

**ECOLOGICAL CORRELATES:
ENDOPHAGOUS INSECTS AND PLANTS IN FYNBOS**

by

Mark G. Wright

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FRONTPIECE

Top: *Sphenoptera* species (Coleoptera: Buprestidae) larva and pupa, infructescence inhabitants of Proteaceae, from *Protea repens*.

Middle: A stem-borer of *Protea* species, *Erioderes candezei* (Coleoptera: Cerambycidae).

Bottom: Stem-galls on *Protea nitida*, harbouring larvae of *Afrotibica* sp. (Coleoptera: Curculionidae/Apionidae).



ABSTRACT

The objective of this study was to investigate endophagous insect species richness in Fynbos. The influences of plants as determinants of insect occurrence were given special attention.

The endophagous insects associated with Proteaceae in Fynbos were compared to endophage assemblages from northern, non-Capensis Proteaceae. The Cape Fynbos genus *Protea* is utilized by many more insect taxa than the non-Fynbos species. The high diversity of host plants in Fynbos appears to have contributed to generating high, local endophagous insect diversity.

Influences of regional climate, biotope and host-plant characteristics on the frequency of occurrence of insect borers exploiting *Protea* species was investigated in Fynbos. Distinct differences in frequency of encounter of the various insect taxa were recorded for the various host-plants studied. This variability was primarily accounted for by physical host-plant characteristics (infructescence and seed-set variables). These findings have important implications for evolution of insects associated with these plants, as well as for the conservation of insects and in pest control programmes on indigenous cut flowers.

The relative species richness of endophagous and ectophagous insects in Fynbos was compared. Gall-forming insects (Diptera: Cecidomyiidae), were found to be considerably more speciose than other feeding guilds, showing that the ratio of endophages to ectophages in sclerophyllous vegetation types is high. The intimate relationship that endophagous insects have with their host plants tends to habitat specialization. These insects are therefore likely to undergo radiation together with their host-plants.

Species richness of gall-insects in Fynbos was investigated to establish whether insect richness was proportional to plant species richness. The relationship between gall-insect species richness and plant-species richness was investigated. Fynbos harboured more

gall-insect species than other Cape Floristic Region vegetation types. Gall-insect species richness was positively correlated with plant-species richness. Plant species richness appears to have contributed to the evolution of a rich gall-insect fauna in the region. Fynbos gall-insect species richness is comparable to other sclerophyllous vegetation types globally, underscoring the importance of this vegetation type as a centre of galler diversification.

Finally, the importance of plant species richness as a determinant of gall-insect species richness was investigated by comparing different sclerophyllous vegetation types under the same climatic conditions. Gall were sampled from Fynbos and Karoo vegetation. Fynbos had higher gall-insect species richness, correlated with plant-species richness. Plant-species richness, or the distal factors that generated it, appear to have contributed significantly to the radiation of gall-insects in this region.

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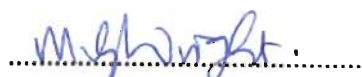
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DISCLAIMER

I hereby declare that the work presented in this thesis is my own. Where applicable, the work of others has been acknowledged. I also declare that this these has not been submitted to any other University.

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CHAPTER 1

REVIEW OF FYNBOS HISTORY AND ECOLOGY, WITH REFERENCE TO ASPECTS GERMANE TO INSECT SPECIES RICHNESS.

Summary

1. Historical and ecological aspects of the Cape Fynbos are summarized and predictions made regarding expected species richness of ectophagous and endophagous insects utilizing the vegetation.
2. The sclerophyllous nature of the vegetation is likely to have restricted ectophaga radiation, but should favour endophaga (borer and gall insect) radiation. This summary serves as a basis upon which hypotheses are based and tested separately.

Introduction

The Cape Floristic Region (CFR) is a distinctive southern African phytogeographical unit, recognized as a distinct Floral Kingdom (Goldblatt 1978, Cowling & Holmes 1992). A high level of plant endemism is typical, and the region has one of the highest recorded plant species densities in the world (Cowling & Holmes 1992). The Cape Fynbos is a major component of the CFR, with numerous endemic species and some families peculiar to the flora (Cowling & Holmes 1992). The CFR, and Fynbos in particular, is of great interest in terms of biodiversity conservation, a source of economically important plants and as a source of information on the evolution of species richness (Ref on cons, Donaldson & Scott 1994, Cowling *et al.* 1992). The flora, particularly the Fynbos, has been well studied (see Cowling 1992) and a reasonable understanding of its history and ecology has been attained.

The fauna is generally less spectacular in terms of diversity, abundance and endemism, although certain groups (amphibians and reptiles notably), have relatively high diversity and endemism in the region. Most faunal groups in Fynbos appear to be relatively insignificant from a ecosystem function perspective, with the exception of insects (Johnson 1992, Wright 1993), and some birds and small mammals that are pollinators (Rebelo 1987). Interactions between the flora and insects have been shown to be of ecological and evolutionary significance (Bond & Slingsby 1983, Johnson 1992, Wright 1993). In spite of their importance, little is known of the diversity and ecology of insects in the flora, and the factors that influenced the evolution of insects associated with plants in the region. As these aspects are important in terms of ensuring the conservation of insects in the region, we need to understand how insect diversity in the Fynbos is related to plant richness and other prevailing ecological factors.

The aim of this paper is to review historical and ecological aspects of the Fynbos and to identify factors that may have promoted or limited insect radiation. Comprehensive reviews of these aspects relevant to plant radiation and richness in Fynbos have been published recently (see Cowling 1992). What follows is a summary of these, underscoring aspects pertinent to the evolution of insects in the flora.

Fynbos evolution:

Historical aspects:

The Fynbos, famous for its high plant-species richness, is a sclerophyllous flora occurring on nutrient-poor soils in the south-western corner of Africa (Taylor 1978). The soils and landscapes are geologically ancient, and the mediterranean-type climate with hot dry summers and wet winters relatively recent (Deacon *et al.* 1992), creating a situation where old biota have been subjected to recent selective pressures. There is no evidence of glacial activity having occurred in the region. The topography is often very complex, with mountains separated from each other by relatively deep valleys (Taylor 1978). Edaphic conditions are also variable. For example, in some cases small patches of limestone soils are dispersed within a sandstone-derived landscape (Cowling & Bond 1991).

Some of the biota are older than the summer dry climate, being remnants of floras that retreated to more hospitable northern climates from the region during times of climatic change (Deacon *et al.* 1992). Attempts have been made to explain the richness of the Cape flora as an accumulation of species resulting from migrations and retreats of northern floras between Ice Ages (see van Zinderen Bakker 1978, Taylor 1978). Other theories argue that present affinities of the Cape flora with Australia and South America cannot be explained by the theory of a northern origin; many typically Cape taxa have never been recorded in the north (Taylor 1978). However, a number of taxa provide reasonable evidence of having a northern origin (Beard 1952, Goldblatt 1972, Rourke 1972). Certain taxa certainly evolved in the region after becoming isolated in the mountainous areas and subjected to subsequent climatic changes (Taylor 1978). A number of neoendemic species are also encountered on younger soils, suggesting that edaphic conditions played an important role in plant speciation (Cowling *et al.* 1992?). The present flora therefore appears to be the result of both isolation of plant species following climatic change and also subsequent speciation within the region.

Highest plant diversity in the Fynbos occurs in areas of greatest terrain diversity (Oliver *et al.* 1983) and with the highest rainfall (Linder 1991). Terrain diversity, edaphic factors and climate have been postulated to have played a central role in generating upland

centres of species richness and ensuring their persistence (Deacon *et al.* 1992). These upland areas are of moderate height. Therefore, extreme cold on mountains was never a limiting factor and the more mesic nature of these areas would have offset the effects of arid periods (Deacon *et al.* 1992). The complex topography of the area would have encouraged extensive plant speciation under these conditions of geographic isolation and with short gene transfer distances. Together with climatic variability during the Quaternary period, high rates of speciation, low rates of extinction and habitat variability could account for the high species richness and endemism encountered today (Taylor 1978, Linder 1985, Deacon *et al.* 1992, Cowling *et al.* 1992).

Other studies have suggested that soil type was of overriding importance, as their data indicate that climate appears to have had little effect during the last 15 000 years (Meadows & Sudgen 1991). They propose that speciation in the flora could have been promoted by variability in post-fire recruitment, or extinction may have been retarded because environmental changes did not exceed species survival thresholds (Meadows & Sudgen 1991). This essentially agrees with the proposal of Deacon *et al.* (1992) that upland areas were climatically moderate enough to allow survival of species that found refuge there. If longer term climatic variability (during the Quaternary) is taken into account, the accumulated effect may well have resulted in the present richness.

The importance of fire in the Fynbos was accentuated by the advent of the mediterranean-type climate during the Pliocene . When forest vegetation became less prolific in the region during the Miocene, fire evidently became a major selective force (Deacon *et al.* 1992). The biology of many Fynbos species became adapted to fire and selection produced a "pyrophylic" vegetation (Cowling 1987, Deacon *et al.* 1992). Recurrent fire has been postulated to have been an important driving force in speciation in the Fynbos, acting as an isolating mechanism by fragmenting plant populations (Cowling 1987). The resulting disruptive selection would have resulted in rapid evolution of isolated demes into specialized species (Cowling 1987).

Deacon *et al.* (1992) conclude that present day Fynbos communities do not date back to the Cretaceous period. They suggest that the present alliances of taxa are the result of

biogeographical remoteness and environmental selection in coastal and mountain habitats that were isolated by aridity during the Pleistocene. This, combined with climatic variability during the Quaternary period (Axelrod & Raven 1978) provides an explanation for the present distribution and richness in historic terms.

Ecological aspects: Species richness patterns in the Fynbos can be accounted for by contemporary environmental conditions (Linder 1991, Cowling *et al.* 1992). There is a concentration of Capensis species in the extreme south west of the CFR. This region also has the highest species: genera ratio, and a higher level of endemism than the south east of the CFR (Cowling & Holmes 1992). It has been suggested that this concentration of CFR elements in the south west is the result of the longer ecological gradients and greater edaphic complexity encountered there than in the south east (Oliver *et al.* 1983). Cowling & Holmes (1992), however, argue that studies excluding these two variables still support the pattern, suggesting that present climate and edaphic conditions alone are not adequate to explain present-day species patterns. They contend that historic explanations must be invoked to explain the high south-western species richness adequately, and agree with others that many genera and families became extinct since the onset of modern climatic patterns. Under the drier modern conditions, pre-adapted sclerophyllous taxa underwent dramatic speciation. Cowling & Holmes (1992) also suggest that during glacial periods, south-western Fynbos would have been exposed to wetter conditions than in the south-east, and would have persisted and expanded. This would have allowed a longer period for speciation in the south-west. In the south-east, drier conditions would have prevailed during glacials, restricting Fynbos to refugia. Too little time has since elapsed for western taxa to have invade the east and augmented species richness. These hypotheses suggest that present-day Fynbos richness patterns cannot be elucidated in terms of contemporary conditions alone.

Imp. It is generally accepted that most plant speciation in Fynbos was allopatric, based on the high species turnover across landscapes (Goldblatt 1978, Kruger & Taylor 1979). There is some evidence that isolation could occur over relatively short distances, in areas with complex edaphic conditions, making the possibility of sympatric speciation a reality for

habitat-specialist plants (Linder 1985, Cowling & Holmes 1992). This could occur within a short period in suitable areas.

Factors other than climatic and edaphic conditions may have also played an important role in generating plant richness in Fynbos. Short gene flow and dispersal distances are factors that are liable to have contributed to plant speciation. The majority of Fynbos plant species have short dispersal distances, primarily as a result of short-distance seed dispersal by ants (Bond & Slingsby 1983, Slingsby & Bond 1985, Cowling *et al.* 1992) and to a lesser extent, short distance pollen transfer by insects (Wright *et al.* 1988, Wright *et al.* 1992). Insects may also have contributed to plant speciation in other, less commonly-recognized ways. Pollinator shifts and concurrent changes in floral features may result in allometric responses, and could presumably contribute towards reproductive isolation and speciation (Johnson 1992). Insects also influence potential reproductive output of plants by destroying seed reserves (e.g. Coetzee & Giliomee 1987, Wright *et al.* 1988) and evidently have selected for seed storage strategies that reduce seed predation in *Protea* spp. (Proteaceae) (Mustart *et al.* 1995, Wright 1994). Insects thus have the potential to influence plant fitness in Fynbos.

Ecological disturbances and Fynbos speciation: Disturbance is arguably the most important catalyst of speciation (Vrba 1980). Fire is the primary disturbance factor in Fynbos (Cowling 1987), and is often used as a management tool in the conservation of Fynbos (Van Wilgen 1984). Recurrent fire in Fynbos is likely to have had an important influence in driving speciation (Cowling 1987). Burning results in fragmentation of plant populations, and specialized taxa should speciate rapidly if they are continually separated, particularly in areas with complex soils and diversity of climatic habitats (Cowling 1987). These fragmented populations are subjected to a range of pressures and local post-fire extinction is not unusual (Cowling 1987), imposing ruthless selective pressures. Fire also acts as one of the most important selective agents in the evolution of plant life-history traits (Cowling 1987). This has profound implications for insects associated with the plants, particularly if they are associated with the reproductive parts of plants.

From an insect's perspective, Fynbos is a taxonomically highly heterogenous, low nutrient, disturbance-prone flora with a climate characterised by seasonal drought. The rest of this paper explores a number of factors that are recognized as important influences on insect evolution, with reference to the Fynbos situation.

Factors influencing insect radiation: The following are of cardinal importance in generating/explaining insect evolution: 1) overcoming nutritional obstacles; 2) habitat and host specialization; 3) enemy free space; 4) geographical effects; 5) contending with hygrothermal stress; and 6) historical contributions. Each of these factors will be briefly discussed below, highlighting characteristics of Fynbos that may have been important.

1) Nutritional obstacles: Fynbos is distinguished by its low nutrient status, making it of little value as a source of nutrition for large mammals (Joubert & Stindt 1979). Levels of nitrogen and water in the leaves of *Protea* spp. are so low as to be of sub-optimal value as food for insects (Wright & Giliomee 1992). The sclerophyllous characteristics of Fynbos have been suggested to influence insects, particularly ectophagous groups (e.g. Lepidoptera) by early workers in the region (Marloth 1913), and this hypothesis has been upheld by more contemporary work (Cottrell 1985).

A flora of such extreme sclerophyllous, low nutrient status should be a suitable substrate for the radiation of endophagous insects (Price *et al.* 1987), such as gall formers and borers. The disproportionately nutrient-rich seeds (de Lange *et al.* 1993, Esler *et al.* 1989) of Fynbos plants, often stored for long periods on plants (Le Maitre & Midgley 1992) provide a suitable and predictable resource for insects such as seed-feeding borers. A relatively high number of endophagous species may thus be expected to have evolved on Fynbos shrubs. However, this guild of insects require a safe and predictable source of plant material (Fernandes & Price 1991), as they have long life cycles and cannot move between plants. Periodic fires in Fynbos would mitigate against the development of a rich assemblage of insects with these requirements. Gall insects and borers are presumably killed during fires (Wright 1993), and the post-fire environment is one in which otherwise apparent plants vanish, except in small refugia (Cowling 1987). These

small refugia may be as important in inducing insect speciation as they are for plant speciation (Cowling 1987). A factor important to plant speciation may thus further encourage speciation of insects that are well adapted to the nutritional limitations of Fynbos plants. This possibility is accentuated when it is considered that endophagous insects demonstrate high host fidelity (Gaston *et al.* 1992), and are thus habitat specialists.

2) Habitat and host specialization: Host specialization has been shown to negatively influence species richness in aphids owing to their inability to survive for even short periods without food and their inefficient host location capabilities in the plant-species rich tropics (Dixon *et al.* 1987). However, adult Fynbos borers (Coleoptera and Lepidoptera; Coetzee & Giliomee 1987b) and gall insects (mostly Cecidomyiidae: Diptera; M.G. Wright unpub. data, in prep) are relatively strong fliers, and therefore likely to be reasonably successful in locating hosts once emerged. This factor is not likely to be important to less-specialized ectophagous insects. Host specialization by insects in Fynbos may have contributed to speciation of endophagous taxa. Cowling *et al.* (1992) argue that plant speciation may have been driven by habitat specialization combined with other factors, as plants adapting to local habitats may undergo incidental speciation. Insects subjected to the same conditions may well have undergone speciation in a similar manner. They may have even been able to speciate more rapidly than plants, as their life cycles are considerably shorter.

3) Enemy-free space: It has been asserted that generalist natural enemies of insects have played a central role in determining phytophagous insect evolution (Bernays & Graham 1988). Cornell (1983) has shown that enemy-free space was the selective force allowing a rich diversity of gall forming wasps to co-occur in the western USA. This may well be true in an environment well suited to the survival of natural enemies of insects. However, it has been suggested that certain guilds of insects (gall formers) are able to circumvent climatic conditions inclement to parasitoids and entomopathogenic fungi and radiate extensively under these conditions (Fernandes & Price 1992). It has indeed been shown that parasitoid pressure appears to have had no effect on gall-insect radiation on certain sclerophyllous, drought adapted plants in the USA (Waring & Price 1989). It

seems reasonable to assume that natural enemies of the insects are unable to thrive under these conditions, creating an enemy-free environment for the gall insects.

envio Fynbos is subjected to a summer drought and hot conditions, with strong winds being prevalent in many areas (Taylor 1978). These climatic conditions may well be suboptimal for parasitoids, creating the enemy-free environment that endophagous insects should be able to flourish in. This is most likely to be true for more arid parts of the Fynbos. However, relatively high levels of parasitism of a *Lasioptera* sp. (Diptera: Cecidomyiidae) have been recorded in more mesic localities (M.G. Wright, unpublished data).

4) Geographical effects: Geographical isolation is generally considered to be a prerequisite for speciation (Mayr 1963). Most plant speciation in Fynbos is thought to have occurred under allopatric conditions (Kruger & Taylor 1979), with edaphic variability and topographical complexity as sources of geographic isolation. Sympatric speciation of plants in Fynbos may conceivably have occurred in some areas where conditions were suitable (Cowling *et al.* 1992).

envio Insect radiation is also influenced by geographic effects, not only isolation, but other variables such as elevational gradients (e.g. Wood & Holstead 1984, Fernandes & Lara 1993). The Fynbos region is characterised by relatively long ecological gradients (elevational and hygothermal) (Cowling *et al.* 1992), and many plant species have restricted ranges, often occurring on isolated mountains or on patches in areas with variable soils (Hall & Veldhuis 1985, Cowling *et al.* 1992). It is therefore possible that insect populations may be isolated by geographic effects or by host plant fidelity, and could have speciated considerably under these conditions.

5) Hygothermal stress: Insects are prone to desiccation, and overcoming this duress has been suggested to be of great importance in their evolution and adaptation to new host plants (Southwood 1972). Fernandes & Price (1988) have identified escape from hygothermal stress as the main factor encouraging endophagous insect radiation on sclerophyllous plants. The endophagous life style allows the insects to escape otherwise

deleteriously low moisture constraints, and to speciate broadly. Escaping hygrothermal stress, together with being able obtain adequate nutrition is thought to be central in permitting gall insects to radiate and become abundant in otherwise hostile habitats. This aspect should be an important consideration for Fynbos insects, and provides further reason to expect a diverse endophagous entomofauna.

6) Historical contributions: The geological history of a region is of great importance in determining present day-faunas (e.g. Schlinger 1974, Gagné 1984). The evolutionary history of plants also contributes to the divergence and contemporary patterns of insect host-plant use (Armbuster 1992). Indeed, historical influences are probably major factors that have contributed to insect evolution in the Fynbos, especially as this has been the case with the plants (Cowling *et al.* 1992).

hist. The dramatic climatic changes that have occurred in the region and the resulting distribution of plants may have also had a major influence on the insects. Studies of stag beetles in the region (*Colophon* spp., Lucanidae: Coleoptera) have suggested that speciation in the genus occurred in the lowlands, and that present-day distributions are accounted for by beetles retreating into mountain refugia following the advent of a drier climate in the region (Endrödy-Younga 1988). No distinct evolutionary relationship with the flora is evident in this case. Similarly, ectophagous Lepidoptera endemic to the region also show no evidence of having "co-evolved" with elements of the flora (Cottrell 1985). It is, however, conceivable that insects with intimate host-plant relationships would be more profoundly influenced by changes in plant richness. Endophagous insects, with their characteristically close host-relationships, are thus most likely to have developed a relatively rich fauna in the region (Cottrell 1985, Gaston *et al.* 1992).

