fynbos and the vegetation of three neighbouring biomes (grassland, subtropical thicket, and Nama-karoo), and to test for a general relationship between plant diversity and insect diversity across these biomes.

**Location** South-western to south-eastern South Africa.

**Methods** We conducted seasonal plant surveys and sweep insect sampling in 10 × 10 m plots in the Baviaanskloof Conservation Area (Eastern Cape), where all four biomes occur. We also conducted once-only collections in the core area of each biome.

**Results** Fynbos plots had insect diversity values similar to those of grassland and subtropical thicket (a dense, evergreen and spinescent shrubland with a high abundance of succulents and climbers), and significantly higher than Nama-karoo (an open, semiarid shrubland). A remarkably strong positive relationship was found between plant and insect species richness.

**Main conclusions** Previous generalizations were based on a few insect groups (e.g. butterflies, under-represented in fynbos), but ignored published results on other groups (e.g. galling insects, which are in fact over-represented in this vegetation). We show that, overall, insect diversity in fynbos is comparable to that of neighbouring biomes. Fynbos vegetation does not represent a significant exception from the broad positive relationship between plant diversity and insect diversity.

## Keywords

Cape Floristic Region, diversity relationships, fynbos, insect diversity, insects, plant diversity, South Africa.

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## INTRODUCTION

Phytophagous insects comprise a substantial proportion of the world's fauna (Mitter *et al.*, 1988). Global diversity estimations for this group have been made using plant species numbers as the predictor, assuming high degrees of host plant specificity (e.g. Erwin, 1982). Recent studies suggest that levels of host specificity may be lower than thought previously (Novotný *et al.*, 2002), and that most of the high values reported for plant–insect correlation at medium and large spatial scales are owing to similar responses to environmental factors in the two groups, and not to a direct, causal relationship (Hawkins & Porter, 2003). In this context, it is not clear if the diversity relationship between phyto-

phagous insects and plants is stronger than that between all insects and plants. Overall, studies on insect–plant diversity relationships are available for a limited range of geographical regions, spatial scales, and insect groups, with most studies addressing single insect groups and spatial scales, and mainly in northern temperate regions (see Strong *et al.*, 1984 and references therein; Siemann *et al.*, 1997; Knops *et al.*, 1999; Haddad *et al.*, 2001).

South Africa is one of the world's foremost centres of plant diversity and endemism, the greatest concentration of plant species occurring in a sclerophyllous, fire-prone shrubland known as fynbos. The south-western corner of the country, dominated by fynbos but containing enclaves of other biomes, is known as the Cape Floristic Region (CFR; Goldblatt & Manning, 2000). It

has been stated repeatedly that the Cape fauna does not parallel the flora in species richness or endemism (Cottrell, 1985; Johnson, 1992; Giliomee, 2003). Although numerous animal endemics occur there, the overall proportion is lower than that for plants. Moreover, in most animal groups surveyed (mainly vertebrates), total diversity is low in the Cape compared to the subtropical regions to the north-east of the CFR (Low & Rebelo, 1998).

Fynbos is thought to have an especially poor insect fauna (Johnson, 1992; Giliomee, 2003), suggesting a deviation from the generally good large-scale relationship between plant and insect diversity (see Hawkins & Porter, 2003). The supposedly low insect diversity in fynbos relates presumably to sclerophylly and chemical defences against herbivory (Johnson, 1992; Giliomee, 2003), but there have been few studies to back this up, and these refer to limited sets of plant species (e.g. Coetzee *et al.*, 1997). Moreover, diversity data are available for a small proportion of the insect fauna (e.g. there are few butterfly species in the Cape, even fewer associated with typical fynbos plants; Cottrell, 1985). However, in some other phytophagous insect groups, the data available suggest that species diversity and endemism are extremely high in fynbos (e.g. Hemiptera: Cicadellidae; Davies, 1988a,b).

Several other biomes occur in the CFR, often in interdigitation or mosaics with fynbos. These include grassland (centred north-east of the CFR), subtropical thicket (a dense, evergreen and spinescent shrubland with a high abundance of succulents and climbers, centred to the immediate east of the CFR), and Nama-karoo (an open, drought-deciduous shrubland, centred to the north of the CFR) (Low & Rebelo, 1998; Fig. 1). It is generally assumed that these biomes are characterized by higher palatability than fynbos, given their lower levels of sclerophylly and lower content of chemical repellents (Johnson, 1992; Owen-Smith & Danckwerts, 1997).

