Mark G. Wright · Michael J. Samways

Insect species richness tracking plant species richness in a diverse flora: gall-insects in the Cape Floristic Region, South Africa

Abstract The Cape Floristic Region (CFR) is one of the most plant-species-rich regions in the world. It is also a warm temperate region and hypothetically should have high gall-insect species richness, making it interesting to investigate the relationship between the insects of the region and the rich flora. 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. 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. Fynbos harboured significantly more gall-insect species than other CFR vegetation types. 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. Fynbos GSR is comparable to other sclerophyllous regions of high GSR globally, corroborating that this vegetation type is conducive to gall-insect diversification. There is likely to be a high percentage of gall-insect endemism in the Fynbos, as might be expected from the high host fidelity of this insect group.

Key words Gall-insects · Cape Floristic Region · Fynbos · Species richness

M.G. Wright (✉)
Agricultural Research Council,
Roodeplaat Vegetable and Ornamental Plant Institute,
Private Bag X1, Elsenburg 7607, South Africa

M.J. Samways
Invertebrate Conservation Research Centre,
Department of Zoology and Entomology,
University of Natal, Private Bag X01,
Scottsville 3209, South Africa
Fax: + 27 21 8085440; e-mail: mark@igs5.agric.za

Introduction

Sclerophyllous vegetation around the world tends to harbour high gall-insect species richness (GSR) (Fernandes and Price 1991). This pattern has been attributed to the capacity of this guild of insects to circumvent nutritional and/or toxic restrictions of sclerophyllous plants (Cornell 1989), as well as to the availability of a safe and predictable environment in the form of long-lived leaves and stems, and to the negative influence that xeric conditions have on natural enemies (parasitoids and entomo-pathogenic fungi, Fernandes and Price 1991; Waring and Price 1989). Globally, xeric, sclerophyllous floras harbour the most taxonomically diverse gall faunas (Price 1991), a pattern which Fernandes et al. (1994) attributed to environmental harshness, i.e. thermohygral stress/elevation. A strong positive correlation between GSR and plant richness has already been documented for the Unites States (Fernandes and Price 1988), but was rejected as a factor explaining or generating the evolution of gall diversity. Plant species richness was rejected because the patterns observed prevailed even in samples with no change in plant-species richness, where single plant species hosted numerous gall-insect species. As most galler richness in the study of Fernandes and Price (1988) was supported by only one plant species at many of their sites, certain plant taxa may have been conducive to galler radiation, rather than plant richness generating gall-insect diversity.

The hypothesis that the factors which generated high plant richness would also contribute to the evolution of gall-insect 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 and Docters van Leeuwen (1926) were analysed 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. This tendency for sclerophyllous vegetation types is attributed to gall insects being able to concentrate nutrients in galls (thus circumventing low nutrient levels), fungal pathogens being scarce in these habitats and persistence of plant parts (Fernandes and Price 1991). However, certain characteristics of fynbos may have militated against the evolution of a rich gall insect assemblage. In particular, the plant species richness of fynbos is exceptionally high (Cowling et al. 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 large areas of resources due to combustion may also make the flora less suitable as a resource for gall-insects. It is also possible that plants resprouting after fire may provide a valuable resource to gall-insects utilizing leaves (Vleira et al. 1996). Plant predictability in time and space have been postulated to be important attributes for the evolution of gall-insect richness (Fernandes and Price 1991). However, the highly diverse, xeric, sclerophyllous, nutrient-impoverished nature of fynbos makes it a potentially suitable substrate for a diverse gall fauna. An overall impression of average numbers of plant species for each vegetation category in the CFR is given in Table 1; note that Table 1 includes all growth forms (e.g. geophytes), while the present study only considered shrubs. Fynbos has a greater number of shrub species than any other of the vegetation types listed. 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.

Table 1 Average number of plant species in various vegetation types within the Cape Floristic Region, for 1000-m² plots. Standard errors are given in parentheses, where available. Data are from Cowling et al. 1992 and Geldenhuis and MacDevette 1989

Vegetation type	Number of plant species
Fynbos – west	66.5 (20.6)
Fynbos – south	64.5 (16.8)
Fynbos – east	66.2 (15.0)
Renosterveld shrublands[a]	84.2 (29.8)
Karroid shrublands – west[b]	71.0 (23.6)
Karroid shrublands – east[b]	55.9 (8.7)
Valley bushveld	58.7 (18.3)
Afromontane forest – southwest[c]	17.0

[a] Dominated by geophytes in terms of richness (Moll et al. 1984)
[b] These values include succulents and geophytes, a substantial proportion of the diversity
[c] Data for 100-m² plots

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 vegetation types.