Also of great importance is the contribution that other floras may have made to the entomofauna of the region. Many northern floras have evidently contributed to the present-day Fynbos as a result of climatic change and retreating ranges of plants (see above). In the same way that sclerophyllous plant species that were pre-adapted to the modern climate of the area appear to have speciated in Fynbos, insects already associated with them may have remained in the area, contributing to the regional species

pool (Lawton 1984) and undergone further radiation as a result of geographical influences as well as host-plant diversification or extinction (Mitter *et al.* 1991). The climatic variability that was prevalent during the Quaternary period may have had a profound influence on the entomofauna, as it probably did on plant evolution (Deacon *et al.* 1992). In this way, a residual insect assemblage, preadapted to the modern conditions, could have undergone radiation as dramatic as that of the flora.

Conclusions

The low abundance and biomass (Schlettwein & Giliomee 1987) of ectophagous insects in Fynbos is likely to be the result of the poor quality of Fynbos plants as insect food. Ectophagous insect species richness is also not high. All indications are that endophagous insects should have a relatively high species richness in this Flora. Factors which may have influenced endophage richness are the high plant richness or the factors that generated it, the sclerophyllous nature of the vegetation, variable climatic conditions in geological time and the pyrophylic nature of the vegetation. Each of the chapters in this thesis therefore explore the species richness of endophagous insects associated with Fynbos, and explore the possibility of correlations between plant species richness and plant attributes that may have influenced endophage evolution.

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CHAPTER 2

BIOGEOGRAPHY AND SPECIES RICHNESS OF ENDOPHAGOUS INSECTS ASSOCIATED WITH PROTEACEAE IN SOUTH AFRICA.

Summary

1. The endophagous insects associated with Proteaceae of the Cape Fynbos were compared to endophage assemblages from more northern non-Capensis Proteaceae.
2. Insects were collected from Proteaceae in the Cape on a regular basis and additional records obtained from insect collections. Northern samples were collected more opportunistically or records were obtained from collections or through personal communication.
3. The Cape Fynbos genus *Protea* is utilized by many more insect taxa than the non-Fynbos *Protea* species. The Fynbos Proteaceae has very few species in common with the northern Proteaceae, yet each has many of their own distinct species. This suggests that the Fynbos endophage insect fauna is distinct from that of the other regions.
4. It appears that the high diversity of host plants in the Fynbos has contributed to generating high, local endophagous insect diversity.

Introduction

The Cape Floristic Region (CFR) has great floral richness, with a plant species density that exceeds many tropical rain forests and other mediterranean-type ecosystems (Cowling *et al.* 1992). The vegetation of the Fynbos biome contributes the majority of the species in the CFR. Because of the high species richness of the region, the CFR is of great interest in terms of the study of biodiversity.

Fynbos is typically sclerophyllous, occurring on nutrient-impoverished soil (Taylor 1978), and has a high percentage of plant species endemism. Many of the endemic Fynbos plant species are threatened with extinction (Hall & Veldhuis 1985). Many of these species have very local distributions, and high species turnover (gamma diversity) is typical in Fynbos. The Fynbos is also a fire-prone/adapted biome (Taylor 1978), and controlled burning is applied in many areas as a management tool, aimed at maintaining plant diversity and productivity (van Wilgen 1984).

Studies have shown that insects play an important role in the biology of Fynbos plants (e.g. Johnson 1992, Wright 1993). However, little is known about the ecological requirements of the endemic insects intimately associated with their host plants. Whether any true "Fynbos insects" exist is uncertain. The contribution that the very high plant richness of the area may have played in generating insect richness is unknown. Cottrell (1985), for example, analyzed the host plant / larval associations of Fynbos-endemic Lycaenidae (Lepidoptera), and showed that there was no indication of any intimate evolutionary association between these insects and the Fynbos plant species. Other taxa (e.g. Vespidae; Hymenoptera, Lucanidae; Coleoptera) are well represented in the region, but do not necessarily show any indication of having radiated in response to the high plant diversity (Gess 1992, Endrödy-Younga 1988). It is possible that the sclerophyllous, xeric, low nutrient status of the vegetation is an unsuitable resource upon which ectophagous insects were unable to radiate extensively (Cottrell 1985). Possibly however, endophagous insects, by virtue of their being able to escape inclement environmental conditions and/or manipulate low nutrient plant material to their benefit, have close plant-associations in the Fynbos.

The aim here was to examine the biogeography and richness of endophagous insects associated with a typical Fynbos plant family, the Proteaceae. Key questions addressed were 1) Are any endophagous insect taxa on Proteaceae endemic to Fynbos? 2) How does their species richness compare to endophages on Proteaceae in other areas? 3) Are serotinous (seed stored in cones) Proteaceae utilized by a wider range of endophages than are non-serotinous species?

Materials and methods

Study plants: The family Proteaceae is well represented in southern Africa, with most species occurring in the Fynbos (Vogts 1982, Rourke 1980). The Fynbos species can be considered true Capensis species, that have evolved in the region (J.P. Rourke, pers. comm.). A number of genera and species also occur to the north-east of the Fynbos, in savanna vegetation and mountainous areas floristically similar to Fynbos (Fig. 1). This provides the opportunity to compare Fynbos/ Capensis plant species to species with non-Fynbos species, in terms of their insect communities.

Insect collection: Surveys of endophagous insects associated with a number of Proteaceae were conducted in the Fynbos (Fig. 1) from 1991 to 1994, usually in the March-May period. Proteaceae in Kwazulu-Natal and the Mpungalanga (previously eastern Transvaal) were collected once during 1991 (April) and twice during 1992 (April and October). An intensive, seasonal investigation was conducted in the Fynbos during 1991-1992. This entailed visiting six study sites (see Wright 1993 and Fig. 1) on a three-monthly basis (December, March, June, September) and sampling 250 infructescences, stems, leaves and buds from three *Protea* species in each site per visit. Stems, leaves and buds were examined for the presence of borers or gall insects *in situ*. The infructescence samples were returned to the laboratory, dissected and examined for the presence of borers. Whenever possible, larvae were collected and reared to adult to aid identification. In addition to *Protea* spp, other genera (mainly *Leucospermum* and *Leucadendron*) were sampled on an opportunistic basis.

Museum collections of insects (South African Museum, Cape Town, Transvaal Museum and National Collection of Insects, Pretoria) were consulted for additional records of

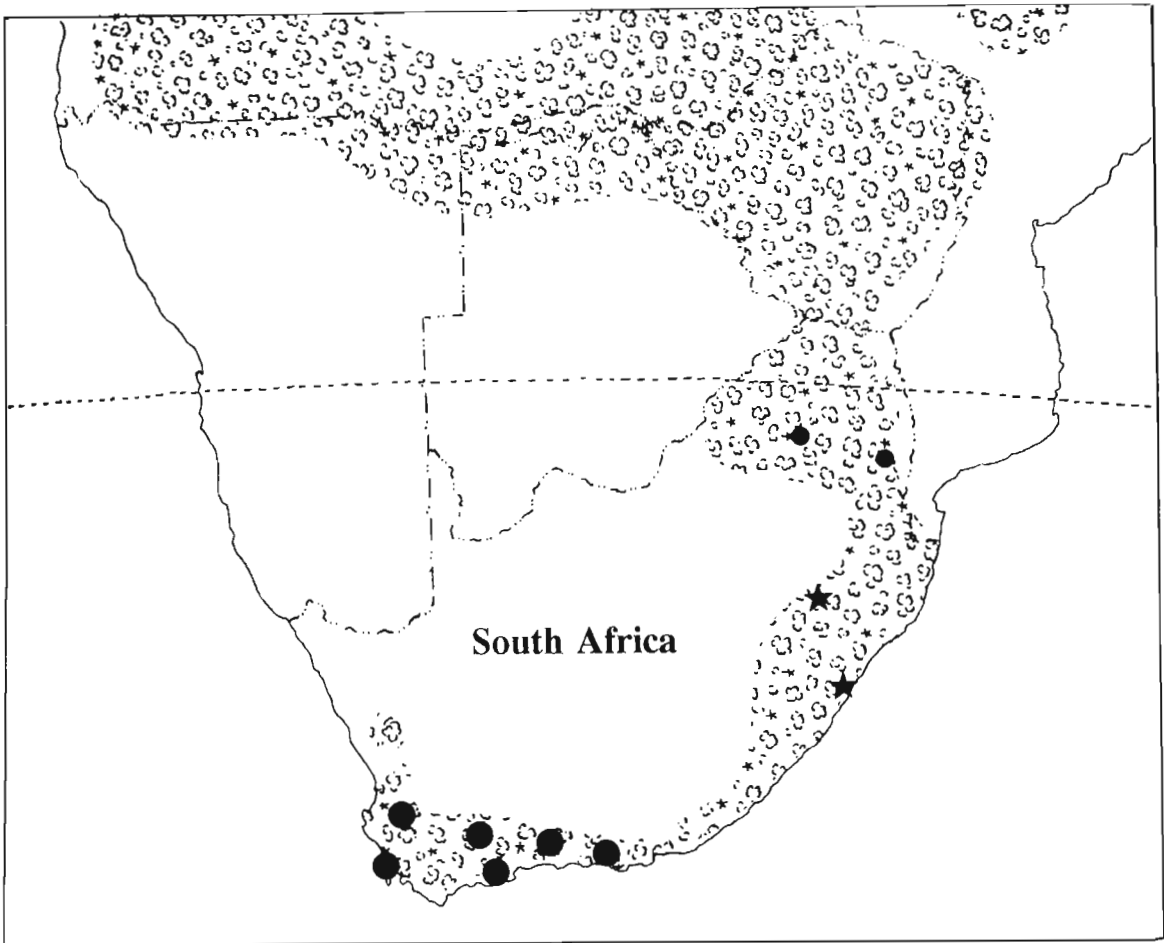


Figure 1. Distribution of Proteaceae in Southern Africa, with the location of six intensive study sites in the Fynbos indicated (●), as well as other sites in Kwazulu-Natal (★) and Mpumalanga (●).

insects recorded from Proteaceae. Checklists of insects compiled for various areas (Coetzee 1989, Visser 1992, Pajor pers. comm.) were also referred to. Finally, a collection of insects from Proteaceae (Agricultural Research Council, Elsenburg, South Africa) also served as a source of records dating as far back as 1960.

Data analysis: Presence-absence lists of the above insects were compiled. Sorting of insect taxa by host plant and locality was done by arranging the data in a two-way classification table. This was done to establish whether any clearly distinct group of insect taxa was associated with Fynbos Proteaceae. Number of endophagous species associated with *Protea* spp. from the three regions were compared, and Sorensons coefficient of similarity calculated for each pair of regions. This similarity coefficient was chosen because it requires only presence/absence data, suitable for the present study. Other require frequency of occurrence data, which were not available for this study, as many of the data were collected from preserved insect collections.

As non-serotinous *Protea* species lack the long-lived infructescences upon which many borer species depend (Coetzee & Giliomee 1987), a comparison of number of endophage species utilizing both serotinous and non-serotinous Fynbos *Protea* spp was made. The endophage species richness for weakly/non-serotinous *P. nitida* was compared to moderately serotinous *P. repens*, which has a comparable geographical distribution. Data used were from the intensive seasonal survey detailed above and from Coetzee (1984, 1989) and Visser (1992). This was done to establish whether this trait was important in terms of determining endophage richness on the plants.

Results

Cape *Protea* spp. were utilized by at least 13 insect species that were absent from the other regions sampled (Table 1). The Kwazulu-Natal and Mpungalanga *Protea* spp sampled were relatively depauperate in terms of number of species associated with them (Table 1, Fig. 2). The *Leucopsermum* and *Leucadendron* spp. sampled (only in the Cape) had unique endophage assemblages, sharing only two species with the Cape *Protea* spp. and none with the northern species. The taxa recorded on the Proteaceae have never

Table 1. List of endophagous insects occurring on Cape *Protea* spp. (CP), Kwazulu-Natal *Protea* spp. (NP), Mpungalanga *Protea* spp. (MP), *Leucospermum* spp. (Ls) and *Leucadendron* spp. (Ld). ⁺Insects listed here were identified at least to genus level and to species where possible (see Appendix 1).

Accession No. ⁺	CP	NP	MP	Ls	Ld
37	*	-	-	-	-
248		-	-	-	-
402	*	-	-	-	-
1	*	-	-	-	-
22	*	-	-	-	-
198	*	-	-	-	-
344	*	-	-	-	-
297	*	-	-	-	-
350	*	-	-	-	-
542	*	-	-	-	-
Cec1	*	-	-	-	-
480	*	-	-	*	-
102	*	-	-	-	*
229	*	-	-	-	*
248	*	*	-	-	-
295	*	*	-	-	-
118	*	*	-	-	-
129	*	*	-	-	-
1523	*	*	-	-	-
75	*	*	*?	-	-
38	*	*	*	-	-
Cydi	-	*	-	-	-
Olet	-	*	-	-	-
Cyd1	-	*	-	-	-
Olet(ind)	-	*	-	-	-
Cossid	-	*	-	-	-
Enat	-	*	*	-	-
Capy	-	-	*	-	-
1178	-	-	-	*	-
100	-	-	-	*	-
155	-	-	-	*	-
407	-	-	-	*	-
556	-	-	-	*	-
Cec3	-	-	-	*	-
1180	-	-	-	*	-
Psil	-	-	-	*	*
Sphe	-	-	-	*	*
197	-	-	-	-	*
531	-	-	-	-	*
Cec2	-	-	-	-	*
Total No spp.	21	14	4	10	7

* Present; - Not recorded.

been recorded on other host plants, as far as could be determined from museum records, with the exception of *Erioderes candezei* Lmr. (Coleoptera: Cerambycidae).

The endophage assemblage on Cape *Protea* spp. was more similar to the Kwazulu-Natal assemblage than to the Mpungalanga assemblage; *Protea* spp. of the latter region also had considerably less insect species than the other areas sampled (Fig. 2).

Protea nitida was utilized by two more insect taxa than *P. repens* (Table 2). Curiously, as *P. nitida* leaves are rather ephemeral, one of these was a leaf galling Cecidomyiidae. Only one more infructescence species was harboured by *P. nitida* than by *P. repens*.

Table 2. Endophagous insects utilizing *P. nitida* (non/weakly serotinous) and *P. repens* (moderately serotinous)

Insect taxon	<i>P. repens</i>	<i>P. nitida</i>
Hemiptera:		
Psyllidae	*	- (leaf galler)
Coleoptera:		
Buprestidae:		
<i>Sphenoptera</i> spp.	*	* (infructescence borer)
Scarabaeidae:		
<i>Genuchus</i>	*	* (infructescence borer)
Curculionidae:		
<i>Euderes</i>	*	* (bud/infructescence borer)
<i>Tanaos</i>	-	* (infructescence borer)
<i>Afrotibicina</i> sp.	-	* (stem galler)
Lepidoptera:		
Lycæinidae:		
<i>Capys</i>	*	* (bud borer)
Oecophoridae:		
<i>Orophia</i>	*	* (shoot/bud borer)
<i>Argyroploce</i>	*	* (shoot/bud borer)
Tineidae:		
<i>Tinea</i>	*	* (infructescence borer)
Diptera:		
Cecidomyiidae:		
<i>Resseliella proteae</i>	*	* (bract colonizer)
Indet. Cecidomyiidae	-	* (Leaf galler)

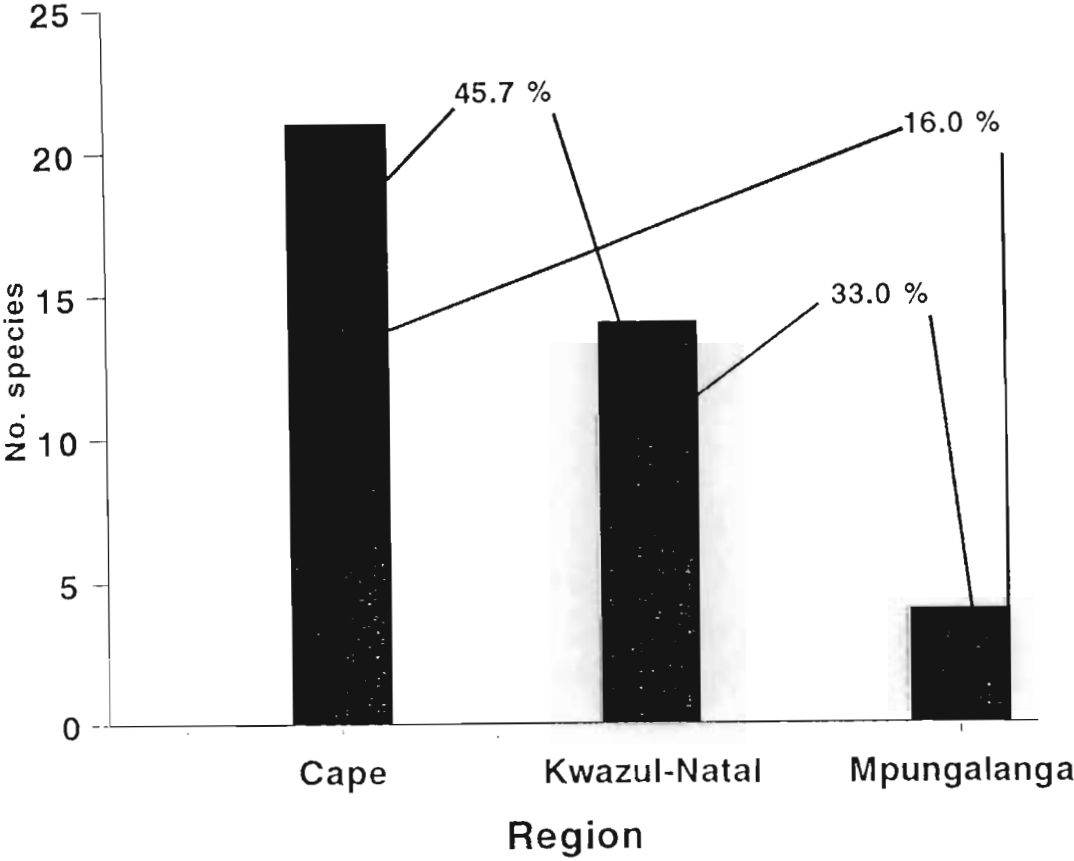


Figure 2. Number of species of endophagous insects (borers and gallers) on *Protea* species in South Africa. Sørensen coefficients of percentage similarity are shown for the different localities.

Discussion

The results showed that the Cape Proteaceae clearly had a greater richness of endophagous insects than the more northern plants. Certain groups, e.g. the Curculionidae were well represented in the Cape samples, with one genus (*Euderes*) occurring on Kwazulu-Natal *Protea* spp. Lepidoptera species were more commonly associated with both Fynbos and non-Fynbos species. Some taxa, notably the Buprestidae (*Sphenoptera* spp.) were absent from the northern samples. This is significant as these insects were, in many cases, among the most abundant borers recorded on the Cape *Protea* spp. (e.g. Wright 1993, Chapter 3). This genus is also widely distributed in Africa (Bellamy 1986, Bellamy & Scholtz 1986, Bellamy *et al.* 1988), so their absence from the northern samples is curious. The Buprestidae associated with other Proteaceae genera (*Leucospermum*, *Leucadendron*) were either from a separate genus (*Psiloptera*), or in the case of the genus *Sphenoptera* were distinguishable as separate species (C.H. Bellamy, pers. comm). This situation suggests that these insects may have speciated in response to variation and availability of host plants. They were not absent from the non-serotinous *P. nitida* in the Cape, so the fact that the northern *Protea* species have ephemeral infructescences does not explain their absence from these plants.