The juxtaposition of these biomes in the CFR offers opportunities for investigating the effects of differences in plant diversity (as well as biomass, morphology and biochemistry) on the species richness of their insect faunas. The only published diversity comparisons across different biomes in the CFR refer to one eco-

logically defined insect group, namely gall-forming insects (Price *et al.*, 1998; Wright & Samways, 1998). These studies contradicted the generalization of low insect diversity in fynbos, this biome emerging consistently as the most species-rich. The studies also reported a generally good correlation between plant and insect species richness values. It is, however, conceivable that this would not hold for other insect groups, gall-forming insects being particularly diverse in sclerophyllous vegetation worldwide (Price *et al.*, 1998).

This study aims to fill gaps in our knowledge of plant–insect diversity relationships in the Cape. Specifically we set out to: (i) compare the richness of the fynbos insect fauna with that of adjacent vegetation, at the plot and biome scale; and (ii) test for a general (cross-biome) relationship between plant and insect diversity.

## MATERIALS AND METHODS

We conducted comprehensive sweep insect collections and plant surveys for 10 × 10 m plots in fynbos, grassland, subtropical thicket and Nama-karoo. For convenience, subtropical thicket and Nama-karoo will be referred to as thicket and karoo, respectively. Table 1 provides a brief characterization of the biomes. In each biome, we collected both in the geographical core area [with the exception of fynbos, biome core areas fall outside the CFR; see Cowling *et al.* (1989) for core biome definition], and in (or adjacent to) the Baviaanskloof Conservation Area in the south-eastern CFR, where all the biomes co-occur in a relatively small area. Therefore we sampled a total of eight localities (Fig. 1; also see Appendix S1 in Supplementary Material). The other southern African biomes (desert, succulent karoo, forest, savanna) are not represented, or only marginally so, in the Baviaanskloof. As these may also require different insect collection methods (forest), they were not included in this study.

In each of the eight localities we sampled eight 10 × 10 m plots in four sets of two adjacent plots. We selected sets 100 m apart at both ends of a 1 km transect (giving four sets in total). Therefore,

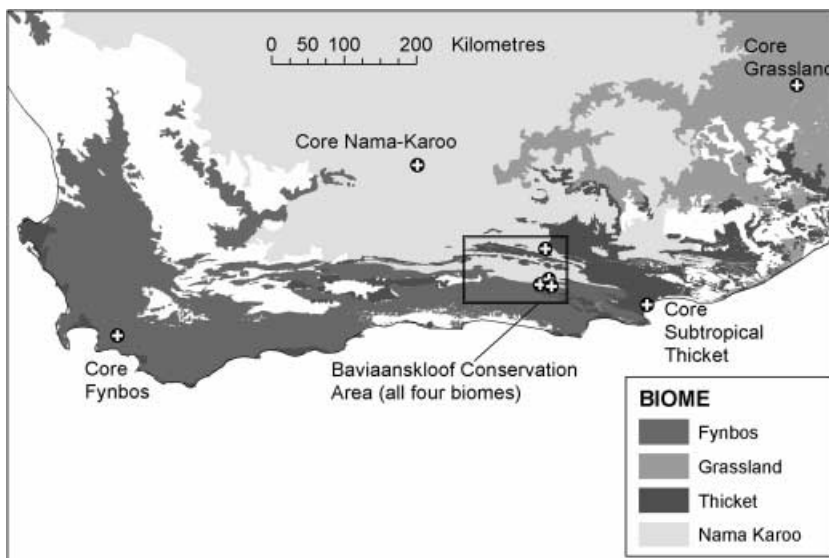


Figure 1 The Cape Floristic Region of South Africa, showing the distribution of the four biomes sampled in this study (Low & Rebelo, 1998). One locality was sampled in the core area of each biome, and all four biomes were sampled in the Baviaanskloof Conservation Area. White areas on the map (biomes that were not sampled) represent succulent karoo (west and centre), forest (along the central part of the south coast) and savanna (east).