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

Gall-insect species richness

GSR was sampled throughout the CFR in the following vegetation categories (Moll et al. 1984): mesic (seasonally waterlogged) and dry mountain fynbos; limestone lowland fynbos; renosterveld; valley bushveld; Afromontane forest and karroid shrublands. Estimates of GSR were made using a modification of the method of Fernandes and Price (1988), sampling up to 600 shrubs per transect because of high plant species richness. Only shrubs were sampled in all categories except Afromontane forest, where trees were sampled as well. The architecture of the shrubs sampled was similar in each vegetation type, viz. shrubs no taller than 1.2 m with typically small, sclerophyllous leaves. Gall species were counted by searching entire plants for the presence of insect galls. Plants were searched with great care, so that inconspicuous galls were detected. Voucher specimens of all galls collected are deposited in a collection at Elsenburg, South Africa. Recognizable taxonomic units (RTUs, Beattie and Oliver 1994) of gall-insects were separated on the basis of gall morphology and host-plant species (Ananthakrishnan 1984; Cornell 1985). Galls with similar morphology on closely-related sympatric host plants (e.g. similar *Erica* spp., Ericaceae) were considered to be con specific (this occurred in few cases, and no more than one species per transect was excluded in this way). Samples of 300–600 randomly selected woody shrubs were examined at Fynbos sites along transects c. 10 m wide. This sample size was considered adequate as species-effort curves for plants were generally saturated at 300–400 plants sampled (Fig. 1). Only 300 karoo shrubs and renosterbos shrubs were sampled per transect as the plant species richness (excluding geophytes and succulents, i.e. shrubs only) in these vegetation types was approximately half that of fynbos. In three cases, only 300 shrubs were sampled for fynbos. Species-effort curves of GSR were saturated after 300–400 plants were sampled (Fig. 2); Mann-Whitney tests indicated that 300 plant samples were not significantly different ($P > 0.05$) from 600 plant samples, and for these reasons where only 300 plants were sampled are included in this study. Valley bushveld and Afromontane forest were sampled by examining the accessible canopy (usually up to c. 1.8 m) of 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, and that time spent searching was equal to that in fynbos. On one occasion, 150 trees were sampled in forest, but this yielded results that were no different to sampling only 30 trees. Random selection of plants was done by 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 Species-effort curves for number of plants collected per transect for four sites with medium to high plant species richness
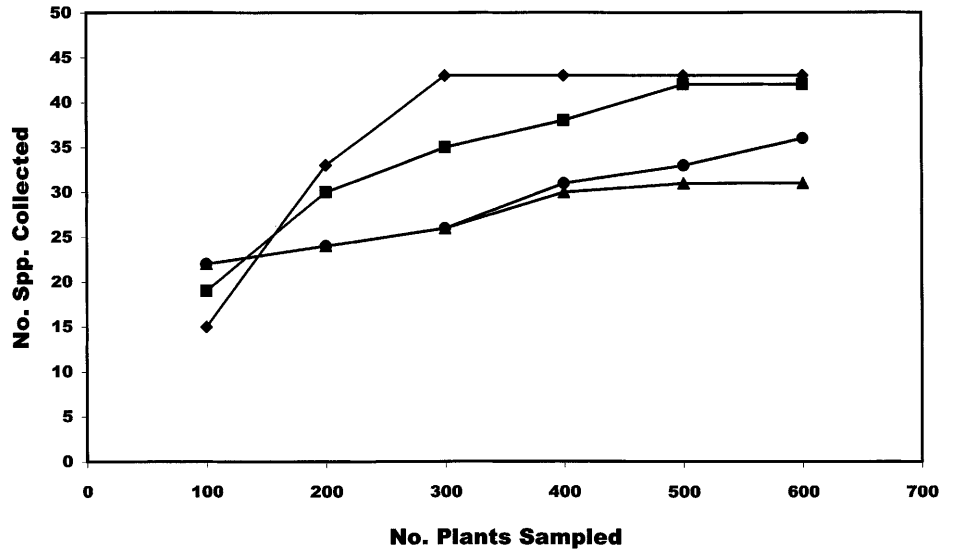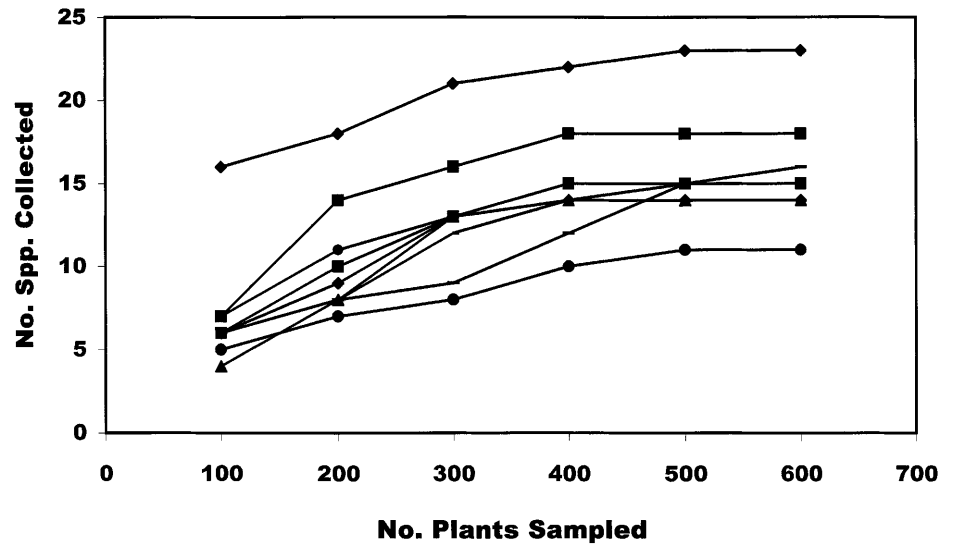