A number of hypotheses have been proposed to explain the number of herbivorous insect species utilizing plants. One is that of Lawton (1984, also see Compton *et al.* 1989) that plants accrue herbivorous insects from a regional pool. A plant occurring in an area with a poorer pool of potential colonizers would have less species. This does not explain the absence of *Sphenoptera* from South African *Protea* spp., as the genus does occur on other plants in areas where it is absent from Proteaceae. A more tenable explanation is that larger, more speciose plant groups are utilized by a larger number of herbivorous species (e.g. Fernandes 1992). The impressive radiation of the Proteaceae in the Cape Fynbos may thus have been the catalyst for endophage speciation on them. The plant-age hypothesis (Southwood 1961) is less likely to be relevant here, as northern Proteaceae are presumed to be ancestral (J.P. Rourke, pers. comm.) and therefore at least as old as the most primitive Cape species. The taxonomic and structural diversity of Proteaceae in the Cape would therefore be the most feasible explanation for the richness of endophagous insects associated with them. The relatively low number of Cape insect taxa shared with northern *Protea* spp. (8 with Kwazulu-Natal samples, 2 with Mpungalanga samples) may indicate a relatively ancient discontinuity in the distribution

of the genus. One of these genera, *Argyroplce* (Lepidoptera; Oecophoridae) has putative Gondwanan affinities with Australian moths on Proteaceae there, suggesting an early association (Herrera in litt). Cladistic analysis of genera common to the various areas would provide more conclusive evidence regarding the history of the group.

Another consideration is that the Fynbos had a complex origin, with many phytochoria contributing plant taxa to the flora (Axelrod & Raven 1978). It is possible that these receding floras provided a relatively rich pool of insects which could colonize plants in the Fynbos. The same factors that generated plant speciation may have contributed to the evolution of a rich, associated insect fauna. The xeric, sclerophyllous, low nutrient nature of Fynbos is well suited for the evolution of a rich endophage entomofauna (Fernandes & Price 1991).

It is conceivable that both geographical and plant-mediated speciation in insects may have occurred in Fynbos, particularly among those insects with high host-plant fidelity. Endophagous insects in general exhibit a high degree of host fidelity (Gaston *et al.* 1992), and are therefore extreme habitat specialists. They could therefore radiate in response to variation in host plants and geographical isolation (e.g. Wood 1980, Vrba 1980). This hypothesis is tested as a separate study.

It is also clear that the Cape Proteaceae harbour a rich and distinct endophagous entomofauna. Other groups of insects, e.g. the Cicadellidae and Lygaeidae (Hemiptera) which are "semi"-endophagous (sap-suckers) also display a large degree of uniqueness in close association with Fynbos plants (Slater 1964, Davis 1988). This is in contrast with ectophagous insects which do not have close associations with the flora (e.g. Cottrell 1985). Selected groups of endophagous insects on Proteaceae provide a suitable study to evaluate the importance that plant richness has played in generating insect richness in the flora, in a similar way shown for other insect groups in other floras (e.g. Gess 1992).

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Appendix A. Insect taxa listed in Table 1 as accession numbers. These are listed separately as Table 1 is not sorted according to taxonomic groups, but according to host plant utilization.

1523 = *Orophia ammopleura* (Lepidoptera; Oecophoridae); 1178 = *Calamia irididescens* (Lepidoptera; Arctiidae); 1180 = *Derolomus* sp. (Coleoptera; Derolomidae); 102 = *Conopia platyuriformis* (Lepidoptera; Ageriidae); 197 = Curculionidae, gen et sp indet; 531 = Diptera, gen et sp indet; 1248 = Coleoptera, gen et sp indet; 97 = Diptera, gen et sp indet; 100 = Momphidae, gen et sp indet; 155 = *Centorrhynchus* sp. (Coleoptera; Curculionidae); 407 = Gelechiidae, gen et sp indet; 480 = *Resseliella proteae* (Diptera; Cecidomyiidae); 556 = Gelechiidae, gen et sp indet; 37 = *Afrotibica* sp. (Coleoptera; Curculionidae); 38 = *Capys alphaeus* (Lepidoptera; Lycaenidae); 198 = *Euderes lineicollis* (Coleoptera; Curculionidae); 248 = *Argyroploce* sp. (Lepidoptera; Oecophoridae); 188 = *Eucosma* sp. (Lepidoptera; Eucosmidae); 402 = *Protaephagus capensis* (Lepidoptera; Incurvariidae); 1 = *Sphenoptera* spp. nr *sinuosa* (Coleoptera; Buprestidae); 75 = *Phyllocnistis* sp. (Lepidoptera, Phyllocnistidae); 229 = *Epichoristodes acerbella* (Lepidoptera; Tortricidae); 344 = *Himatium* sp. (Lepidoptera; Cossoninae); 118 = *Genuchus hottentottus* (Coleoptera; Scarabaeidae); 129 = Psyllidae gen et sp indet; 350 = Lepidoptera, gen et sp indet; Cec1 = Cecidomyiidae, gen et sp. indet; Enat = *Euderes natalis* (Coleoptera; Curculionidae); Cydi = *Cydia* sp. (Lepidoptera; Tortricidae); Olet = Olethreutinae (Lepidoptera; Tortricidae); Cossid = Cossidae gen et sp. indet.; Capy = *Capys alphaeus* (Lepidoptera; Lycaenidae); Cec3 = Cecidomyiidae gen et sp indet; Sphe = *Sphenoptera* sp. (Coleoptera; Buprestidae); Psil = *Psiloptera albomarginata* (Coleoptera; Buprestidae); Cec2 = Cecidomyiidae gen et sp indet.

CHAPTER 3

HOST-PLANT CHARACTERISTICS AS DETERMINANTS OF INSECT-BORER ASSEMBLAGES ON *PROTEA* SPECIES (PROTEACEAE) IN THE CAPE FYNBOS

Summary

1. The influence of regional climate, biotope and host-plant variables on the frequency of occurrence of insect borers associated with infructescences of *Protea* species in the species-rich flora of the Cape Fynbos was investigated.
2. Large samples of infructescences (n = 1000) were collected on a seasonal basis and borers identified and quantified.
3. Data were analysed using DECORANA and CANOCO so as to correlate environmental variables with borer occurrence.
4. Distinct differences in frequency of occurrence of the various insect taxa were recorded on the various plant species studied.
5. These differences were primarily accounted for by physical host-plant characteristics (infructescence and seed set variables), and secondarily, by biotope variables and climatic factors.
6. Fynbos plant characteristics therefore play a major role in determining insect abundance. They also have important implications for the conservation of insects, as well as possibly providing a basis for host-plant mediated differentiation in the insects.

Introduction

Various attempts have been made to explain the diversity and abundance of insects in ecosystems. Variables including plant family size (Fernandes 1992), host-plant age in geological history (Southwood 1960), plant distribution (Strong 1974), climatic harshness (Fernandes & Price 1991), plant chemistry (Schultz 1988) and natural enemies (Bernays & Graham 1988) have all been identified as elements which may influence phytophagous insects. Identifying the relative roles of various biotic and abiotic factors will help elucidate aspects of present-day insect abundance. With the current emphasis on conservation of biodiversity, and also the increasing need to manage insect populations (in both natural systems and agro-ecosystems), it becomes important to understand what influences the presence/absence of insects.

The Cape Fynbos, the species-rich, sclerophyllous, fire-prone vegetation of the southwestern tip of Africa (Taylor 1978), is renowned for its remarkable plant-species richness and its environmental correlates (Cowling 1992, Cowling & Holmes 1992, Linder 1991). Conservation areas in this region are primarily devoted to the conservation and management of this flora (van Wilgen *et al.* 1992, Jordaan *et al.* 1991, Wright 1993).

Insects associated with Fynbos plants play an important ecological role as pollinators, seed dispersers, seed predators and as folivores (Johnson 1992, Wright 1993). However, the effect of abiotic and biotic influences (e.g. plant community structure, host plant attributes) on insect abundance and local diversity in this important flora are essentially unknown. This study therefore aimed to determine the relative importance of abiotic factors (local climate) and abiotic factors (biotope characteristics and host-plant characteristics) as determinants of abundance of larvae of insect borers utilizing infructescences (seed storage structures of serotinous Proteaceae) of *Protea* species in Fynbos. This guild of insects was chosen because of: 1) Their ecological significance as seed predators (Coetzee & Giliomee 1987a, Wright 1993), 2) Their intimate association with their host plants - this means that no error can be made in relating the insects to their hosts, and, 3) Endophagous insects often have a high degree of host-fidelity (Gaston *et al.* 1992).

Materials & Methods

Six study sites distributed from the east to the west of the Fynbos biome (Table 1) were selected to provide a range of environmental conditions, ranging from close to the ocean to arid mountainous areas. In each site, at least three *Protea* species were selected for investigation (Table 1).

Table 1. Study sites and *Protea* species used as study plants. (Abbreviations in parentheses refer to Figures 1 & 2)

Locality	Grid reference	<i>Protea</i> spp. sampled
Cederberg Wilderness Area	32°25'S 19°10'E	<i>P. magnifica</i> (CBPM) <i>P. laurifolia</i> (CBPL) <i>P. nitida</i> (CBPN)
Silvermine Nature Reserve	34°05'S 18°26'E	<i>P. repens</i> (SMPR) <i>P. nitida</i> (SMPN) <i>P. lepidocarpodendron</i> (SMPL)
Anysberg Nature Reserve	33°29'S 20°42'E	<i>P. repens</i> (ABPR) <i>P. punctata</i> (ABPP) <i>P. lorifolia</i> (ABPL)
De Hoop Nature Reserve	34°26'S 20°25'E	<i>P. repens</i> (DHPR) <i>P. obtusifolia</i> (DHPO) <i>P. sussanae</i> (DHPS) <i>P. neriifolia</i> (DHPN)
Grootswartberge	33°22'S 22°03'E	<i>P. repens</i> (GSPR) <i>P. nitida</i> (GSPN) <i>P. lorifolia</i> (GSPL)
Kareedouw	33°59'S 24°15'E	<i>P. eximia</i> (KDPE) <i>P. coronata</i> (KDPC) <i>P. neriifolia</i> (KDPN)

Equal-aged (10-15 years old) plants were sampled at all sites. Random collections of infructescences which are the habitat for a range of insect borer taxa (Coetzee & Giliomee 1987b) were made for each plant species at each site every three months. A sample of 250 infructescences was collected from each plant species at each sampling date (i.e. 1000 per year). At least 25 plants were sampled during each collection. In the laboratory, all insect borers present were counted and reared to adult for identification. This approach was used to avoid some of the usual limitations of insect-plant studies (e.g. Futuyma & Gould 1979), such as sampling only at limited times of the year, or spurious host identification.

To evaluate the role of abiotic and biotic variables, climate, biotope structure and host-plant characteristics were quantified. Climatic data were obtained from meteorological stations closest to the study sites. Meteorological variables measured were: 1) Maximum and minimum temperature, 2) Relative humidity, 3) Wind speed, 4) Sunlight hours per day, 5) Rainfall and 6) Evaporative potential.

Biotope characteristics were measured for each site. Three randomly selected 100 m² quadrants were marked out at each site (using the random quadrat method of Sampford 1962) and the following variables measured: 1) Maximum plant height, 2) Average plant height, 3) Number of Proteaceae individuals, 4) Number of study plants and 5) Number of woody plant species.

Host plant characteristics considered were: 1) Presence/absence of resins on infructescence bracts, 2) "Openness" of infructescence, 3) Wall thickness of infructescence, 4) Average number of seeds per infructescence, 5) Average percentage seed set, and, 6) Variability in seed set. Resin presence was quantified as 1 = abundant resin on bracts of infructescence or 0 = resin absent/minimal. Extent of "openness" of infructescences was quantified on a scale of 1 (open) to 4 (florets/seeds enclosed by dried bracts). Infructescence wall thickness was measured at the base of the bracts (using digital callipers), on ten randomly selected infructescences for each plant species. Number of seeds and percentage seed set were determined by counting number of seeds and number of infertile florets in undamaged infructescences (n = 10) of each species.

Percentage seed set was calculated as in Wright (1994). Variability in percentage seed set was calculated for each species as a coefficient of variance (Zar 1984).

Frequency of encounter of the various insect taxa on host plants at each locality was compared using contingency tables (Zar 1984). The null hypothesis that 'all plant species sampled per site would be equally utilized by borers' was tested. Host plants and localities were ordinated using Detrended Correspondence Analysis (DCA, Hill 1979), and an initial attempt to describe the ordination axes was made by correlating climatic, biotope and host-plant variables with ordination scores. Further analysis with Canonical Community Analysis (CCA/CANOCO, Ter Braak 1987) was applied. This multivariate technique ordinated samples (sites and host plants) and taxa (insect borers) along gradients (axes), thus elucidating contribution of each to explaining variance in the insect assemblage. These gradients are linear combinations of the various environmental variables which contribute significantly to explaining variation in the data set. CCA results are presented as biplots of samples and taxa, with vectors plotted simultaneously, which indicate the importance of environmental variables. Correlation matrices are also calculated for all environmental axes and variables (Ter Braak 1987). Autocorrelated environmental variables were excluded from the analysis.

Results

The insect taxa and numbers of individuals collected are listed in Table 2. Contingency table analysis showed that the frequency of encounter of the insect taxa on the host plants was uneven (Table 3). The DCA showed that the samples were distributed along axes which accounted for 51% of the variation (Fig. 1). The ordination scores were primarily correlated with plant characteristics (Table 4). Environmental and biotope variables did not show a correlation of more than 0.48, except variation in plant height and density of host plants (Table 4). Variables which accounted for the first two DCA axes were: 1) Variance in plant height, and, 2) A range of infructescence variables. The third DCA axis was primarily a function of host-plant density (Table 4). CCA clearly indicated that plant characteristics contributed to variation in host-plant exploitation by

Table 2 Insect taxa and number of individuals collected from *Protea* spp. in six study sites in the Cape Fynbos. Data are pooled counts for four samples (of n = 1 000 infructescences for each plant in total) taken at three-monthly intervals

Taxa	Cederberg			Kareedouw			Anysberg NR			Grootswartberge			Silvermine NR			De Hoop NR			
	P.mag	P.nit	P.lau	P.exi	P.cor	P.ner	P.lor	P.rep	P.pun	P.lor	P.rep	P.nit	P.rep	P.nit	P.lep	P.rep	P.ner	P.sus	P.obt
<u>Coleoptera:</u>																			
Buprestidae: <i>Sphenoptera</i> spp.	7	29	24	64	111	71	196	64	6	16	78	42	2	3	1	13	18	31	171
Scarabaeidae: <i>Genuchus botentottus</i>	2	2	1	3	26	52	47	193	30	19	100	42	224	1	56	88	25	0	68
Curculionidae: <i>Euderus lineicollis</i>	2	114	9	42	15	3	0	67	11	0	36	153	0	35	8	3	0	0	6
Apionidae: <i>Tanais</i> sp.	0	4	0	7	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Lepidoptera:</u>																			
Oecophoridae: <i>Orophila amnopleura</i>	0	1	1	11	13	5	4	2	1	1	6	3	18	1	8	7	1	14	5
Tortricidae: <i>Angropyge</i> sp.	0	37	0	1	1	0	4	75	0	0	44	81	1	356	0	22	0	2	0
Tineidae: <i>Tinea</i> sp.	57	0	2	35	62	25	2	5	0	5	2	16	2	2	1	11	5	5	18
Sesiidae: <i>Conopia platyuriformis</i>	1	1	29	21	44	0	64	0	8	51	58	0	3	10	24	0	62	14	61
Noctuidae: <i>Bostra conspiciatilis</i>	0	0	3	0	0	1	8	8	0	0	0	6	3	3	2	3	1	6	7

P.mag = *Protea magnifica*; P.nit = *P. nitida*; P.lau = *P. laurifolia*; P.exi = *P. eximia*; P.cor = *P. coronata*; P.ner = *P. neriifolia*; P.lor = *P. lorifolia*; P.rep = *P. repens*; P.pun = *P. punctata*; P.lep = *P. lepidocarpodendron*; P.sus = *P. sussanae*; P.obt = *P. obtusifolia*; NR = Nature Reserve

borers (Fig. 2; Table 5). Climatic variables also played a role, but never with a correlation of more than 0.55 (Table 5).

Table 3. Summary results of contingency table analyses of frequency of encounter of various insect borer taxa on *Protea* species in six study sites

Site	χ^2	d.f.	P
Cederberg	255,6	16	< 0,001
Kareedouw	143,6	16	< 0,001
Anysberg Nature Reserve	379,6	14	< 0,001
Grootswartberge	348,8	14	< 0,001
Silvermine Nature Reserve	793,6	14	< 0,001
De Hoop Nature Reserve	367,0	21	< 0,001

Infructescence wall thickness and "openness" were negatively correlated with variability in insect occurrence. Other plant/ infructescence variables, such as seed set characteristics were also correlated with the ordination scores for the first two CCA axes (Table 5).

Table 4. Weighted correlation coefficients (for variables > 0,50) for correlations between biotope, climatic and host-plant variables and DCA ordination scores on DCA axes

Variable	Axis 1	Axis 2	Axis 3
Variability, host height	0.44	0.61**	0.05
No. of Proteaceae spp.	0.22	0.25	-0.67**
Infructescence openness	-0.63**	-0.63**	0.62**
Wall thickness	-0.71**	-0.62**	-0.45
% Seed set	-0.35	-0.53*	0.45
No. of seeds	-0.50*	-0.53*	-0.06
Variability, seed set	-0.59**	-0.58**	0.01

* P < 0.05; ** P < 0.01

Table 5. Weighted correlation coefficients (for variables > 0.50) for correlations between biotope, climatic and host plant variables and CCA ordination scores

Variable	Axis 1	Axis 2
Wind speed	0.55*	0.14
Maximum temperature	-0.29	0.50*
Variance, maximum temperature	-0.24	0.50*
Minimum temperature	-0.31	0.50*
Infructescence openness	-0.74**	-0.38
Wall thickness	-0.79**	-0.24
% Seed set	-0.50*	-0.42
No. of seeds	-0.52*	0.47
Variability, seed set	-0.56*	0.21

* P < 0.05; ** P < 0.01

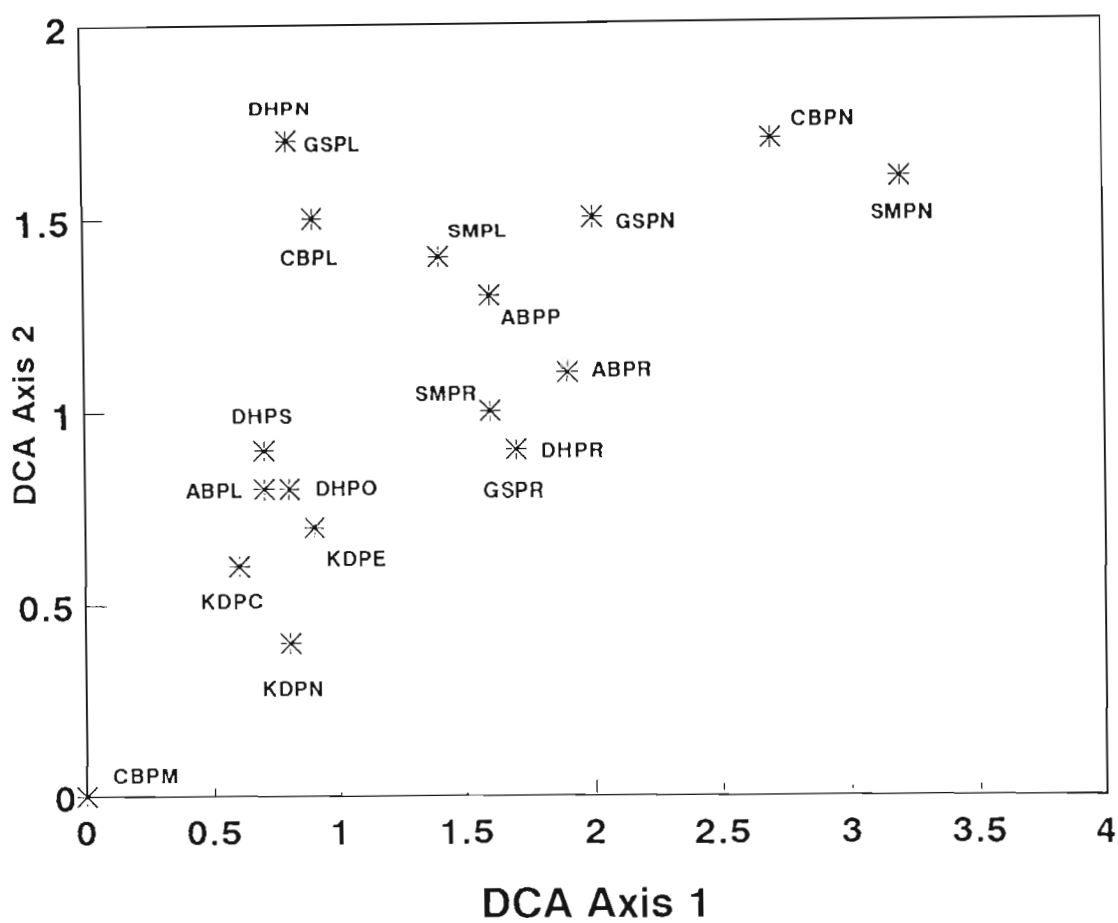


Figure 1. Detrended correspondence analysis ordination of *Protea* spp. in various study sites, based on the frequency of occurrence of insect borer species. See Table 1 for an explanation of abbreviations.