**Table 1** General description of the biomes (based on Cowling *et al.*, 1989; Low & Rebelo, 1998; Vlok *et al.*, 2003)

Biome	Major growth forms	Rainfall	Forage palatability	Plant species richness	
				Local (1 m <sup>2</sup> )	Regional
Fynbos	Evergreen shrubs, evergreen hemicryptophytes (restioids)	200–3000 mm yr <sup>-1</sup> winter/non-seasonal	low	5–35	7316
Grassland	Seasonal hemicryptophytes (graminoids)	400–2000 mm yr <sup>-1</sup> , summer	moderate–high	5–25	3788
Thicket	Evergreen shrubs, succulent shrubs, lianas	200–800 mm yr <sup>-1</sup> , equinoctial	high	1–15	1558
Karoo	Dwarf deciduous shrubs, seasonal hemicryptophytes	100–520 mm yr <sup>-1</sup> summer–autumn	moderate–high	1–15	2147

64 plots (two per set, four sets per transect, two transects per biome, four biomes) were sampled that covered a broad range of spatial scales (cf. Wu & David, 2002). We collected our data in 2002–03, at the time of year when plant and insect activity peaked at each locality: October in the Baviaanskloof and core fynbos; February in core grassland; December in core thicket; and April in core karoo. To include insects with various seasonal emergence patterns, we conducted additional collections in the Baviaanskloof, in April, July, and December 2002 (four replicate plots during each collection season, in each biome).

We identified all plants to genus level, and more than 90% to species level; the rest we defined as morphospecies. All insects were identified to family level, and within families we defined morphospecies using broad external morphology (Oliver & Beattie, 1996). We counted adults and nymphs from each heterometabolous morphospecies in each sample. Only adult holometabolous insects were considered.

To compare species richness for the four biomes, we used plant and insect presence/absence data at various spatial scales in Kruskal–Wallis comparisons followed by Dunn's *post-hoc* test. To test for a general plant–insect diversity relationship, we regressed insect diversity against plant diversity. For plant taxonomy, we followed Germishuizen & Meyer (2003); for insect taxonomy, Scholtz & Holm (1985), with the additional recognition of the collembolan orders Symphyleona and Entomobryomorpha (D'Haese, 2003), Strepsiptera (Whiting & Wheeler, 1994), and Mantophasmatodea (Klass *et al.*, 2002). We defined trophic guilds according to the predominant feeding habits at family level (same references), and explored the relationship between various guilds and plant diversity using correlation analyses.

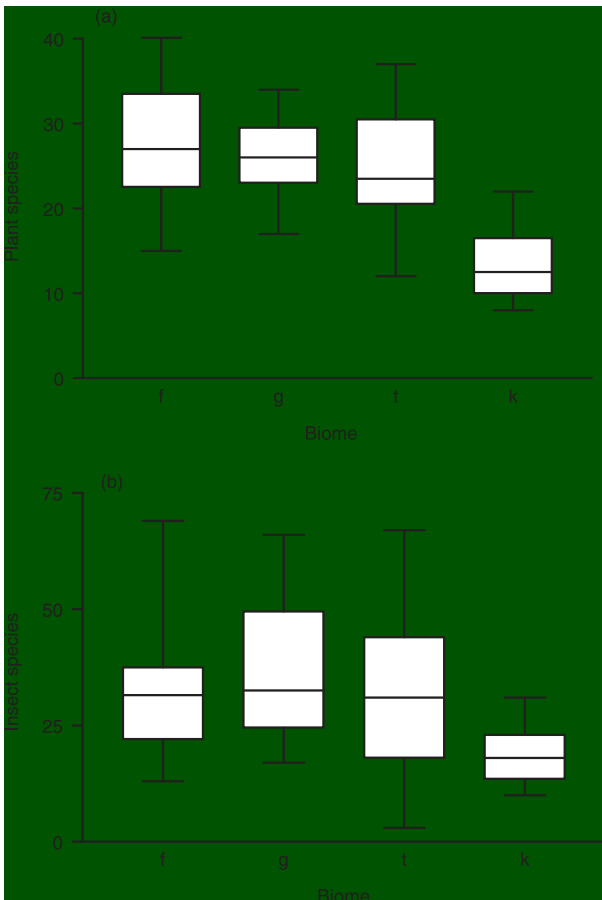
## RESULTS

In total, we recorded 480 plant species (belonging to 234 genera in 71 families) and 754 insect morphospecies (belonging to 162 families in 20 orders; 412 phytophagous, 225 predaceous/parasitic, and 117 detritus feeders). The largest plant families were Asteraceae (65 species), Poaceae (52), Restionaceae (28), Aizoaceae (24), and Crassulaceae (21); the largest genera were *Erica* (Ericaceae;