Fig. 2 Species-effort curves for number of gall insect species collected on five transects with high and low gall-insect species richness (GSR)

(Fig. 3) 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.

Relationship between GSR and plant species richness

Regressions and correlations between GSR and plant species richness were calculated for all vegetation-type samples together and separately for 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).

Environmental gradients

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
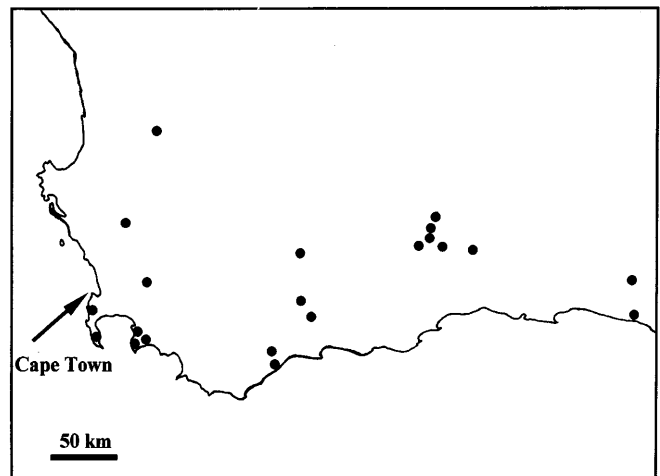

Fig. 3 Distribution of sites sampled for gall-insect richness (GSR) in the Cape Floristic Region (CFR, fynbos sites only)

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.

Comparisons

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

Results

GSR in the CFR

The majority of galls recorded were caused by Cecidomyiidae (Diptera), with Tephritidae (Diptera), Buprestidae (Coleoptera), Apionidae (Coleoptera), Psyllidae (Hemiptera) and Cynipidae (Hymenoptera) galls being rare. Fynbos harboured significantly higher average number of gall-insect species than other CFR vegetation types ($F_{3;27} = 6.91$; $P < 0.002$). Overall average numbers of species of gall-insect recorded for the various components of the CFR are shown in Fig. 4. GSR peaked in the centrally-located parts of the region, in mesic fynbos of moderately high plant species richness. If the CFR is divided into a western and eastern region (*sensu* Cowling and 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.

Relationship between GSR and plant species richness

Regression analysis indicated that variation in plant richness accounted for a substantial proportion of GSR for all CFR vegetation ($y = 0.51x - 2.20$; $r^2 = 81.9\%$; $F_{1;30} = 135.93$; $P < 0.0001$) as well as for fynbos only ($y = 0.52x - 2.60$; $r^2 = 68.4\%$; $F_{1;20} = 43.26$; $P < 0.0001$; Fig. 5). Regression analysis of ratio of GSR: plant richness as a variable dependent on plant richness showed that a multiplicative model ($y = 0.11x^{0.39}$; $P < 0.005$; $r^2 = 24.4\%$) best accounted for variability in the ratio. This indicates that the ratio reached a "plateau", i.e. GSR did not continue to increase in a linear manner, but levelled off at high (>30 species) 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 (the "plateau" referred to above) indicated a non-significant linear relationship ($y = 0.31 + 0.004x$; $r^2 = 8.9\%$; $P = 0.18$), with a slope not significantly different from zero ($P > 0.05$). The Spearman's rank correlation was not significant for these data ($r = 0.27$; $P = 0.21$).