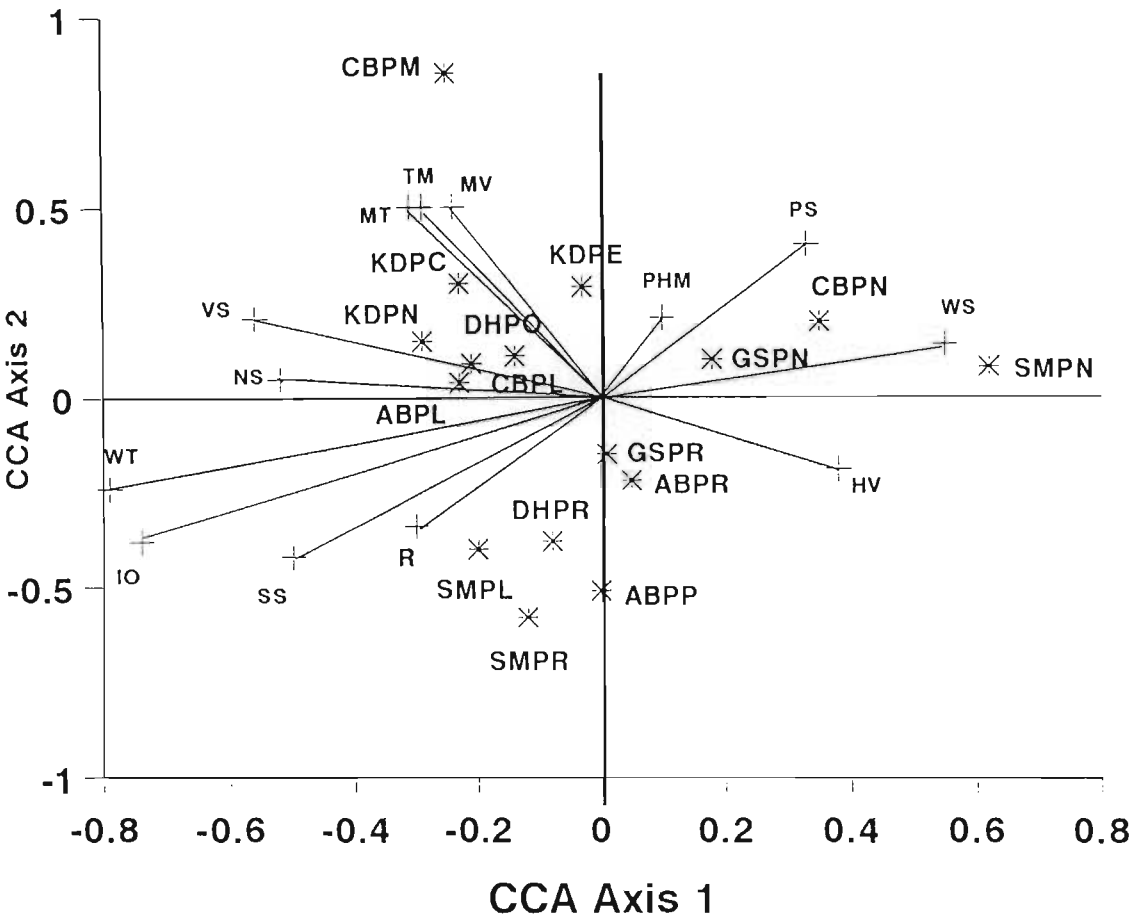


Figure 2. Canonical correspondence analysis ordination of *Protea* spp. in various study sites, based on the frequency of occurrence of insect borer species and climatic, biotope and host plant variables (shown as vectors in the biplot). (Abbreviations for sites and host plants listed in Table 1; TM = maximum temperature, MT = Minimum temperature, MV = variability in temperature, WS = wind speed, PHM = maximum plant height, PS = No. of Proteaceae, HV = variation in plant height, R = resin presence on infructescence, SS = % seed set, VS = variation in seed set, NS = average number of seeds set, IO = infructescence openness, WT = wall thickness.)

Discussion

The clear differences in host-plant utilization by borer taxa within localities suggests that host-plant effects are an important determinant of borer occurrence on *Protea* species. The results clearly indicate that the local taxonomic composition of the host-plant community determined insect-borer assemblages. This has important implications for the evolution of insect host-races or species. Guttman *et al.* (1981) suggested that insect host-specificity can be maintained by local host-plant abundance and their narrow ecological preferences. Opler (1974) and Janzen (1968) have suggested that host plants could act as evolutionary islands, particularly large individual plants or patches of plants.

It has even been proposed that host-induced disruptive selection could lead to sympatric or parapatric speciation in insects with specialized feeding habits (Maynard Smith 1966, Bush 1975).

Limited information is available on host-specific insect species occurring on *Protea* species. Weak evidence from Coetzee (1989) suggests that *Sphenoptera* species (Coleoptera: Buprestidae) are host specific, and could provide evidence of host-mediated differentiation. The study here, however, provides the first solid evidence that differential host selection occurs and may be an important evolutionary influence on insect borers in Fynbos.

This is highly significant, considering that endophagous insects generally show high host fidelity (Gaston *et al.* 1992) and are therefore highly likely to be strongly influenced by changes in host-plant abundance. In some cases, certain taxa were absent from certain host plants (Table 2). If their preferred host plants in a certain locality were dramatically reduced in numbers, the insects could be excluded from that locality. Rapid, short-term changes in plant community structure as a result of too-frequent fire, habitat destruction, commercial flower picking and invasive plants (van Wilgen *et al.* 1992) could therefore have a major deleterious impact on the insects associated with these proteas. Sterling *et al.* (1992) showed, for example, that leaf miner assemblages in Britain were strongly related to plant species composition, and were altered by changes in plant community structure. This effect should be considered when

management of an area leads to changes in plant community. More widespread, community-level repercussions may also occur. For example, Janzen (1978) suggests that host-specific seed predators maintain plant species richness and the loss of such species could, conversely, have a negative effect on local plant-species richness.

From the DCA, it is clear that host-plant characteristics determined frequency of occurrence of the borers. The first DCA axis was a function of infructescence "accessibility" (i.e. openness and wall thickness) to insects. The second DCA axis was accounted for by variance in plant height and infructescence characteristics. The third DCA axis was mainly accounted for by Proteaceae diversity within study sites. The negative correlation between insect occurrence and infructescence openness may be a parasitoid-mediated effect. Open infructescences are likely to be more accessible to parasitoids, which limit borer numbers. If this is the case, larval survival on the host, rather than host selection is important (Langor & Spence 1991). The negative correlation with wall thickness indicates that young, emergent larvae may be limited in their ability to penetrate infructescences, supporting the host-selection hypothesis. Also, the negative correlations of borer occurrence with seed set, point to variability in seed set influencing plant use by borers (Wright 1994). The clear influence of host plants is emphasized by host plants, rather than localities, being grouped in the DCA (Fig. 1).

CCA ordination of the samples further confirmed the overriding importance of host plant characteristics. Wind speed played a relatively small role in defining the first CCA axis, but infructescence characteristics were most strongly correlated with frequency of occurrence of insects, as in the DCA. The CCA illustrates more clearly the tendency for similar hosts to exhibit more congruent borer assemblages. CCA has previously been shown to be valuable in identifying ecological determinants of insect species occurrence and abundance (e.g. Penev 1992, Sterling *et al.* 1992). Penev (1992) showed that the application of this technique can lead to the elucidation of otherwise confounding data, identifying environmental conditions independent of climate that played a role in influencing insect assemblages. The present study has, likewise, shown that variables independent of climate and biotope can significantly influence insect abundance.

The importance of interactions between host-plants and insects appears to be largely peculiar to endophagous insects. Courtney and Chew (1987) showed that host-plant communities were not good predictors of abundance of adult Pieridae (Lepidoptera). They identified habitat type as the primary factor determining host use by insects. A study of soil-dwelling and free-living beetles on heathland (Webb *et al.* 1984) also showed that habitat variability (i.e. structural diversity of vegetation) influenced insect diversity. Their study concerned organisms that were not intimately associated with specific host plants. The combined effect of biotic and abiotic variables was also demonstrated in the present study, but plant characteristics were consistently identified as being of cardinal importance. The intimate relationship of borers with their host plants is likely to be the reason for the overriding influence of host plant characteristics, with pairwise insect-host relationships being particularly important.

Consideration of the subtle ecological requirements of insects is essential for management of the Fynbos flora (Wright 1993). Furthermore, it is also important to understand the effect of anthropogenic disruption of communities, and the long-term ramifications. For example, Sterling *et al.* (1992) show that changes in plant community can profoundly alter insect communities. Ensuring that habitats remain intact remains the ideal and often most practical umbrella insect conservation measure (Samways 1992). However, management may also be important. Periodic disturbance by fire is essential in Fynbos, to ensure that plant diversity and productivity are maintained (van Wilgen *et al.* 1992). Determining whether host-specific insects are present (and could be deleteriously influenced), is therefore important.

Management implications: Fynbos ecosystems are seldom managed for faunal diversity. This is because few mammals and birds are endemic to the flora. Only animals with relatively close associations with the flora (e.g. geometric tortoises) and an endemic antelope (bontebok) have received special attention (van Wilgen *et al.* 1992). Yet endophagous insects are intimately associated with the flora, and often play an important ecological role (Johnson 1992, Wright 1993). Owing to their intimate association with their hosts, they are likely to be subject to dramatic disruption when management practices change plant communities. Burning an area of Fynbos will exclude borers

associated with *Protea* infructescences for at least as long as it takes newly recruited plants to mature (3 - 10 years). It has also been shown that too-frequent burning leads to local extinction of slow-maturing Proteaceae (van Wilgen & Kruger 1981), with significant implications for insects intimately associated with them. Results of this study have shown that *Protea* spp. present in a host-plant community are important determinants of borer occurrence, as are host-plant characteristics.

The requirements of these insects must be considered if they are to be adequately conserved. Management burns should clearly not be applied too frequently or over areas large enough to cause the exclusion of any borer species. Planning to burn in this manner will necessitate surveys of borer species in an area intended for burning. As these insects are associated with some of the slowest maturing Fynbos plants, they are likely to function as "umbrella" species in terms of conserving other insects associated with more rapidly maturing plant species. Borers on *Protea* spp. could also provide a useful "indicator" group for assessing the effects of management and for comparative insect community studies. Lawton & Gaston (1989) have suggested that an "indicator" group should be well defined, with an adequate number of species. The insect borer community on *Protea* spp. appears to be highly suitable for such use.

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CHAPTER 4

HIGH RATIOS IN ENDOPHAGOUS TO ECTOPHAGOUS INSECTS SPECIES RICHNESS IN THE SCLEROPHYLLOUS AFRICAN CAPE FYNBOS

Summary

1. This study examines the relative species richness of endophagous and ectophagous insects in the African Cape Fynbos, a sclerophyllous, plant-species rich flora.
2. Sweep-samples of ectophagous insects were compared to gall insect richness sampled on transects comprising 600 plants. Data were analysed by comparing number of species collected per family and feeding guild. Species diversity for different guilds was compared using species rank/abundance curves.
3. Endophagous, gall-forming insects (Cecidomyiidae: Diptera) were found to be considerably more speciose than other feeding guilds, showing that the ratio of endophages to ectophages in sclerophyllous vegetation types is high.
4. Families with a semi-endophagous feeding habit (e.g. Cicadellidae), and some with an endophagous part of the life cycle (e.g. Curculionidae), were intermediate in species richness.
5. Gall forming Cecidomyiidae were numerically dominant as well as more speciose in most study sites, with lower diversity in sites with high plant species richness.
6. The intimate relationship that the endophagous insects have with their host plants tends to habitat specialisation, thus, making them likely to undergo radiation together with their host plants. It is postulated that this relationship has led to higher rates of speciation in endophagous insects than other feeding guilds in Fynbos.

Introduction

Cornell (1989) hypothesized that endophagous insect species should be particularly abundant relative to ectophagous species in resource-poor habitats where plants have heavy "defences" against insects. He proposed that heavy defense levels on plants do not necessarily reduce the number of species associated with them, but can have a dramatic effect on the guild structures of herbivores that utilize the plants. Endophagous insects have the ability to avoid physical defences and to circumvent the problem of low plant nutrient quality (Cornell 1989, Craig *et al.* 1986). These supposed defences would usually deter ectophages (Scriber & Slansky 1981). These are traits which provide endophagous insects, relative to ectophages, with the potential to radiate extensively on nutrient-poor plants.

The Cape Fynbos is a typically sclerophyllous, mediterranean-type climate flora (Taylor 1978) on extremely nutrient-poor soils (Deacon *et al.* 1992). The vegetation is also of low nutrient value, and is a suboptimal food source for insects (Wright & Giliomee 1992). Cottrell (1985) suggests that the extremely low nutrient value of Fynbos plants has precluded the evolution of butterfly endemics with intimate host plant relationships in the region, and suggests that endophagous or long life-cycle taxa should be more prolific. The Fynbos thus presents an ideal flora to test the predictions of Cornell (1989). The aim of this study, therefore, was to quantify relative endophage and ectophage species richness in Fynbos to test this hypothesis. It is also the first attempt to measure insect species richness in Fynbos as a flora rather than investigating a limited group of plant taxa (e.g. Wright & Giliomee 1991, Coetzee *et al.* 1987, Visser 1992).

Materials and methods

Study sites were located at Rooiels (34°20'S, 18°50'E), Steenbras River Mouth (34°13'S, 18°50'E), in the Kogelberg Wilderness Area (34°13'S, 18°53'E), Cape of Good Hope Nature Reserve (34°15'S, 18°25'E) and Oudekraal (33°59'S, 18°21'E). These sites are all in areas of high plant diversity (Cowling & Holmes 1992, Oliver *et al.* 1983).

The following feeding guilds of insects were recognised: endophages (gall insects, Diptera: Cecidomyiidae); sap-suckers (Hemiptera and Thysanoptera); leaf chewers

(Coleoptera, Lepidoptera, Orthoptera, Phasmatodea); and taxa with an endophagous developmental stage ("semi-endophages": Coleoptera: Curculionidae; Cerambycidae; Elateridae, Lepidoptera: Phyllocnistidae) (see Cornell 1989). Gall insects were sampled from each site using a modification of the method of Fernandes & Price (1988): at each site, 600 individual woody shrubs were chosen randomly and examined for the presence of galls in leaves, buds or stems. Herbs and trees were not sampled. Other groups were collected by sweep netting three 100m-long transects in each site between December 1994 and March 1995. Peak numbers of ectophagous insects occur at this time of year in Fynbos vegetation (Wright & Giliomee 1991, Visser 1992). Collections were made on at least three to four occasions from each site. Transects for gall insects and sweep-netting were approximately equal in area, allowing a more statistically acceptable comparison of number of species collected. Ectophagous insects were stored in 70 % ethyl alcohol and deposited in a voucher collection of Fynbos insects (Agricultural Research Council, Elsenburg, South Africa). Gall insect species were separated on the basis of gall morphology and host plant (Anathakrishnan 1984, Fernandes & Price 1988). Voucher specimens of all galls recorded were also deposited in the Fynbos insect collection. Ectophagous insects were sorted and identified to family level. Beyond that, specimens were sorted to recognizable taxonomic units ("morphospecies"). Number of species per order and family as well as per feeding guild were compared. As only Cecidomyiidae were used to quantify endophagous richness, an inadequate comparison would have resulted from pooling numbers of species for the other guilds, as many more families were collected for them. Average number of species per order, family and guild were compared by ANOVA, using Tukey pairwise comparisons (Zar 1984). Species abundance was analyzed by plotting log abundance of species against species rank, arranging species from most to least common in abundance (Magurran 1988). Only Cecidomyiidae, Hemiptera and Coleoptera were used for rank-abundance curves as other taxa were scantily represented in the data set.

Results

Number of species collected for each family and guild are shown in Table 1. A total of 28 families were recorded. ANOVA showed that the gall forming Diptera contributed the greatest number of species. Other orders were not significantly different in number of species collected, although the Coleoptera and Hemiptera tended to be slightly more speciose than other orders (Fig. 1). At family level, the Cecidomyiidae contributed the greatest number of species, with the Cicadellidae, Curculionidae and Chrysomelidae contributing an intermediate group (Table 1). Gall insects were the most species rich

Table 1. Number of species of each family and guild of insects collected from the five sites

Family (guild)	Site					x
	R	SR	K	C	O	
Diptera:						
Cecidomyiidae (E)	9	16	7	9	16	11.4a
Hemiptera:						
Cicadellidae (S)	1	5	6	3	10	5.0b
Pentatomidae (S)	-	2	2	1	1	1.2c
Lygaeidae(S)	1	2	2	2	6	2.6c
Miridae (S)	1	2	1	1	2	1.4c
Scutellaridae (S)	-	-	1	-	-	0.2c
Phyrochoridae (S)	-	3	1	-	-	0.8c
Fulgoroidea (S)	-	1	2	1	1	1.0c
Tingidae (S)	1	1	1	-	1	0.8c
Cercopidae (S)	-	-	1	-	1	0.4c
Cicadidae (S)	-	-	1	-	-	0.2c
Coleoptera:						
Chrysomelidae (C)	2	1	3	4	2	2.4bc
Curculionidae (P)	2	1	6	3	6	3.6b
Cerambycidae (P)	1	1	1	1	-	0.8c
Melolonthinae (C)	-	1	-	1	1	0.6c
Nitidulidae (C)	-	-	2	1	1	0.8c
Elateridae (P)	-	-	1	-	-	0.2c
Lepidoptera:						
Geometridae (C)	2	2	1	2	1	1.6c
Phyllocnistidae(P)	-	-	-	1	-	0.2c
Psychidae (C)	-	1	1	1	-	0.6c
Lymantriidae (C)	-	1	-	-	-	0.2c
Pyalidae (C)	-	1	-	-	-	0.2c
Thysanoptera:						
Tubilifera (S)	1	1	-	1	2	0.6c
Thripidae (S)	-	-	1	-	-	0.2c
Orthoptera:						
Acrididae (C)	1	1	1	1	1	1.0c
Lentulidae (C)	-	-	1	1	1	0.6c
Tettigoniidae (C)	-	-	1	-	-	0.2c
Phasmotodea:						
Phasmidae (C)	-	-	-	1	-	0.2c

R = Rooiels; SR = Steenbras River Mouth; K = Kogelberg Wilderness Area; C = Cape of Good Hope Nature Reserve; O = Oudekraal

E = endophagous; S = sap-sucker; C = chewer; P = "partially" endophagous.

x = average number of species; averages followed by different letters are significantly different (ANOVA, LSD $P < 0.05$).