16 species), *Crassula* (Crassulaceae; 13), *Asparagus* (Asparagaceae; 11), *Hermannia* (Malvaceae; 11), and *Senecio* (Asteraceae; 10). In the case of insects, the largest orders were Coleoptera (202 species), Hymenoptera (193), Hemiptera (151), Diptera (73), and Orthoptera (42), and the best-represented families were Chrysomelidae and Curculionidae (Coleoptera, 44 species each), followed by Cicadellidae (Hemiptera; 30), Encyrtidae (25) and Eumolpidae (23; both in Hymenoptera). Taxonomic representation varied greatly across biomes. Poaceae and Asteraceae were among the most diverse plant families in grassland, thicket and karoo, but fynbos plots were dominated by three characteristic families (Ericaceae, Proteaceae, Restionaceae). Differences between the insect faunas of the biomes were less pronounced, with phytophagous coleopteran (Curculionidae, Chrysomelidae) and hemipteran (Cicadellidae) families, as well as parasitic wasps (Encyrtidae, Eulophidae), dominating the samples from all four biomes (see also Appendices S2 and S3 in Supplementary Material.).

Kruskal–Wallis comparisons for plot-scale data indicated significant differences in species richness among the four biomes. Karoo samples were poorer in species than fynbos, grassland, and thicket, in both plants and insects ( $P < 0.001$  for plants;  $P < 0.05$  for insects), while the differences between the three last-mentioned biomes were not significant (Fig. 2). Total (biome scale) species richness was highest in grassland and fynbos, which had almost equal numbers in both groups (fynbos: 168 plants and 311 insects; grassland: 171 plants and 294 insects). Thicket ranked third, with 116 plants and 248 insects, while karoo had the lowest numbers, with 81 plants and 131 insects.

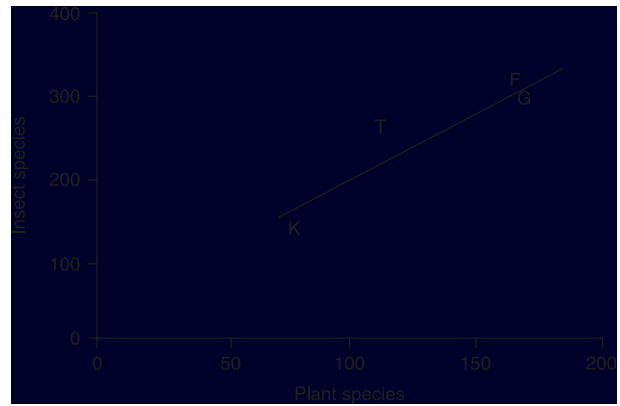
There was a good linear relationship between the total numbers of plant and insect species recorded at the biome scale (Fig. 3;  $n = 4$ ;  $r^2 = 0.90$ ;  $P = 0.05$ ), although less variation was explained at the plot scale ( $n = 64$ ;  $r^2 = 0.14$ ;  $P = 0.002$ ), and when the seasonal collections from the Baviaanskloof Conservation Area were excluded ( $n = 4$ ;  $r^2 = 0.76$ ;  $P = 0.13$ ). When considering trophic guilds separately, correlation with plant species richness was similar for phytophagous and predaceous/parasitic insects, and slightly higher in the case of the detritus feeders. A much higher correlation was noted between phytophagous insects and predaceous/parasitic insects (Table 2).



**Figure 2** Species diversity for plants and insects for 10 × 10 m plots in four southern African biomes (f: fynbos; g, grassland; t, thicket; k, karoo; *n* = 16; shown are ranges, central 50% of the values, and medians; data combined from the Baviaanskloof Conservation Area and core biome areas).