Environmental gradients

Multiple factor (elevation and aspect) ANOVA for the Grootswartberg data showed a slight but non-significant increase in GSR with increasing elevation ($F_{1;3} = 5.12$; $P = 0.12$), and no significant difference ($F_{1;1} = 4.77$; $P = 0.12$) in GSR on north- (mean = 10.8 species.) or south- (mean = 15.5 species) facing slopes (Tukey multiple range tests). Plant richness was significantly higher on south slopes (mean = 32.0 species) than on north slopes (mean = 20.8 species, $F_{1;1} = 11.27$; $P < 0.05$). The ratio of gall-insect species to plant species remained relatively constant, however (north: 0.52; south: 0.48). 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

Fig. 4 Average (±SE) numbers of gall insects recorded in five vegetation types sampled in the Cape Floristic Region ($F = 691$; $P < 0002$)
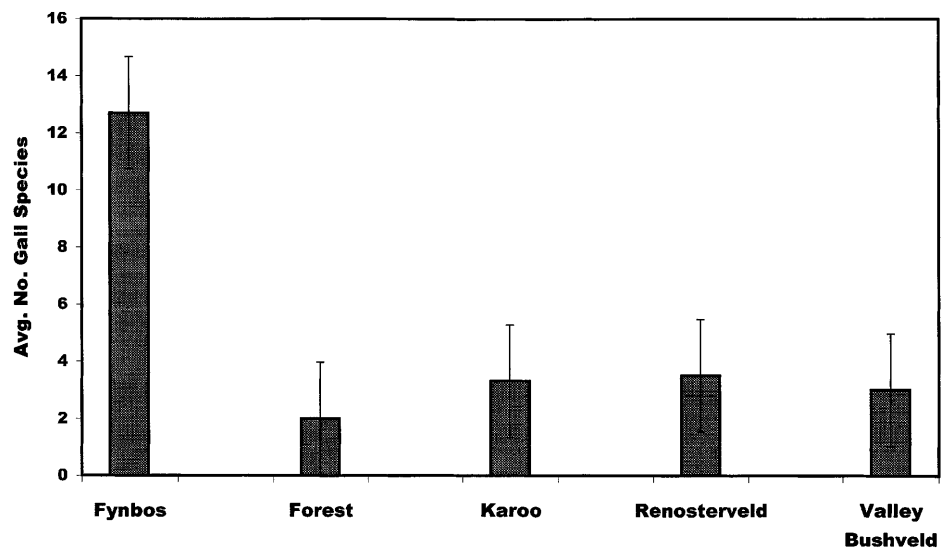
Fig. 5 Relationship between gall-insect species richness (GSR) and plant richness in samples from Fynbos vegetation ($y = 0.52x - 2.60$; $r^2 = 68.4\%$; $F = 43.26$; $P < 0.0001$)
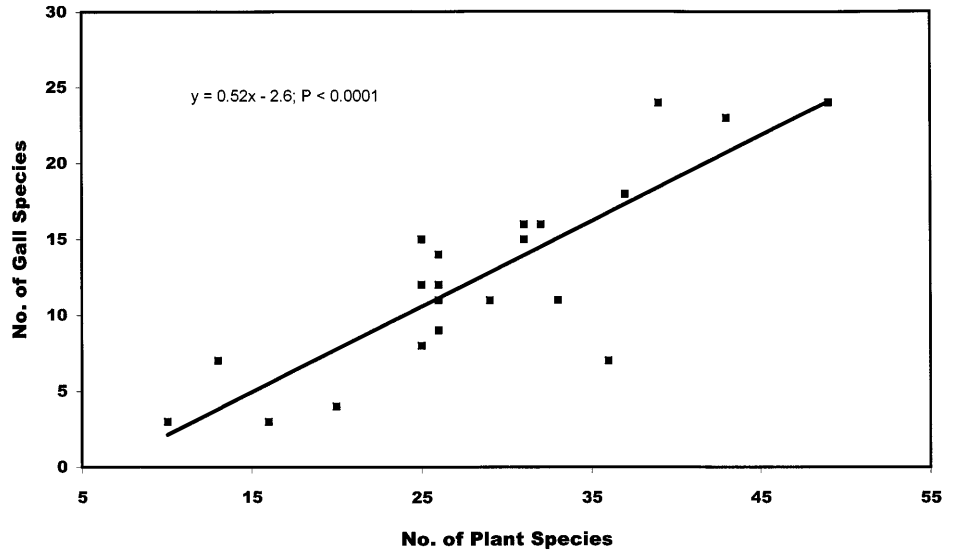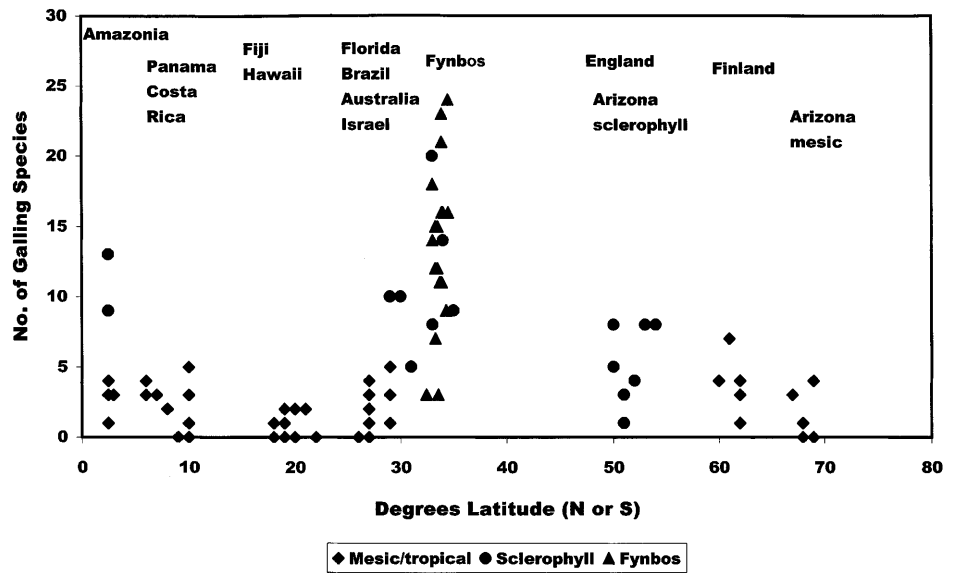