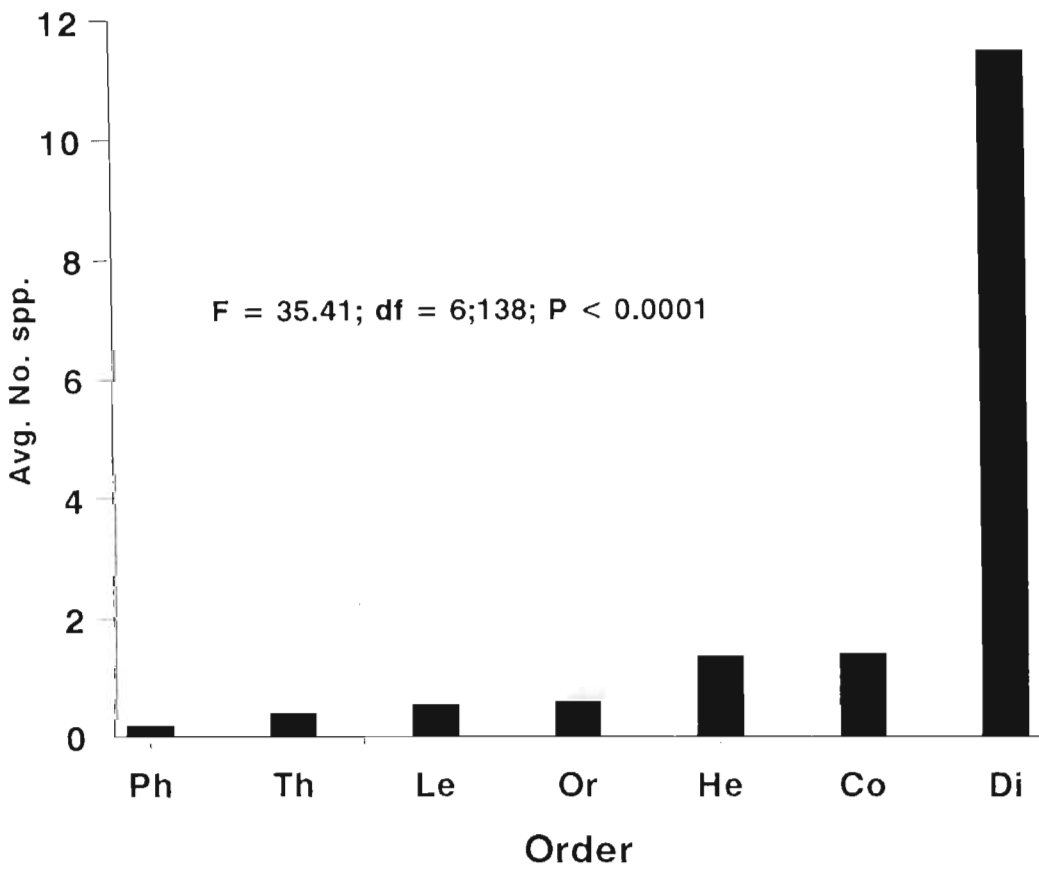


Figure 1. Species richness of various orders of insects collected from five Fynbos sites in the southwestern Cape. (Ph = Phasmatodea, Th = Thysanoptera, Le = Lepidoptera, Or = Orthoptera, He = Hemiptera, Co = Colopetera, Di = Diptera.)

guild, with sap-suckers and "semi-endophages" slightly, but not significantly, more speciose than leaf chewers (Fig. 2).

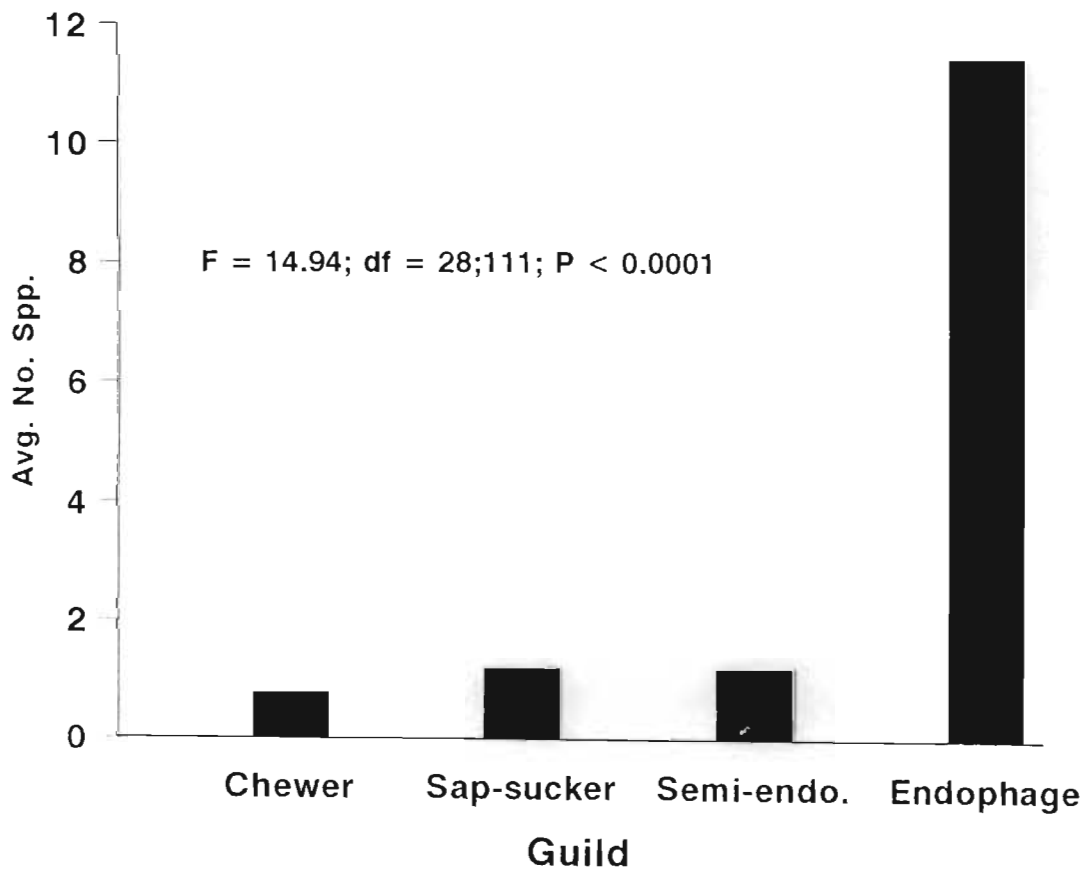


Figure 2. Number of species per feeding guild for Fynbos vegetation at five sites in the southwestern Cape.

The rank-abundance curves for the five study sites showed differences in species richness and diversity between localities. The Cape of Good Hope Nature Reserve and Steenbras River sites showed that Cecidomyiidae were numerically dominant, and also contributed a greater number of species (Fig. 3A,B). The differences in number of species shown here is also shown in Table 1. The other three sites showed less dominance in number of individuals of Cecidomyiidae, and they were again more speciose in the Rooi Els samples (Fig. 3C). In the Oudekraal and Kogelberg samples (Fig. 3D,E), Hemiptera contributed more species.

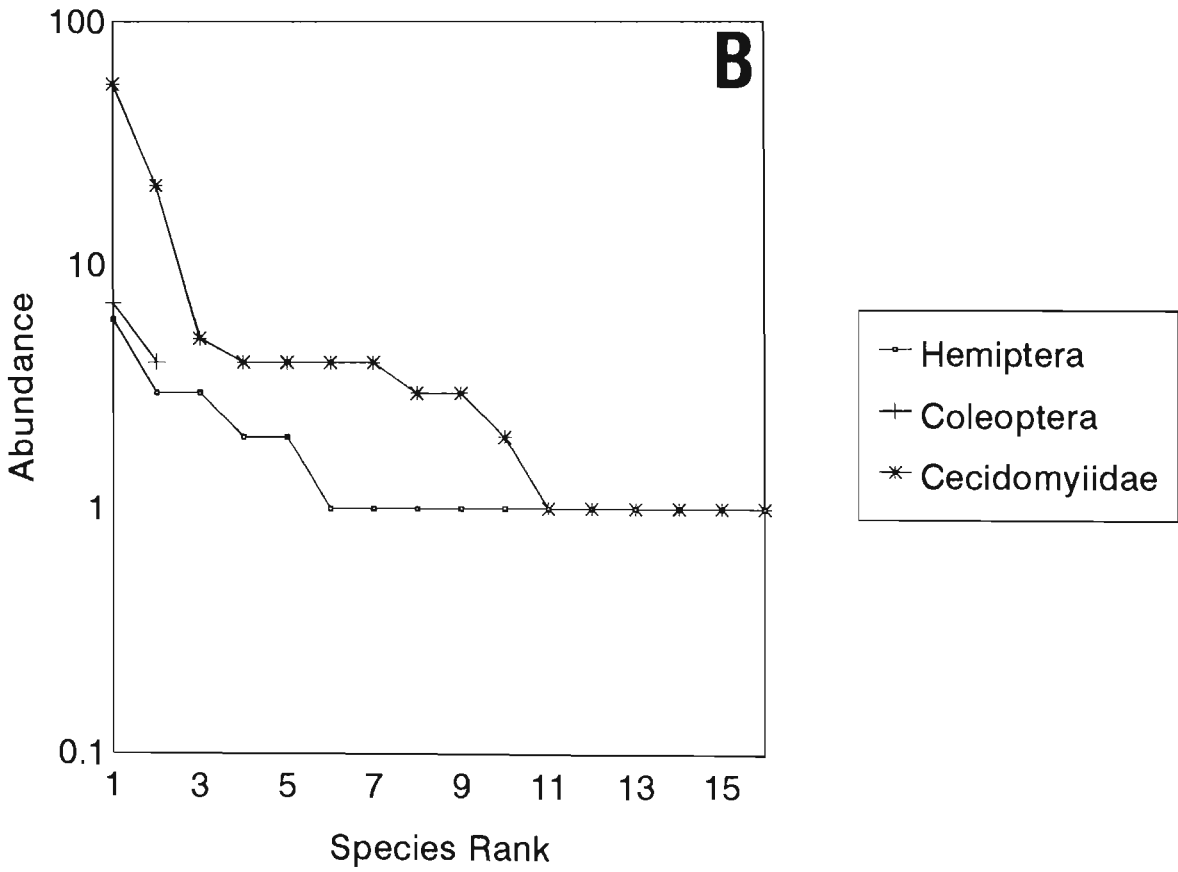
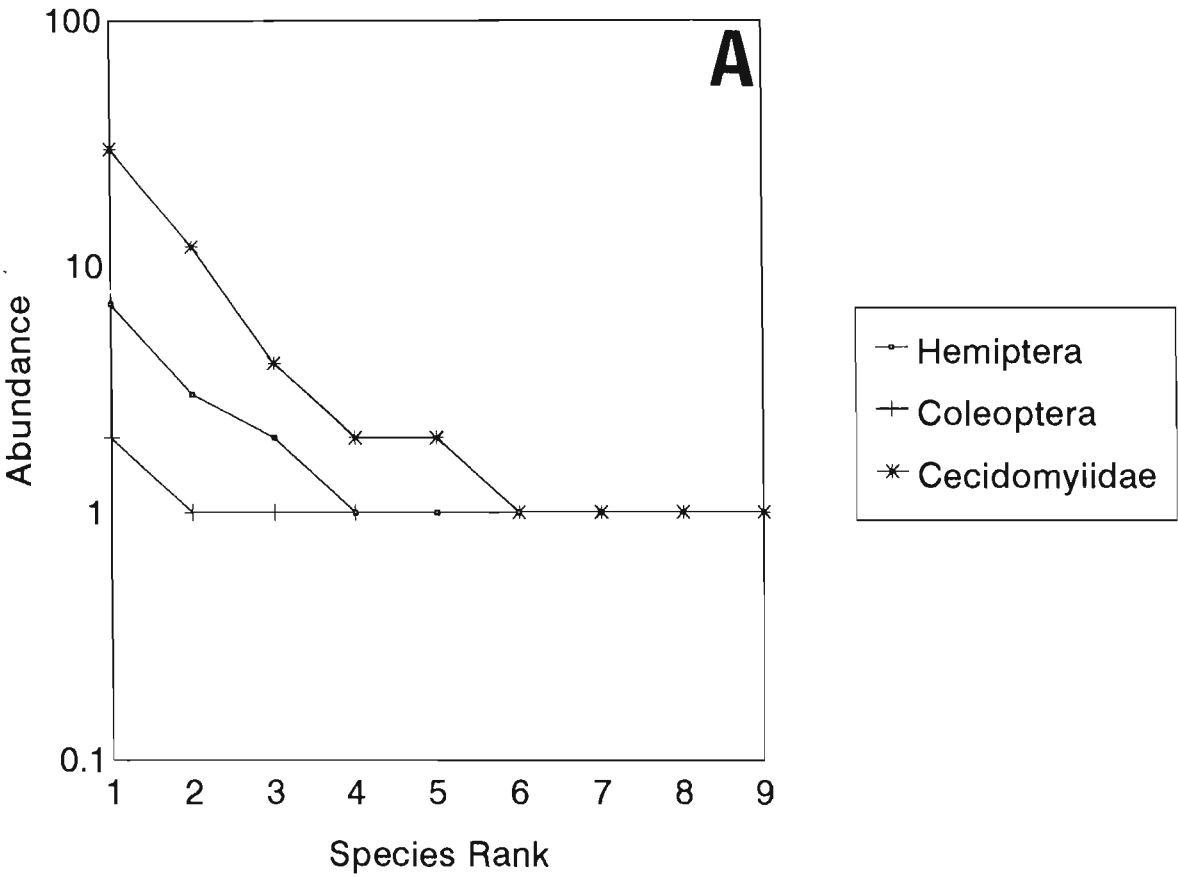
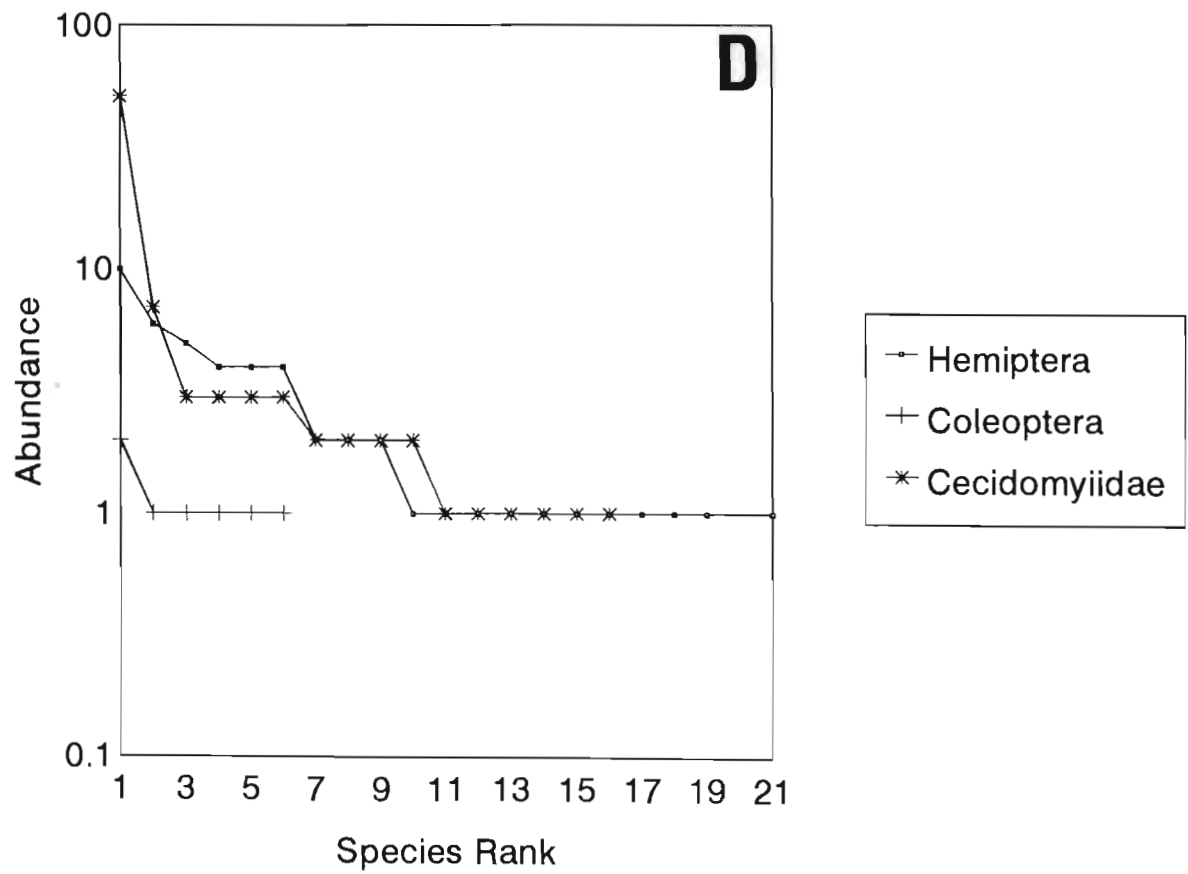
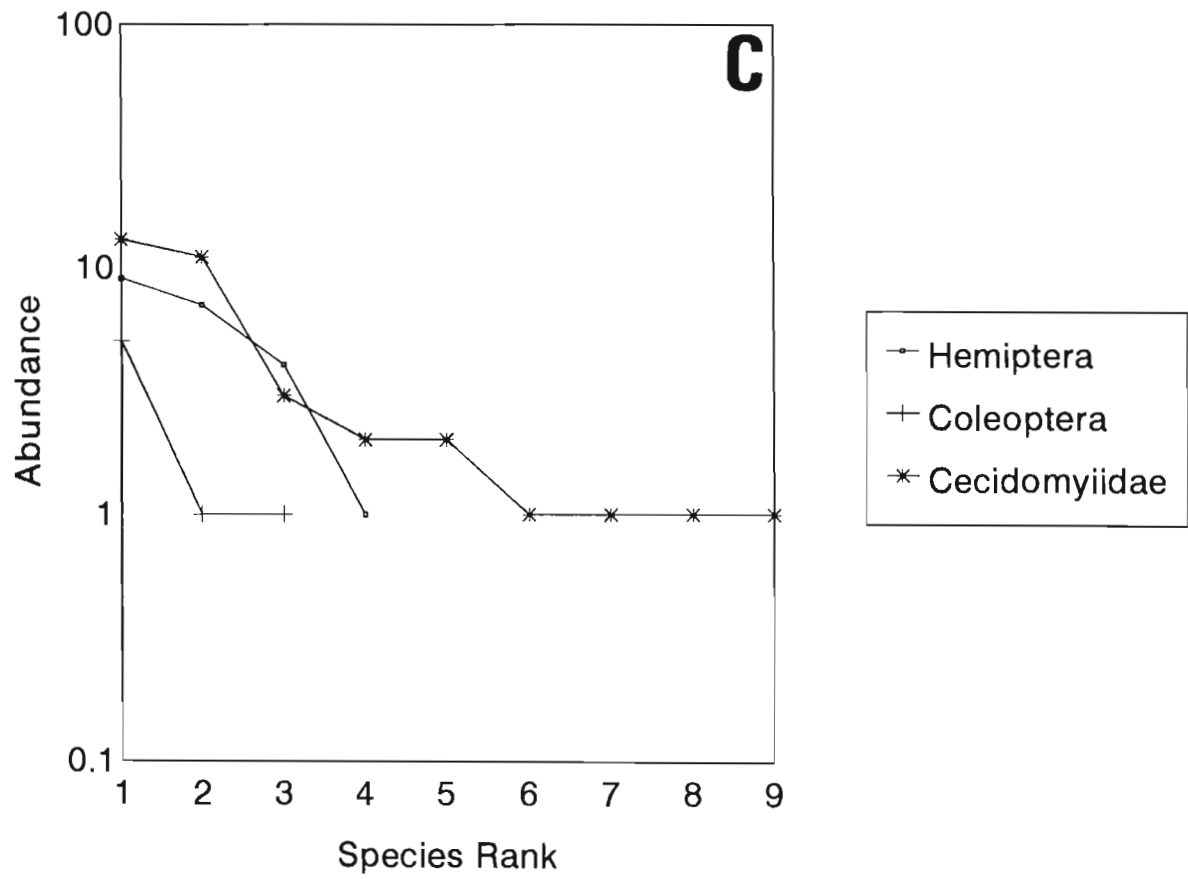
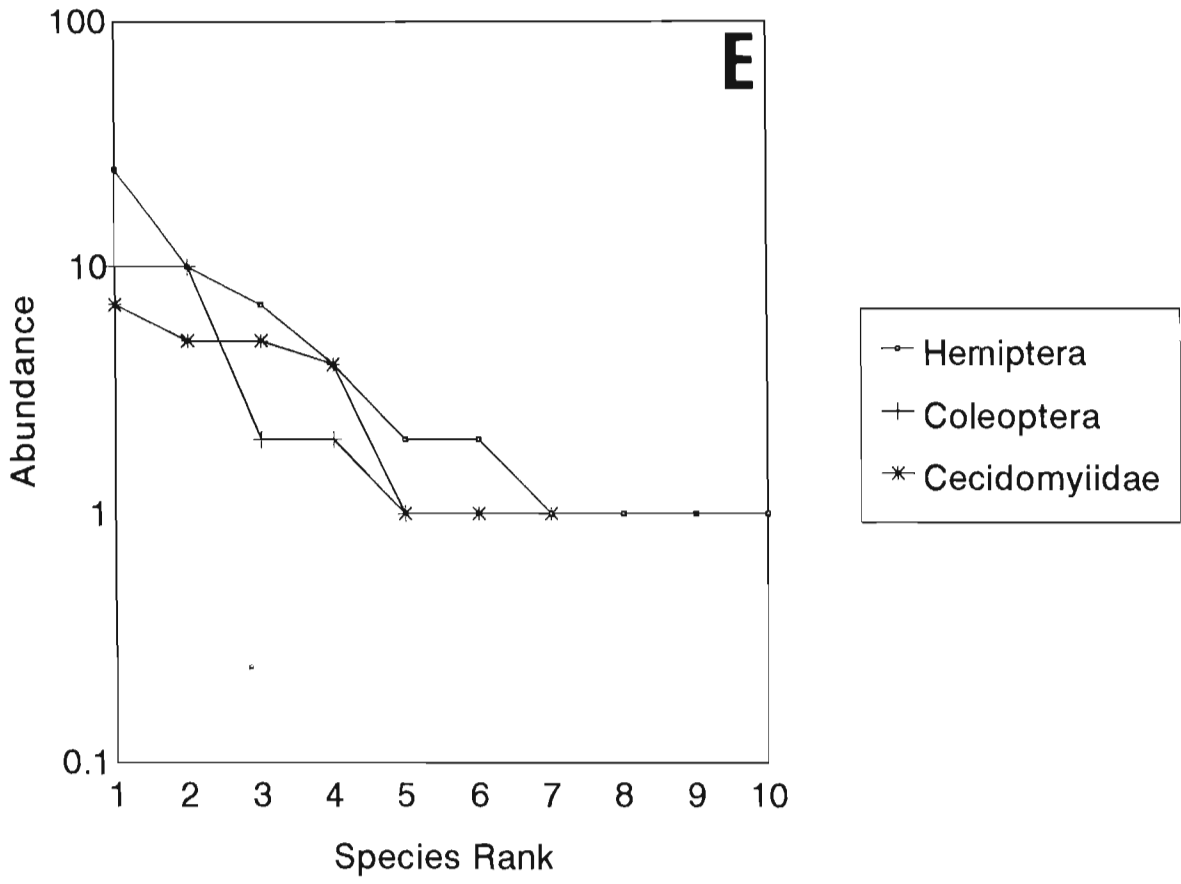


Figure 3A-E. Species rank/abundance curves for Coleoptera, Hemipetera and Diptera (Cecidomyiidae) for five study sites (A: Cape of Good Hope Nature Reserve, B: Steenbras River; C: Rooi Els; D: Oudekraal; E: Kogelberg).