**DISCUSSION**

While the plant surveys were highly reliable, the method used here does not cover the complete spectrum of insects in the surveyed vegetation, or even in the plots under consideration. Omitted from our survey are all insects living in the soil, on the soil surface, and at levels lower on the plants than the height at which we sampled. Among the insects that live on the upper parts of the plants, the highly mobile species, such as the butterflies, larger dipterans and hymenopterans, are likely to have escaped collection. It could also be argued that sweeping is not consistently



**Figure 3** Diversity relationship between plant and insect species across the four biomes. Included are year-round collections from the Baviaanskloof Conservation Area and peak season collections from the core biomes; *n* = 4, each point pooling data for 26 plots; F: fynbos; G: grassland; T: thicket; K: karoo.

efficient across different vegetation types (see Janzen, 1973). Further differences could result from the levels of insect activity at the various collection times, as much as we tried to minimize these by collecting under similar weather conditions. Other problems can arise by underestimating species numbers due to wrong morphospecies definition, although such errors are likely to be consistent across biomes (Oliver & Beattie, 1996).

Nevertheless, we have assumed that these limitations have not seriously affected the patterns observed. The high insect diversity values recorded in fynbos (especially at large scales), while contradicting earlier generalizations (e.g. Johnson, 1992), are consistent with available data on gall-insects (e.g. Hemiptera: Psyllidae; Coleoptera: Apionidae; Diptera: Tephritidae), which are more diverse in fynbos than in thicket and karoo (Wright & Samways, 1998). High fynbos insect richness is indicated here for a much broader spectrum of taxa, less than one-quarter of all species recorded being potentially gall-forming. Among the other biomes, grassland insect diversity was remarkably similar to that recorded in fynbos. Thicket insect diversity was high at the plot scale (Fig. 2), but there was less variation between the two localities, compared to the other biomes. This related to the smaller geographical area covered by thicket (Fig. 1), and was reflected in a slightly lower biome-wide value, compared to fynbos and grassland (Fig. 3). It is conceivable that savanna entomofauna represents a combination of grassland and thicket elements; typical African savanna may be richer in insects than any of the biomes considered here (see Krüger & McGavin, 1998).

	Plant species	Insect species (detritophages)	Insect species (phytophages)
Plant species	—	—	—
Insect species (detritophages)	0.43	—	—
Insect species (phytophages)	0.31	0.54	—
Insect species (predaceous/parasitic)	0.30	0.54	0.71

**Table 2** Correlation values (*r*) between the number of plant species and the number of insect species in three trophic categories, calculated at plot scale (*n* = 64). All values are significant at *P* < 0.05

Karoo insects had the lowest species diversity of the four biomes. However, it is possible that the diversity of species not sampled in this study — e.g. ground-dwelling species such as Tenebrionidae — is greater in the karoo than the other biomes (see Koch, 1955).

Pollinators were probably under-sampled in this study, as many of them are active fliers likely to escape sweep collections. Those which were sampled reliably (especially beetles: Melyridae, Scarabaeidae, Nitidulidae) were actually most diverse and most abundant in fynbos (see Appendix S3 in Supplementary Material). This corroborates previous findings indicating a high diversity in fynbos for insect groups important in pollination (see Gess, 1992 for pollen wasps), while contradicting suggestions of pollinator limitation in fynbos (Johnson & Bond, 1997).

We show that insect diversity in fynbos is not low when compared to other Cape biomes. However, perhaps insects are generally less diverse in the Cape, compared to other parts of the world. Unfortunately, standardized collections that would allow for proper comparisons on a global scale are lacking. Nevertheless, by pooling samples either spatially or seasonally, and by restricting analyses to certain insect groups, we were able to compare our data with collections from a few other regions. The thicket insect fauna is (unsurprisingly) impoverished, when compared to rain forest (e.g. Janzen, 1973; average values are twofold in Coleoptera and close to threefold in Heteroptera, although the differences are not significant in either case;  $P > 0.1$ ). Southern African grasslands are poorer than tropical pastures (Janzen, 1973; the same ratios observed in the thicket–rain forest comparisons), but somewhat richer than northern temperate grasslands (e.g. Siemann *et al.*, 1997; by *c.* 20%). All these differences, emerging as not significant here due to small sample size, probably illustrate a real latitudinal gradient in insect species richness, with Cape biomes being neither richer nor poorer than could be expected given their position on the globe.