Discussion

This study clearly indicates that average endophagous insect species richness was higher than other feeding guilds, even than other groups that included an endophagous life stage or feeding mode (i.e. sap-suckers). These data corroborate Cornell's (1989) hypothesis proposing greater endophage species richness in sclerophyllous, nutrient-poor floras, and are in agreement with the proposal of Fernandes & Price (1991) that sclerophyllous vegetation should allow the proliferation of gall forming species. Cornell (1989) suggests that endophagy is promoted by heavily defended plants. However, this is a matter of some controversy (Jermy 1984). Whether plant "defence" has contributed to insect diversification and specialization at all is questionable. Sclerophyllous traits in Fynbos may serve as a coincidental defence mechanism against herbivory (Wright & Giliomee 1992), and the sclerophyllous vegetation may simply provide a more suitable substrate for endophages rather than ectophages. It is interesting to note that the Oudekraal and Kogelberg sites had relatively low gall-insect richness compared to other guilds. The relationship between plant species richness and gall insect species richness is investigated in detail in Chapters five and six.

Fynbos plants are probably serendipitously defended by sclerophyllous adaptations to their environment, rather than by coevolved responses to herbivore pressure (Wright & Giliomee 1992), so the flora possibly provides an under-utilized resource upon which endophages could radiate. Radiation of galls may have been mediated by the presence of the great diversity of plant species characteristic of Fynbos (Cowling & Holmes 1992) or may be the result of exposure to the same selective pressures / speciation processes that generated the floral diversity. Fynbos is characterized by high beta and gamma diversity (species turnover within and at the landscape level, Cowling & Holmes 1992). Plant richness is also strongly correlated with environmental variables and edaphic variability (Linder 1991, Cowling & Holmes 1992, MacDonald & Cowling 1995). Extensive plant speciation in the Fynbos may have been incidental to ecological adaptations of plants in a variable environment.

Vrba's (1980) effect hypothesis may be as relevant to insect speciation as it is to Fynbos plant speciation (see Cowling & Holmes 1992). This hypothesis suggests that selection

for characteristics suited to a certain environment may incidentally drive speciation (Vrba & Gould 1986). Cowling & Holmes (1992) suggest that habitat specialist plants in Fynbos should be prone to speciation under conditions of environmental change, population fragmentation and subsequent divergence in allopatry. The same may be feasible for endophagous insects, which are characteristically host ("habitat") specialists and should therefore be profoundly influenced by the history of their host plants. Higher speciation rates may thus be more plausible for gall insects than for ectophagous insects in Fynbos, both because of the inherent suitability of this type of flora for gallers, and as a result of the considerable plant richness, with high turnover in plant species within landscapes. It has been suggested previously that insects, particularly Diptera, may have radiated with the Cape flora, and possible contributing factors are habitat diversity, varied topography, climatic variability and floristic diversity (Bowden 1978). Coleoptera also appear to have been influenced by ecological conditions in the Fynbos, with many endemic genera, though these tend to be less intimately associated with the flora (Endrödy-Younga 1978). Even other invertebrates, e.g. land-snails, have a relatively high level of endemism in the Fynbos (at least 7 subgenera) with a fairly high number of species (van Bruggen 1978). The patterns of species richness in these groups suggests that both plant diversity and other environmental factors have contributed to the evolution of a distinct entomofauna in the Fynbos.

The role played by plants in generating insect diversity in Fynbos is likely to have been greater in a group such as the Cecidomyiidae, with their intimate host relationships. Host plant speciation/divergence is likely to have affected them, together with other ecological changes. These insects fall into Jermy's (1984) "Type A group": closely related mono- or oligophagous insects on plants that are themselves not necessarily closely related, and probably follow plant evolution sequentially. This is the result of insects becoming particular in food selection (Jermy 1984). Ectophagous insects often also have a tendency to be monophagous, e.g. Chrysomelidae, Curculionidae (Jermy 1984), and these families did tend to be slightly more speciose than other groups in the present study, although substantially less than gall insects. Their radiation in Fynbos may have been limited by factors such as sclerophylly and xeric conditions (Cottrell, 1985; Fernandes & Price 1988).

The relatively high species richness of endophages observed in Fynbos is therefore not unexpected. The results here support the hypothesis concerning the expected richness of different guilds of insects in sclerophyllous, nutrient-poor floras. The results also demonstrate that endophagous insects in the Fynbos are considerably more speciose than other guilds. They are also the guild with the greatest host fidelity and therefore with greatest dependence on their host plants. The maintenance of their species richness is therefore closely connected with the careful management and utilisation of their host plants. Information elucidating the relationship of gall insect richness to plant richness in Fynbos is demonstrated as separate studies (Chapter 5 & 6).

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CHAPTER 5

INSECT SPECIES RICHNESS TRACKING PLANT SPECIES RICHNESS IN A DIVERSE FLORA: GALL INSECTS IN THE CAPE FLORISTIC REGION, SOUTH AFRICA.

Summary

1. The Cape Floristic Region (CFR) is one of the most plant-species rich regions in the world, making it interesting to ascertain whether the insects of the region are proportionally speciose. The relationship between gall- insect species richness (GSR) and plant richness was investigated for the Fynbos and for representatives of vegetation of the whole CFR.
2. Samples (of up to 600 plants per transect for Fynbos) of woody shrubs were investigated for the presence of galls. The species richness of these insects was quantified, as well as plant species richness for each transect. GSR for Fynbos was compared to global figures for GSR.
3. Fynbos harboured significantly more gall-insect species than other CFR vegetation types.
4. GSR was positively correlated with CFR plant richness. GSR also closely tracked plant richness in Fynbos. GSR was not significantly influenced by other variables (elevation and aspect), suggesting that plant richness *per se* was an important factor in generating GSR.
5. Fynbos GSR is comparable to other sclerophyllous regions of high GSR globally, corroborating that this vegetation type is a centre of galler diversification.
6. There is a high percentage of gall-insect endemism in the Fynbos, as might be expected from the high host-fidelity of this insect group.

Introduction

Sclerophyllous vegetation around the world tends to harbour high gall-insect species richness (GSR) (Fernandes & Price 1991). This is attributed to the capacity of this guild of insects to circumvent nutritional and/or toxic restrictions of these plants (Cornell 1989), availability of a safe and predictable environment in the way of long-lived leaves and stems, as well as the negative influence that xeric conditions have on natural enemies (parasitoids and entomo-pathogenic fungi, Fernandes & Price 1991, Waring & Price 1989). Patterns in GSR show that xeric, sclerophyllous floras harbour the most taxonomically diverse gall faunas globally (Price 1991), and that these patterns are best accounted for by environmental harshness, i.e. thermohygral stress/elevation (Fernandes *et al.* 1994). A strong positive correlation between GSR and plant richness has already been documented for the USA (Fernandes & Price 1988), but was rejected as a factor explaining or generating the evolution of gall diversity, as the patterns observed prevailed with no change in plant-species diversity. Furthermore, most galler richness in Fernandes & Price's (1988) study was supported by only one plant species in many of their sites, perhaps suggesting that certain plant taxa are conducive to galler radiation, rather than plant richness being an generating gall-insect diversity.

The hypothesis that the factors which generated high plant richness would also contribute to the evolution of gall richness has not yet been rigorously tested. The only investigation that tackles this problem is that of Fernandes (1992), where the data of Docters van Leeuwen-Reijnvaan & Docters van Leeuwen (1926) were analyzed to relate gall species richness to plant family size. A positive correlation was found, suggesting that host plant species richness, or the factors that led to the generation of high plant richness, may have been instrumental in generating GSR.

The Fynbos biome of the Cape Floristic Region (CFR) is a sclerophyllous and species-rich flora, with characteristically low-nutrient plants on a nutrient-poor substrate (Taylor 1978) and may be predicted to host a diverse gall fauna. However, certain characteristics of Fynbos may have mitigated against the evolution of a rich gall insect assemblage. In particular, the plant species richness of Fynbos is exceptionally high (Cowling & Holmes 1992), and this could reduce the spatial predictability for host-plant location by

stenophagous gall insects. Fynbos is also a typically fire-prone mediterranean-type flora (van Wilgen 1987). Large burns may occur at intervals of 4 - 60 years (Kruger 1977). The abrupt disappearance of resources due to combustion may also make the flora less suitable as a resource for gall insects. Plant predictability in time and space have been postulated to be important attributes for the evolution of gall-insect richness (Fernandes & Price 1991). However, the highly diverse, xeric, sclerophyllous, nutrient-impooverished nature of Fynbos makes it a potentially suitable substrate for a diverse gall fauna. Less speciose, sclerophyllous vegetation types (e.g. Karoo, renosterveld), of the CFR should exhibit gall richness at least equal to that of Fynbos if the xeric environment and sclerophylly are of overriding importance in their evolution. If plant richness or the factors generating it are of cardinal importance, Fynbos may be expected to have a proportionally higher gall richness.

Documentation and elucidation of insect biodiversity patterns has become important (e.g. Erwin 1990, Gaston 1991), and the conservation of insects a priority (Gaston *et al.* 1993). The Fynbos is an appropriate flora to further investigate gall insect richness and its associated environmental variables, providing the opportunity to investigate the possible role of high plant richness and to compare sclerophyllous vegetation types with more mesic vegetations.

The aims of this study were therefore: 1) To document the GSR of the different vegetation types/phytochoria of the CFR; 2) To investigate the relationship between GSR and plant species richness in the CFR; 3) To investigate the effect of environmental gradients in Fynbos on GSR, and, 4) To compare Fynbos GSR with similar data for other regions.

Materials and Methods

1) GSR was sampled throughout the CFR in the following vegetation categories (Moll *et al.* 1984): mesic and dry mountain Fynbos; limestone lowland Fynbos; Renosterveld; Valley Bushveld; Afromontane forest and Karroid shrublands. Estimates of gall insect species richness were made using a modification of the method of Fernandes & Price

(1988). Gall species were counted by searching entire plants for the presence of galls. Recognizable taxonomic units (RTUs, Beattie & Oliver 1994) of gall insects were separated on the basis of gall morphology and host-plant species (Ananthakrishnan 1984, Cornell 1985). Samples of 300 - 600 randomly selected woody shrubs were examined for Fynbos and Karoo sites along transects of *ca.* 10 m wide. In preliminary samples, an accumulative curve of GSR was found to become saturated at 300 - 400 plants sampled. Thirty trees were sampled for each of these sites. Valley bushveld and Afromontane forest were sampled by examining 30 randomly selected trees per site. A sample size of 30 was used for trees to ensure that roughly equal areas were sampled for trees and shrubs. Random selection of plants was done by investigating searching plants as they were encountered along the transects, irrespective of their identity. At each sampling, number of plant species sampled and number of gall insect species present were recorded. Fynbos sites of similar post-fire age were selected. Fynbos sampling sites were selected throughout the Fynbos biome (Fig. 1) to provide an indication of the distribution of gall richness within the biome. Average number of gall insect species were calculated for each vegetation type/phytochorion.

2) Regressions of gall richness dependent on plant richness and correlations between gall- insect species and plant species richness were calculated for all vegetation-type samples together and separately Fynbos samples only. This was done so that the influence of plant species richness could be evaluated for the region as well as for the Fynbos as a plant species-rich vegetation type. To test whether GSR tracked plant richness, the ratio of gall species: plant species was regressed against plant richness for each sample (Gaston 1992).

3) A series of samples were taken in the Grootswartberge Wilderness Area (33°18'S, 22°03'E), along an elevational gradient, sampling 600 plants as above at every 300 m above sea level. Both north and south facing slopes were sampled, so that the effect of aspect on GSR could be gauged. This set of samples included Karroid shrubs, north-facing dry-mountain Fynbos and mesic-mountain Fynbos at higher elevations and on south-facing slopes. Multi-factor ANOVA was used to test for differences in gall richness at different elevations and aspects.

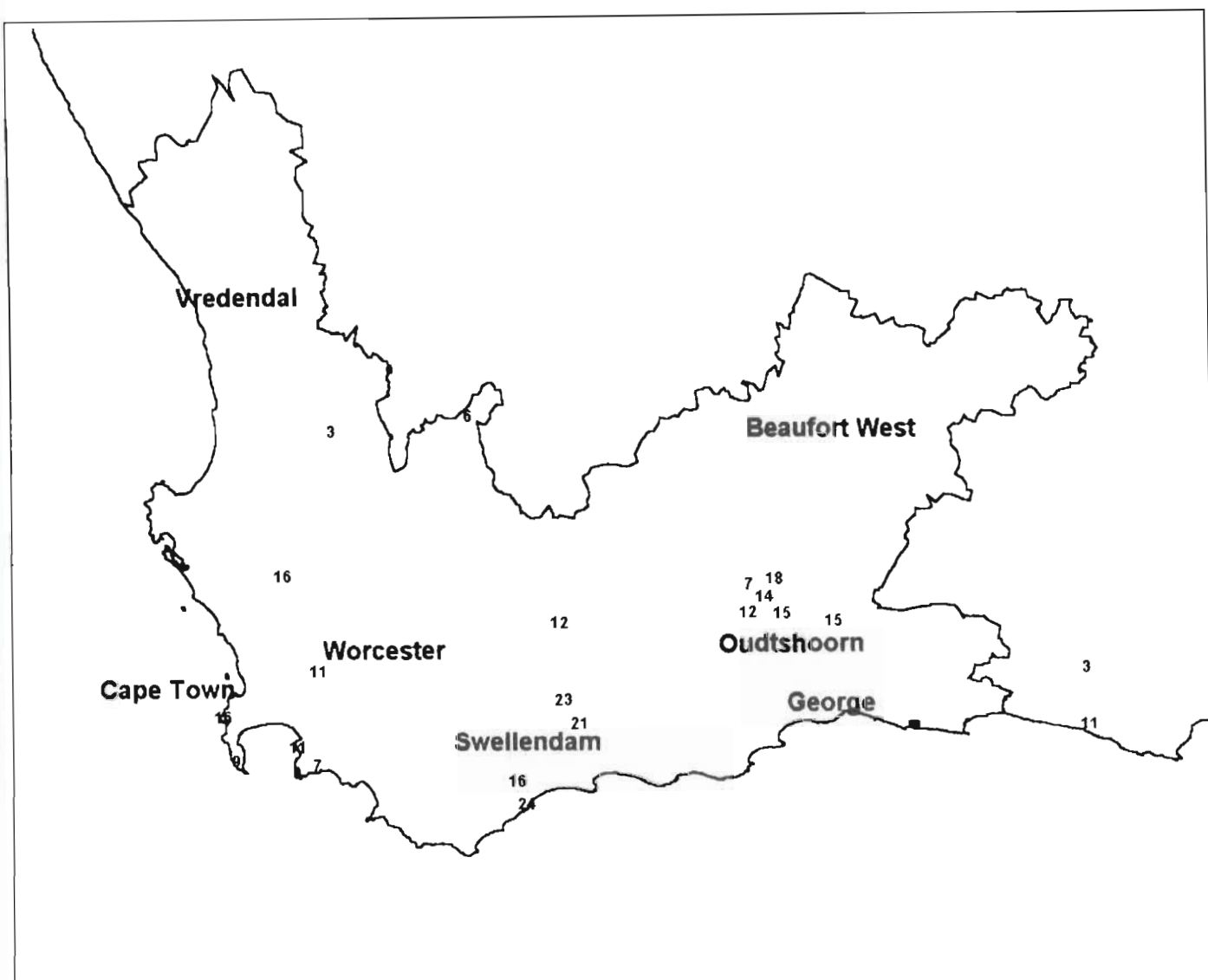


Figure 1. Distribution of sites sampled for gall-insect richness (GSR) in the Cape Floristic Region (CFR). Number of species recorded at each locality is shown.

4) Fynbos GSR was compared with global levels of GSR from Price (1991).

Results

1) GSR in the CFR: Average numbers of species of gall-insect recorded for the various components of the CFR are shown in Figure 2. Fynbos harboured significantly higher average number of gall insect species than other CFR vegetation types ($F_{3,27} = 6.91$; $P < 0.002$). GSR peaked in the centrally-located parts of the region, in mesic Fynbos (Fig 1).

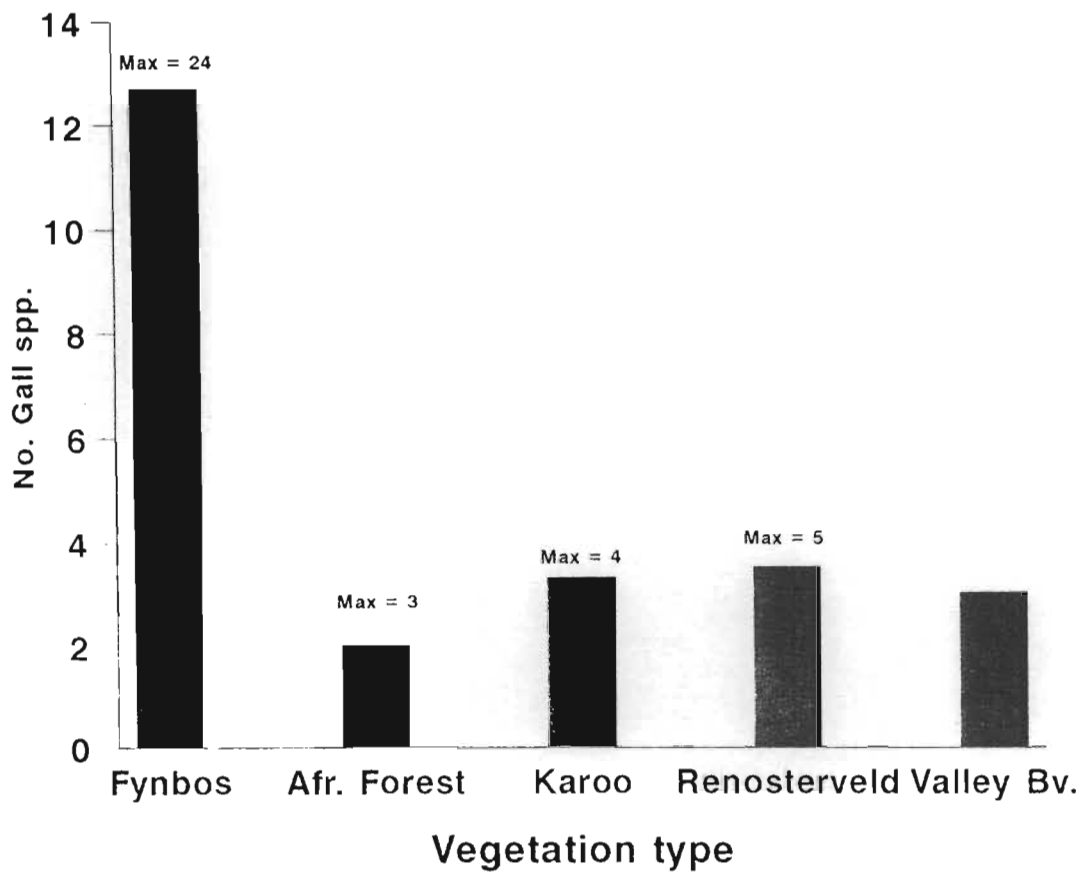


Figure 2. Average and maximum number of gall insects recorded in five vegetation types sampled in the Cape Floristic Region.