A historical comparison with plants is required to discuss the existence of a characteristic and diverse fynbos insect fauna. While fynbos vegetation contains plants of remarkable antiquity, such as the Proteaceae and Bruniaceae (see Goldblatt & Manning, 2000; Linder, 2003), the unusually high plant species diversity in fynbos is of recent origin, going back no longer than 5 Myr, when a strongly seasonal climate became established in the Cape (Linder, 2003). There are also ancient elements among fynbos insects (Endrödy-Younga, 1988; Picker & Samways, 1996), but these probably represent a minority, and much of the fynbos entomofauna may be recent associations. Diversification in fynbos phytophagous insects was certainly influenced by the broad spectrum of host plants that were available, increasing the probability of speciation by host shift, especially in galling insects (Mendonça, 2001). Also, the dissected fynbos landscapes favour geographical speciation in both plants and insects (Endrödy-Younga, 1988; Linder, 2003), although this may be less often the case with well-dispersed plant-inhabiting insects. It is difficult to assess how factors such as edaphic diversity and fire regimes, both seen as essential in fynbos plant diversification (e.g. Cowling, 1987), may impact on insect diversification, given the limited understanding we currently have on insect fire ecology (Parr & Chown, 2003) or edaphic requirements.

The small deviations from linearity observed in the plant–insect diversity relationship (Fig. 3) can be explained in terms of plant biomass and structural complexity, with thicket (higher insect diversity than predicted by plant diversity alone) having the highest cover, height and growth form diversity of the four biomes (Cowling *et al.*, 1994). Karoo vegetation lies at the other extreme, and has lower than predicted insect diversity.

The plot scale considered here, that of  $10 \times 10$  m, is the smallest scale where plant diversity values would be meaningful, considering that, occasionally, individual thicket plants can be large enough to cover half a plot. At this scale, the amount of explained variation was low, perhaps because the presence or absence of plant species with diverse associated insect faunas would have a large influence on the pattern seen between plots. For example, the average grassland plot contained six grass species, accounting for 23% of the plant species diversity, and representing more than 90% of the total plant cover. However, few insect species were actually caught on grasses, many more being associated with the few individuals of *Aspalathus* (Fabaceae) and *Hermania* (Malvaceae). Similarly, in fynbos, flowering *Syncarpha* and *Osteospermum* (Asteraceae) plants represented within-plot centres of insect diversity and abundance (although in fynbos insect abundances tended to be high on most large plants, including Restionaceae, Ericaceae and Proteaceae; S.P., personal observation). The similar correlation values between plant diversity and the diversity of various insect trophic guilds (Table 2) suggest that food resource diversity is not limiting phytophagous insect niches (see also Strong *et al.*, 1984; Novotný *et al.*, 2002; Hawkins & Porter, 2003). Rather, plant structural heterogeneity influences all insect guilds equally (Southwood *et al.*, 1979; Haddad *et al.*, 2001). In contrast, the strong correlation between the diversity of phytophagous and predaceous/parasitic insects (Table 2) indicates a real trophic diversity cascade (see also Krüger & McGavin, 2001; Walker & Jones, 2001), with the diversity of the latter guild being limited by that of the former.

In conclusion, the good relationship between plant and insect species richness is likely to be due to both direct interactions (the plants providing primarily microhabitats and secondarily food for the insects) and parallelism (both groups responding to similar environmental factors and, to a lesser extent, having similar phylogeographical histories). The proportional contribution of these factors is still to be ascertained for a variety of systems, but this study tends to confirm the assertion (Hawkins & Porter, 2003) that the contribution of direct trophic relationships have been overrated previously. In the Cape, insect diversification does not match plant diversification completely, but the main vegetation type, the fynbos, is certainly not as insect-poor as thought previously. The diversity, community patterns, and phylogeographical history of a 'Cape Faunistic Region' are yet to be documented.