2) GSR was significantly positively correlated with plant richness for the CFR ($r = 0.91$; $P < 0.0001$) and for Fynbos alone ($r = 0.83$; $P < 0.0001$)(Fig. 3). Regression analysis indicated that variation in plant richness accounted for a substantial proportion of GSR

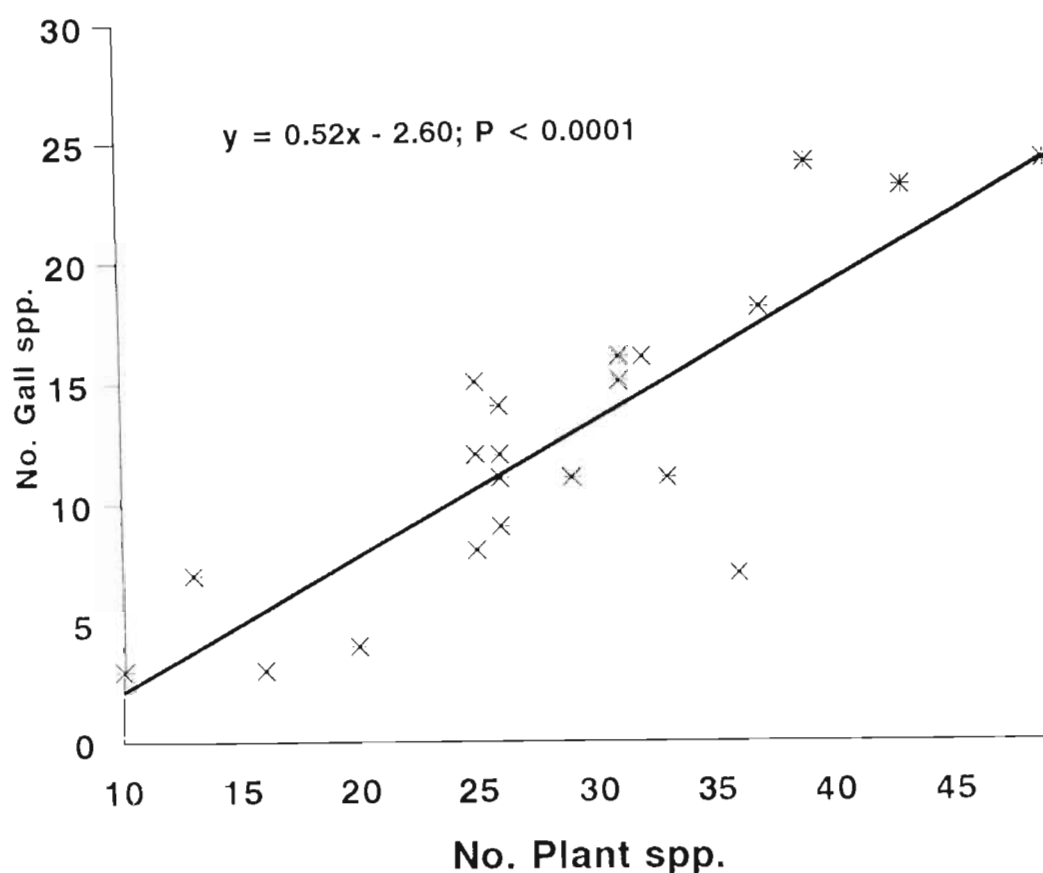


Figure 3. Correlation between gall-insect species richness (GSR) and plant richness in samples from Fynbos vegetation.

for all CFR vegetation ($y = 0.51x - 2.20$; $R^2 = 81.92\%$; $F_{1,30} = 135.93$; $P < 0.0001$) as well as for Fynbos only ($y = 0.52x - 2.60$; $R^2 = 68.39\%$; $F_{1,20} = 43.26$; $P < 0.0001$).

Regression analysis of ratio of GSR: plant richness as a variable dependent on plant richness showed that a multiplicative model ($y = 0.11x^{0.39}$; $P < 0.005$; $R^2 = 24.38\%$) best accounted for variability in the ratio. This indicates a "plateau" being reached by the ratio, i.e. GSR did not continue to increase in a linear manner, but levelled off at

high plant species richness levels. Spearman rank correlation analysis showed a significant correlation between the ratio and plant richness ($r = 0.45$; $P < 0.02$). Regression analysis for the Fynbos data alone indicated a non-significant linear relationship ($y = 0.31 + 0.004x$; $R^2 = 8.91\%$; $P = 0.18$), with a slope not significantly different from zero ($P > 0.05$) (Fig. 4). The Spearman's rank correlation was not significant for these data ($r = 0.27$; $P = 0.21$).

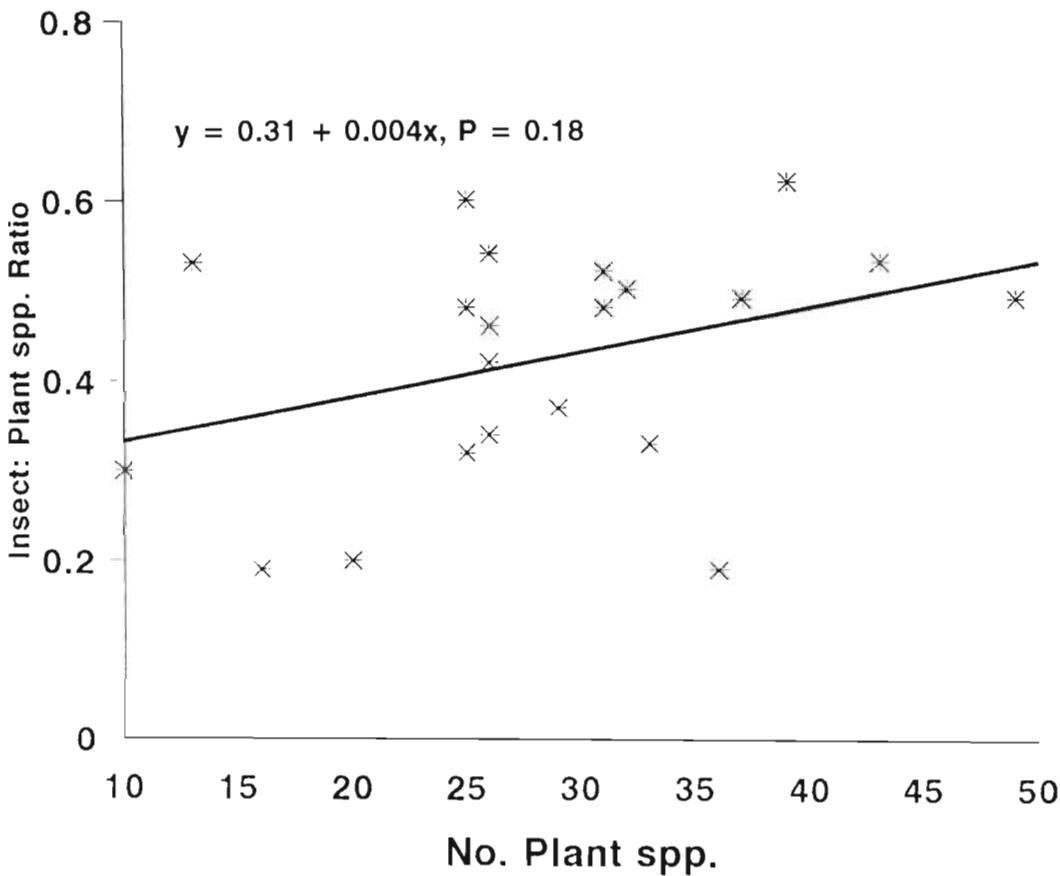


Figure 4. Ratio of gall-insect species richness (GSR): plant species regressed against plant richness.

3) Multiple factor (elevation and aspect) ANOVA for the Grootswartberg data showed a slight but non-significant increase in GSR with increasing elevation ($F_{1,3} = 5.12$; $P = 0.12$; Fig. 3), and no significant difference ($F_{1,1} = 4.77$; $P = 0.12$) in GSR on north- (avg

= 10.8 spp.) or south- (avg = 15.5 spp.) facing slopes (Tukey multiple range tests). Plant richness was significantly higher on south slopes (avg = 32.0 species) than on north slopes (avg = 20.8 spp., $F_{1,1} = 11.27$; $P < 0.05$). Plant richness increased significantly with elevation from dry to mesic mountain Fynbos ($F_{1,3} = 9.70$; $P = 0.05$). Ratio of GSR to plant richness, regressed as a dependent variable on plant richness, across the elevation gradient showed no significant correlation ($y = 0.55 - 0.002x$; $R^2 = 7.99 \%$; $F_{1,2} = 0.17$; $P = 0.72$).

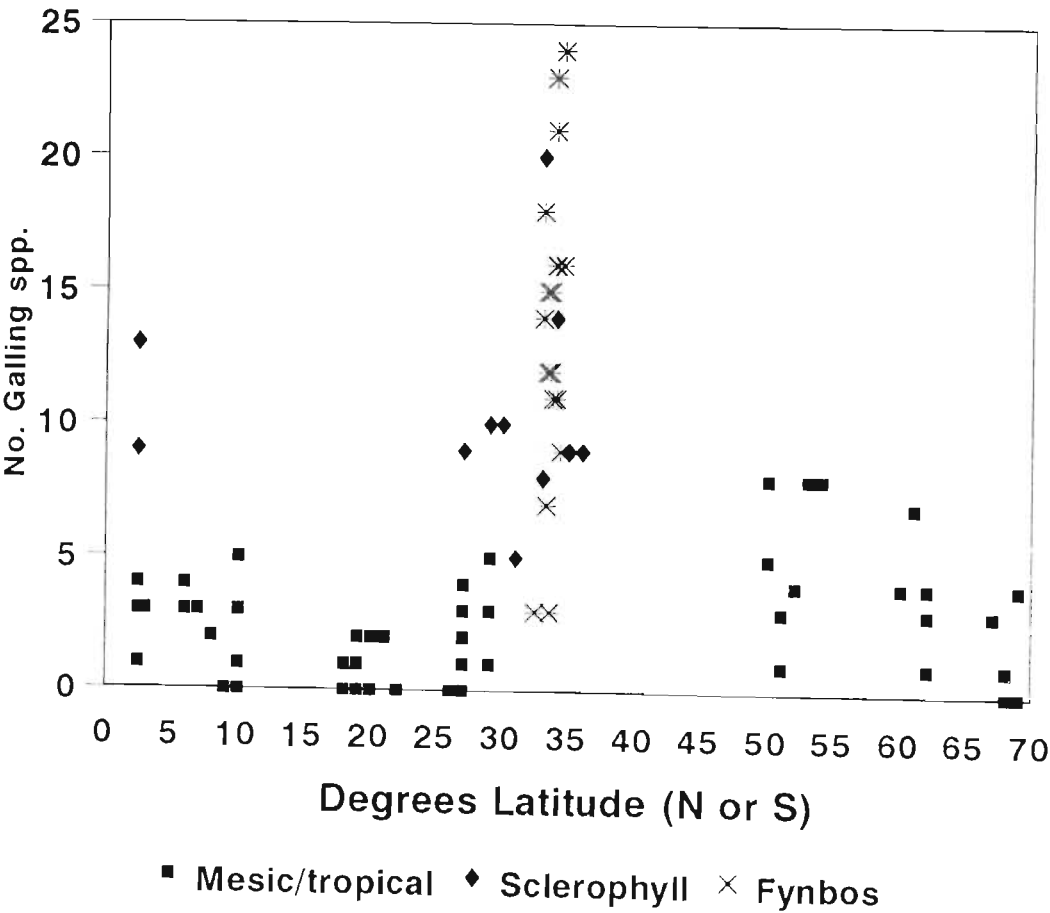


Figure 5. Global gall-insect species richness in a range of floras including Fynbos samples (additional data from Price 1991).

4) GSR was similar to other sclerophyllous floras in warm-temperate areas (Fig. 5), and higher than in most tropical areas, in counts of number of species made using standardized census techniques.

Discussion

Average gall-insect species richness (GSR) was disproportionately higher in Fynbos than in the other CFR vegetation types/phytochoria sampled. Maximum gall-insect species numbers in Fynbos were an order of magnitude higher than for any other CFR vegetation. This suggests that high plant richness, rather than xeric or sclerophyllous vegetation alone, generated the high GSR. This is further reinforced by the distribution of GSR in the Fynbos. Highest GSR was recorded in mesic-mountain Fynbos and limestone-Fynbos in the South Cape (Fig. 1). More xeric, dry-mountain Fynbos sites had intermediate GSR, similar to mesic-mountain sites east and west of the sites with highest GSR. The lowest GSR in Fynbos was recorded in the extreme north-west and east of the biome. If the CFR is divided into a western and eastern region (*sensu* Cowling & Holmes 1992), no significant difference in GSR is evident ($F_{1;20} = 0.61$; $P = 0.45$), because of the centrally-located peak in GSR. There was, however, a clear tendency for the southern mesic Fynbos sites to harbour the highest GSR.

The strong correlation between GSR and plant richness ($r = 0.91$) for the CFR, and for Fynbos alone ($r = 0.83$), is substantially greater than that reported by Fernandes & Price (1988, $r = 0.60$) for their USA samples. This suggests that plant richness in Fynbos may be more important than in other regions, in terms of generating gall insect diversity. This is supported by the fact that other xeric, sclerophyllous floras in the region (Karoo and renosterveld) did not exhibit high GSR.

GSR in the Fynbos contrasts markedly with the pattern described by Fernandes & Price (1988). They found that the pattern of increasing GSR with increasing hygrothermal stress (decrease in elevation), was evident even with no change in plant diversity - in many cases, a single species of plant harboured the majority of GSR in their samples in Arizona. This never occurred in Fynbos; most galled plants had only a single gall

species, and plants rarely had more than two gall species. This suggests that certain plant species were more suitable for gall insect utilization/radiation than others in the Arizona samples. Proportion of Fynbos plant species utilized by gallers was significantly more here in the Fynbos than in Arizona for 1200 m a.s.l. sites and with similar plant richness ($\chi^2 = 8.95$; $df = 1$; $P < 0.05$). However, when plant richness in the Arizona samples was low (4 spp.), proportion of galled species was equal to that of a Fynbos site at the same elevation (305 m) but with high plant richness (44 spp.) ($\chi^2 = 0.04$; $df = 1$; $P > 0.05$; data for Arizona calculated from Fernandes & Price 1988). This suggests that gall insects track plant richness in Fynbos, while this is not the case for the Arizona assemblage. This is further substantiated when the GSR to plant species richness ratio is correlated with plant richness. For all CFR vegetation types together, a plateau was approached, suggesting that galler richness was not reduced by very high plant richness, but increased multiplicatively in proportion to increasing plant richness (a negative relationship between ratio of insect to plant species vs. plant species richness would imply that GSR was lower at high plant richness, see Gaston 1992). The same analysis for the Fynbos data alone showed that there was no significant correlation between the GSR/plant species ratio and plant richness (the plateau in the CFR data set). This clearly indicates that in the plant species-rich Fynbos samples, galler richness increased at roughly the same rate as plant richness. GSR therefore tracks plant richness in Fynbos. These data suggest that plant richness, or the factors responsible for generating plant richness in Fynbos, were important in generating gall radiation.

Plant richness in Fynbos is considered to be largely the result of allopatric speciation in a topographically and edaphically complex region (Cowling & Holmes 1992). Fire may also have played a role in catalyzing speciation in Fynbos by causing vicariance (Cowling 1987), as well as biological factors such as short-distance seed dispersal (Slingsby & Bond 1985) and limited pollen dispersal (Linder 1985, Wright *et al.* 1988, 1991). Insect speciation may have been a response to topographical (geographical) isolation as well as disturbances like fire, or may be the result of host shifts onto new plants which developed as the result of a range of selective forces. Both geographical isolation (Mayr 1963) and genetic differentiation on different hosts (Guttmann *et al.* 1981) are plausible sources of evolutionary change in insects. Gall insects in Fynbos may have radiated

together with their host plants, in which case, high rates of plant speciation in the Fynbos would have generated high GSR, rather than this being simply a response to xeric conditions, which are conducive to gall insect radiation (Fernandes & Price 1991).

The elevation gradient surveyed for GSR showed no significant effect. This may be because it was a relatively short gradient of 1100m, in contrast with those analyzed by Fernandes, Lara & Price (1994) and Fernandes & Price (1988). There was a tendency (albeit non-significant) for GSR to be higher in the more mesic, higher elevation samples, which also had higher plant richness. A smaller variation in vegetation types was also included in the present study than other similar studies. Fernandes & Price (1988) included a wide range of vegetation types. It is possible that vegetation types are differentially susceptible to gall insects, which would explain why an elevational gradient within Fynbos shows less variation than a gradient including desert, chaparral, pinyon/juniper, pines, firs and tundra (see Fernandes & Price 1988). The tendency for GSR to track plant richness along the gradient reinforces the proposal that plant richness and/or its evolution, rather than contemporary ecological conditions, has been important in generating GSR.

The fact that GSR in Fynbos falls within the range expected for warm temperate vegetation (Price 1991), lends support to the hypothesis that sclerophyllous floras in these regions will have high GSR globally. This shows that Fynbos, while considered to be relatively depauperate in endemic, plant-associated ectophagous insects (Cottrell 1985), is likely to be a centre of considerable endemism in terms of gall insects. Gall insects are generally highly host-specific (Ananthakrishnan 1984), which suggests that the GSR recorded here in the Fynbos is a reflection of the turnover in plant community composition. This would imply a high degree of endemism in many areas, considering the high level of host-fidelity exhibited by gall insects.

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CHAPTER 6

GALL-INSECT SPECIES RICHNESS IN AFRICAN FYNBOS AND KAROO VEGETATION: THE IMPORTANCE OF PLANT SPECIES RICHNESS.

Summary

1. The hypothesis that the plant-species rich Fynbos and the less-rich Little Karoo, both xeric ecosystems in South Africa, would support equal levels of gall-insect richness (GSR) was tested.
2. Galls were sampled from Fynbos and Karoo in a valley where adjacent sites with similar climate could be selected.
3. Fynbos had higher GSR, strongly correlated with plant richness.
4. Both Fynbos and Karoo vegetation had galls in equal abundance (galls/plant) showing that neither was a more suitable substrate for colonization by gall insects, but differed in terms of species richness only.
5. Plant species richness, or the distal factors that generated it, appear to have contributed significantly to the radiation of gall insects in these regions.

Introduction

Gall-inducing insects have been the subjects of a range of studies investigating global patterns of species richness and the environmental gradients influencing species richness (see Price 1991 and Fernandes *et al.* 1994 for reviews). These studies have consistently shown that environmental harshness (hygrothermal stress associated with decreasing elevation) and sclerophylly account for the most variation in gall-insect species richness (GSR). Other variables, such as plant species richness and the regulating effects of natural enemies, are considered to be of lesser importance in explaining gall richness and radiation (Fernandes & Price 1988, Waring & Price 1989).

The data indicating harshness as primary generator of GSR were collected in a range of floras, from desert to alpine tundra (Fernandes & Price 1988). Yet the range of floras investigated may have had different evolutionary histories, which may have played an important role in generating/limiting gall-insect radiation. The strong correlation between GSR and plant richness was considered by Fernandes & Price (1988) to have little explanatory value as a force generating gall diversity. Their data showed that most GSR was often supported by a single plant species in a community, and followed a consistent pattern across the elevational gradient they analyzed, irrespective of change in plant diversity.

Historic factors shaping a flora in terms of types (physiognomy) of plants and species compositions of plant communities are as important as contemporary ecological variables, and should be considered when attempting to establish what has led to the generation of species richness (e.g. Ricklefs 1987). To investigate the role of plant richness (or the factors that allowed plant richness to develop), as a factor generating GSR, it is necessary to compare GSR from speciose and non-speciose floras that evolved under relatively similar environmental conditions.

The Fynbos, containing the Capensis elements of the Cape Floristic Region (southwestern Cape, South Africa), and the Karoo (arid semi-desert adjacent to Fynbos), have relatively similar histories: both appear to have undergone geologically recent speciation under recent climatic change and alternating wet and dry climatic conditions

during the Quaternary period (Axelrod & Raven 1978). Fynbos underwent far more dramatic plant speciation in response to edaphic complexity, fire and topographic variation than did the arid Karoo, and consequently has a considerably higher species richness (Gamma diversity). Interestingly, the environmental fluctuations that Fynbos plants were subjected to appears to have increased richness, rather than limit it, as would normally be expected (Tilman & Pacala 1993). Karoo vegetation receives far lower rainfall than Fynbos (Cowling & Holmes 1992) and is of a distinct xeric nature.

A previous study (Chapter 5) of gall-insect species richness (GSR) in the Cape Floristic Region (CFR) and Fynbos alone has shown that Fynbos supports higher GSR than other CFR phytochoria, and that GSR tracks woody plant richness in Fynbos closely. Study sites included in this study were from a wide range of climatic conditions and vegetation types. The results of this work led to the proposal that gall insects had radiated as a response to floral radiation of the Fynbos. This is in contrast to previous work in temperate and tropical regions (Fernandes & Price 1988, Price 1991), which indicated that GSR was primarily a response to xeric conditions, with sclerophyllous vegetation being particularly favourable for gall insect radiation. Plant richness was not considered to have played an important role.

The aim here was to compare GSR in two floras with similar contemporary (xeric) climate, located geographically as close together as possible, but with different levels of plant-species richness. The null hypothesis that GSR would be equal in both vegetation types was tested.

Materials & Methods

Study site: The study was conducted in the Anysberg Nature Reserve (33°29'S, 20°42'E), located in the Little Karoo in South Africa, with remnant patches of Fynbos on top of mountains and adjacent to Karoo vegetation in valleys. This provided the opportunity to compare GSR in Fynbos and Karoo located close together and under very similar climatic conditions. Sampling sites were located adjacent to each other in a shallow valley, so that samples could be taken in both vegetation types at the same elevation.

Gall insect sampling procedure: Six samples of 100 plants each were taken at corresponding elevations opposite each other in Fynbos and Karoo vegetation. Plants were sampled randomly along transects *ca.* 10 m wide and *ca.* 30 m long at each sampling point. Only woody shrubs were sampled in both vegetation types. This was because semi-arborescent growth forms (e.g. *Protea* spp. in Fynbos) were absent from the Karoo sites. Gall species were separated and counted on the basis of host-plant and gall morphology (Cornell 1985, Waring & Price 1989). Number of galls per plant species were recorded for each plant sampled, to establish whether either of the vegetation types was more susceptible to gallers.

A random sample of plant material was taken at each sampling site. These samples were analyzed for nitrogen and phosphorous content (Routine plant & soils analysis protocols, Agricultural Research Council). A soil sample was also taken (to a depth of *ca.* 200 mm, deeper sampling was limited by rocky soils) at each site, and analyzed for nitrogen and phosphorous content. This was done to establish whether there were any differences in nutrients for the sample sites and vegetation. Soil fertility is an important variable with which high GSR may be correlated (Blanche 1994).

GSR and plant species richness was compared by ANOVA for the two vegetation types sampled. The relationship between GSR and plant richness was analyzed using linear regression. Nutrient levels for soils samples were analyzed by Kruskal-Wallis single factor ANOVA (Zar 1984).

Results

Average number of gall species and average number of plant species were significantly higher in the Fynbos samples (Table 1). Approximately twice as many plant and gall-insect species were recorded for the Fynbos samples. The nutrient characteristics of the sites were similar for soil and plants (Table 1).

GSR was positively correlated with woody shrub richness ($y = 1.07 + 0.44x$; $R^2 = 54.78\%$; $r = 0.74$; $P < 0.05$), with a highly significant slope ($b = 0.44$; $t = 3.48$; $P < 0.007$) (Fig 1).

Table 1. Average numbers (± 1 s.e.) of gall species (per 100-plant sample), plant species and soil and plant nutrient data for Fynbos and Karoo sites

Variable	Vegetation type		ANOVA
	Fynbos	Karoo	
Gall spp. (No.)	9.8	5.2	$F_{1,10} = 11.33$
(GSR)	(1.2)	(0.7)	$P < 0.008$
Plant spp. (No.)	19.5	10.0	$F_{1,10} = 32.40$
	(1.5)	(0.7)	$P < 0.0002$
Soil (% N)	0.05	0.03	$U = 3.0$
			$P > 0.07$
Soil P (mg.kg ⁻¹)	8.00	8.50	$U = 0.0$
			$P > 0.10$
Plant (% N)	0.61	0.69	$F_{1,10} = 3.90$
	(0.32)	(0.30)	$P = 0.08$
Plant P (mg.kg ⁻¹)	0.25	0.27	$F_{1,10} = 0.17$
	(0.003)	(0.002)	$P = 0.69$

Galls were equally abundant in both vegetation types ($t = 0.02$; $df = 26$; $P > 0.05$, Fig. 2). The majority of plants were not galled (*ca.* 80 % free of galls) in both vegetation types. Most plants had 1 - 3 galls, with individual Karoo plants harbouring up to 38 galls each.

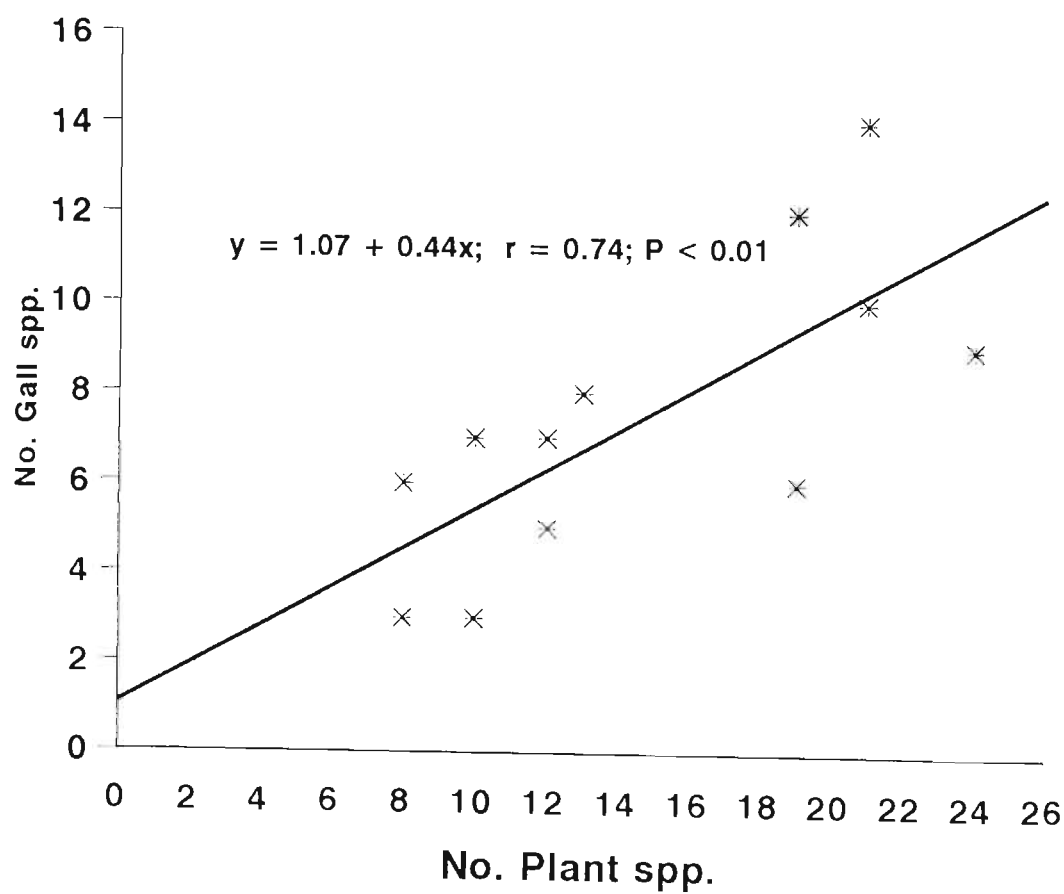


Figure 1. Gall-insect species richness (GSR) plotted against woody shrub richness for Fynbos and Karoo sites in the Anysberg Nature Reserve.

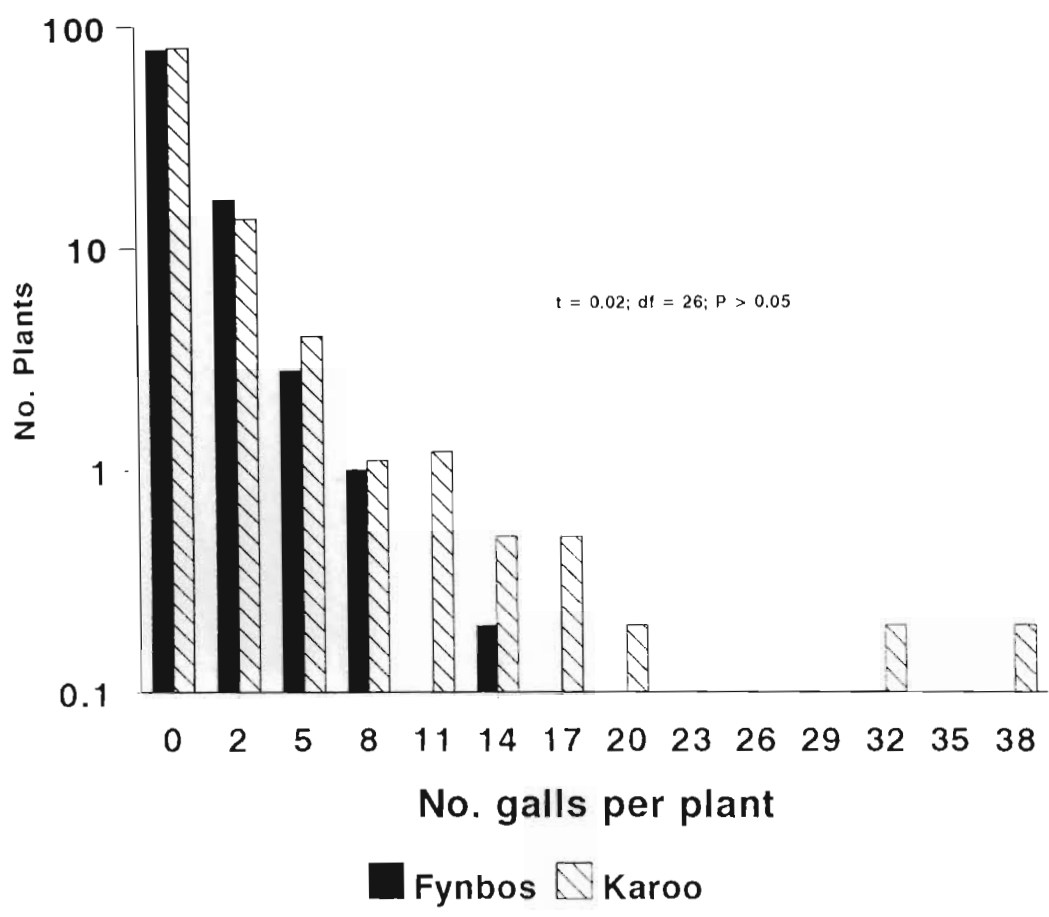


Figure 2. Frequency distribution of gall-insect abundance on Fynbos and Karoo shrubs.

Discussion

These results show clearly that GSR was correlated with plant richness in the study sites. This corroborates the proposal (Chapter 6) that, although xeric, sclerophyllous conditions have been favourable for radiation of gall insects globally (Fernandes *et al.* 1994), the role of host-plant diversity should not be discounted in explaining GSR. Plants in the two vegetation types sampled in this study were equally prone to attack by gall insects (albeit different species), so it is unlikely that either was a more suitable resource for gall insects. Neither was there any significant difference in soil and plant nutrient status in the study sites. This suggests that historical factors, rather than contemporary ecological variables, were responsible for generating higher GSR in the Fynbos. More conclusive of the closeness of insect-plant evolution evidence should be obtained if historical factors are taken into account together with a phylogenetic study of the insects associated with the plants, and of the plants themselves. This will confirm whether any correspondence between the insect and plant cladograms is evident (Farrel & Mitter 1993).

Cowling (1987) and Cowling *et al.* (1992) have suggested that fire and other conditions in Fynbos could have resulted in strong disruptive selection resulting in rapid evolution of isolated plant populations into different species. Gall insects are likely to be influenced by the same variables. As gall insects have considerably shorter life cycles than their host-plants and are extreme habitat specialists, they are likely to undergo speciation at least as rapidly as their Fynbos hosts. The possible importance of plant diversity as a primary factor contributing to the generation and maintenance of GSR is underscored by the results obtained here. No implication of coevolution, where insects place selective pressures on their host plants with reciprocal defence against the insects (Janzen 1980) is made here, but the disruptive selection that is imposed by intimate association with plants in a varying environment is likely to lead to plant-mediated divergence.

Cowling (1978) also noted that post-fire extinction of plant populations is a common phenomenon. This has enormous implications for insects which are intimately associated with plants, as they are likely to be even more susceptible to extinction by fire than plants (Wright 1993). Tscharntke (1994) has presented evidence suggesting that gall

insects require high population numbers to remain viable in an area. This means that gall insects are very sensitive to plant population fluctuations, and that management burning (van Wilgen *et al.* 1992) of small plant populations in Fynbos could result in local extinction of gall insects associated with them. This is particularly relevant in the case of host plants that have become restricted in distribution as a result of population or landscape fragmentation. For example, unidentified Cecidomyiidae occur in only a few populations of the rare host plants, *Audouinia capitata* (Bruniaceae) and *Heliophylla cineria* (Brassicaceae) (J.H. de Lange, pers. comm. and personal observation, M.G. Wright).

Another important consideration is that a proteaceous overstorey Fynbos communities greatly reduces the number of shrub species in the understorey (Cowling & Gxhaba 1990). Recurrent management burning of an area applied at a particular time of year (autumn, the season most beneficial for *Protea* regeneration from seed) can result in domination by Proteaceae (van Wilgen *et al.* 1992). This clearly has negative implications for the maintenance of GSR in an area.

This study has shown that GSR in Fynbos is more likely to be the result of plant radiation within a xeric, sclerophyllous flora, than any other factor. Similar patterns should be sought in other species-rich, sclerophyllous vegetation to further test this hypothesis globally.

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GENERAL CONCLUSIONS

The central objective of this study was to investigate species richness of endophagous insects associated with Fynbos plants. The influence that plant attributes may have on insect assemblages as well as correlations between plant species richness and endophage species richness were given special attention. Five separate key questions were addressed:

1. Are a greater number of insect species associated with Proteaceae in Fynbos than in other regions where this family is less speciose?
2. Are borers associated with *Protea* species in Fynbos influenced by climate, biotope or host-plant characteristics?
3. Does the sclerophyllous Fynbos vegetation harbour a higher number of endophagous insect species than ectophagous insect species?
4. Is gall-insect species richness (GSR) correlated with plant species richness in the Fynbos, and how does GSR in Fynbos compare with other vegetation types, regionally and globally?
5. Does Fynbos vegetation, with high species richness, host more gall-insect species than similarly sclerophyllous, yet less speciose Karoo vegetation under similar climatic conditions?

The first key question was devised to compare regional insect species richness on a plant family (Proteaceae) that occurs in Fynbos (with numerous species), to non-Fynbos species from areas with lower Proteaceae richness. The intention was to discover whether the more speciose Fynbos Proteaceae hosted a greater number of endophage species. This was indeed the case, with Fynbos Proteaceae hosting more than twice as many taxa as the more northern *Protea* species. This suggests that the profusion of Proteaceae species in the Cape vegetation may have contributed to generating high endophage richness.

The potential that *Protea* species may have as evolutionary islands to insects associated with them was considered in Chapter 3, where it was demonstrated that variation in borer assemblages was primarily accounted for by host-plant characteristics, rather than

climatic or biotope variables. Plant characteristics therefore played an important role in mediating insect abundance. This effect may have provided disruptive selective influences on insects, which may have led to host-plant mediated differentiation in the insects.

Vegetation-effects on endophagous insects was investigated by quantifying the species richness of endophages relative to ectophagous insects (Chapter 4) and the relationship between endophage richness and plant species richness (PSR) (Chapters 5 & 6). These studies showed that more species of endophagous insects (Diptera: Cecidomyiidae) than ectophagous species were associated with the vegetation. Furthermore, Fynbos supported more species of gall-insects than other Cape Floristic Region vegetation types. There was a strong positive correlation between GSR and PSR, and the ratio of gall-insect species to number of plant species remained constant with increasing PSR. This shows that GSR tracks plant richness. It is plausible that the gall-insects radiated in response to high PSR and the selective agents that generated it. GSR in Fynbos was found to be similar to GSR in other sclerophyllous vegetation-types globally, underscoring the importance of this type of vegetation in generating GSR.

The importance of PSR as a factor generating GSR was accentuated by results showing that GSR was correlated with PSR in vegetation type with low and high PSR, under similar climatic conditions. These data therefore show that high PSR has contributed to the development of high GSR.

Although Fynbos has characteristics (e.g. low spatial apparancy, disturbance by fire, low nutrient status) that should have moderated the evolution of a rich insect fauna, this study has shown that endophagous insects were more speciose in Fynbos than in adjacent vegetation types. Even plant families that occur in Fynbos and in other biomes harboured more species in Fynbos. It was also shown that borers responded to plant characteristics primarily, rather than climatic, or other ecological variables. The importance of high PSR in generating endophagous insect species richness is thus emphasized.

Various applications may be developed from these findings. A substantial industry is based on the cultivation of Fynbos plants for export as cut flowers. Insects are a major restraining factor in this industry, as they reduce yields and pose a phytosanitary risk. This study has shown that insect borer numbers on *Protea* species vary in response to plant characteristics. This information may be of value in terms of developing new *Protea* cultivars with borer resistance. Numerous gall insects with potential to become phytosanitary pests were also recorded from plants that are commonly grown commercially.

The conservation of insects as a significant components of biodiversity has recently become recognized as an important goal. The intrinsic value of insects as participants in ecological processes aside, it is also recognized that they should be given special attention in conservation programmes as constituents of the biosphere. This suggests that insect conservation *per se* is of cardinal importance. However, as the ecology of most Fynbos insects is unknown, their ecological needs are not taken into account in conservation management planning. This study has shown that Fynbos not only harbours a large number of endophagous insect species, but they are also influenced profoundly by their interactions with the vegetation. As disturbances in Fynbos (e.g. management burning, agriculture, invasive weeds) can severely alter plant communities, they are also likely impact significantly on insects dependent on certain plants in these communities. It is therefore important that ecosystem-based strategies, including the requirements of insects should be considered when management decisions are made. This study has shown, for example, that the taxonomic structure of a plant community influences the occurrence of borers exploiting *Protea* species, and that gall-insect species richness is determined by local plant-species richness. These insects may be deleteriously influenced if management decisions are based solely on considerations addressing plant conservation. Insect conservation in Fynbos needs to be recognized as a management aim in its own right.

Furthermore, this work has shown that plant-species richness is a factor which can not be rejected when attempting to explain the evolution of a rich endophagous entomofauna. The possibility of host-plant mediated race-formation and speciation

having occurred in Fynbos deserves further attention. Elucidation of this process will not only contribute to the understanding of insect evolution, but will also provide further information relevant to the management of insects in specific agricultural systems and conservation areas.

...Ticking away the moments that make up a dull day
Waiting for something or someone to show you the way...

You run and you run to catch up to the sun
But it's spinning around and coming up behind you again...

The sun is the same in a relative way,
But you're older, shorter of breath
And one day closer to death...

(Roger Waters, Pink Floyd - Dark Side of the Moon)