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## REFERENCES

- Coetzee, J.H., Wright, M.G. & Giliomee, J.H. (1997) Anti-herbivore mechanisms of economically-important Proteaceae in the African cape Fynbos. *Journal of Applied Entomology*, **121**, 367–372.
- Cottrell, C.B. (1985) The absence of coevolutionary associations with Capensis floral element plants in the larval/plant relationships of southwestern Cape butterflies. *Transvaal Museum Monographs*, **4**, 115–124.
- Cowling, R.M. (1987) Fire and its role in coexistence and speciation in Gondwanan shrublands. *South African Journal of Science*, **83**, 106–111.
- Cowling, R.M., Gibbs-Russell, G.E., Hoffman, M.T. & Hilton-Taylor, C. (1989) Patterns of plant species diversity in southern Africa. *Biotic diversity in southern Africa: concepts and conservation* (ed. by B.J. Huntley), pp. 19–50. Oxford University Press, Cape Town.
- Cowling, R.M., Mustart, P.J., Laurie, H. & Richards, M.B. (1994) Species diversity, functional diversity and functional redundancy in fynbos communities. *South African Journal of Science*, **90**, 333–337.
- D'Haese, C.A. (2003) Morphological appraisal of Collembola phylogeny with special emphasis on Poduromorpha and a test of the aquatic origin hypothesis. *Zoologica Scripta*, **32**, 563–586.
- Davies, D.M. (1988a) Leafhoppers (Homoptera: Cicadellidae) associated with the Restionaceae. I. The tribe Cephalini. *Journal of the Entomological Society of South Africa*, **51**, 31–64.
- Davies, D.M. (1988b) Leafhoppers (Homoptera: Cicadellidae) associated with the Restionaceae. II. The tribes Athysanini and Paraliminini (Euscelinae). *Journal of the Entomological Society of South Africa*, **51**, 65–80.
- Endrödy-Younga, S. (1988) Evidence for the low-altitude origin of the Cape Mountain biome derived from the systematic revision of the genus *Colophon* Gay (Coleoptera, Lucanidae). *Annals of the South African Museum*, **96**, 359–424.
- Erwin, T.L. (1982) Tropical rainforests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin*, **36**, 74–75.
- Germishuizen, G. & Meyer, N.L., eds (2003) Plants of southern Africa: an annotated checklist. *Strelitzia*, **14**, 1–1231.
- Gess, S.K. (1992) Biogeography of the masarine wasps (Hymenoptera: Vespidae: Masarinae), with particular emphasis on the southern African taxa and on correlations between masarine and forage plant distributions. *Journal of Biogeography*, **19**, 491–503.
- Giliomee, J.H. (2003) Insect diversity in the Cape Floristic Region. *African Journal of Entomology*, **41**, 237–244.
- Goldblatt, P. & Manning, J.C. (2000) Cape plants: a conspectus of the Cape flora of South Africa. *Strelitzia*, **7**, 1–743.
- Haddad, N.M., Tilman, D., Haarstad, J. & Knops, J.M.H. (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. *The American Naturalist*, **158**, 17–35.
- Hawkins, B.A. & Porter, E.E. (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. *The American Naturalist*, **161**, 40–49.
- Janzen, D.H. (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, **54**, 687–708.
- Johnson, S.D. (1992) Plant–animal relationships. *The ecology of fynbos: nutrients, fire and diversity* (ed. by R.M. Cowling), pp. 175–205. Oxford University Press, Cape Town.
- Johnson, S.D. & Bond, W.J. (1997) Evidence for widespread pollen limitation of fruiting success in Cape wildflowers. *Oecologia*, **109**, 530–534.
- Klass, K.-D., Zompro, O., Kristensen, N.P. & Adis, J. (2002) Mantophasmatodea: a new insect order with extant members in the Afrotropics. *Nature*, **296**, 1456–1459.
- Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E. & Groth, J. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, **2**, 286–293.
- Koch, C. (1955) Monograph of the Tenebrionidae of southern Africa. Tentyriinae, Molurini–Trachynotina: *Somaticus* (Hope). *Transvaal Museum Memoirs*, **7**, 1–242.
- Krüger, O. & McGavin, G.C. (1998) Insect diversity of *Acacia* canopies in Mkomazi Game Reserve, north-east Tanzania. *Ecography*, **21**, 261–268.
- Krüger, O. & McGavin, G.C. (2001) Predator–prey ratio and guild conservancy in a tropical insect community. *Journal of Zoology*, **253**, 265–273.
- Linder, H.P. (2003) The radiation of the Cape flora. *Biological Reviews*, **78**, 597–638.
- Low, A.B. & Rebelo, A.G., eds (1998) *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.
- Mendonça, M.D. (2001) Galling insect diversity patterns: the resource synchronisation hypothesis. *Oikos*, **95**, 171–176.
- Mitter, C., Farrell, B.D. & Wiegmann, B. (1988) The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *The American Naturalist*, **132**, 107–128.
- Novotný, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Èiek, L. & Drozd, P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, **416**, 841–844.
- Oliver, I. & Beattie, A.J. (1996) Invertebrate morphospecies as a

- surrogate for species: a case study. *Conservation Biology*, **10**, 99–109.
- Owen-Smith, N. & Danckwerts, J.E. (1997) Herbivory. *Vegetation of southern Africa* (ed. by R.M. Cowling, D.M. Richardson & S.M. Pierce), pp. 397–420. Cambridge University Press, Cambridge.
- Parr, C.L. & Chown, S.L. (2003) Burning issues for conservation: a critique of faunal fire research in southern Africa. *Austral Ecology*, **28**, 384–395.
- Picker, M.D. & Samways, M.J. (1996) Faunal diversity and endemism of the Cape Peninsula, South Africa: a first assessment. *Biodiversity and Conservation*, **5**, 591–606.
- Price, P.W., Fernandes, G.W., Lara, A.C.F., Brawn, J., Barrios, H., Wright, M.G., Ribeiro, S.P. & Rothcliff, N. (1998) Global patterns in local number of insect galling species. *Journal of Biogeography*, **25**, 581–591.
- Scholtz, C.H. & Holm, E. (1985) *Insects of southern Africa*. Butterworth, Durban.
- Siemann, E., Haarstad, J. & Tilman, D. (1997) Short-term and long-term effects of burning on oak savanna arthropods. *American Midland Naturalist*, **137**, 349–361.
- Southwood, T.R.E., Brown, V.K. & Reader, P.M. (1979) The relationship of plant and insect diversities in succession. *Biological Journal of the Linnean Society*, **12**, 327–348.
- Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984) *Insects on plants: community patterns and mechanisms*. Blackwell Science, Oxford.
- Vlok, J.H.J., Euston-Brown, D.I.W. & Cowling, R.M. (2003) Acocks' Valley Bushveld 50 years on: new perspectives on the delimitation, characterisation and origin of subtropical thicket vegetation. *South African Journal of Botany*, **69**, 27–51.
- Walker, M. & Jones, T.H. (2001) Relative roles of top-down and bottom-up forces in terrestrial tritrophic plant–insect herbivore–natural enemy systems. *Oikos*, **93**, 177–187.
- Whiting, M.F. & Wheeler, W.C. (1994) Insect homeotic transformation. *Nature*, **368**, 696.
- Wright, M.G. & Samways, M.J. (1998) Insect species richness tracking plant species richness in a diverse flora: gall-insects in the Cape Floristic Region, South Africa. *Oecologia*, **115**, 427–433.
- Wu, J. & David, J.L. (2002) A spatially explicit hierarchical approach to modelling complex ecological systems: theory and applications. *Ecological Modelling*, **153**, 7–26.

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**Şerban Procheş** is interested in global and southern African biogeography, plant and arthropod community ecology, and plant–insect interactions. Current projects include studies on Cape insects and geophytes, and patterns of phylogenetic diversity in southern African vegetation.

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Editor: Martin Sykes

#### SUPPLEMENTARY MATERIAL

The following material is available online at [www.blackwell-synergy.com/loi/geb](http://www.blackwell-synergy.com/loi/geb)

**Appendix S1** Details on the collection localities and dates

**Appendix S2** Number of plant species per genus recorded in each of the four biomes, and in total

**Appendix S3** Number of insect morphospecies per family recorded in each of the four biomes, and in total



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