Fig. 6 Global gall-insect species richness in a range of floras including Fynbos samples (additional data from Price 1991). Geographic locations where groups of samples were taken (Price 1991) are shown. *Arizona mesic* samples are data for samples corrected latitudinally for height above sea level

correlation ($y = 0.55 - 0.002x$; $r^2 = 7.99\%$; $F_{1;2} = 0.17$; $P = 0.72$), again indicating that number of gall-insect species increased proportionally with number of plant species.

Comparisons

GSR was similar to other sclerophyllous floras in warm-temperate areas (Fig. 6), 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 considerably 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 conditions 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. 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. This supports the hypothesis that GSR in fynbos is a response to plant species richness rather than other environmental variables, with the species rich, but more moist centrally located sites harbouring highest numbers of gall-insect species. It has been shown that high plant species richness in fynbos is strongly correlated with availability of moisture (Linder 1991).

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 and Price (1988, $r = 0.60$) for their United States 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 and 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. In contrast, fynbos plants generally had only a single gall species, and plants rarely had more than two gall species. The fact that certain plant species harboured the bulk of GSR in many Arizona samples suggests that certain plant species were more suitable for gall-insect utilization/radiation than others at these sites. The proportion of fynbos plant species utilized by gallers was significantly higher than in Arizona for sites 1200 m a.s.l. 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 species), proportion of galled species was equal to that of a fynbos site at the same elevation (305 m) but with high plant richness (44 species) ($\chi^2 = 0.04$; $df = 1$; $P > 0.05$; data for Arizona calculated from Fernandes and Price 1988). The more equable distribution of gallers on host plants in fynbos suggests that gall-insects track plant richness in fynbos, while this is not the case for the Arizona assemblage. Equable distribution of gall-insect species on fynbos plants 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 at very high plant richness, but increased multiplicatively in proportion to increasing plant richness (a negative relationship between ratio of insect to plant species and 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). The tendency for the GSR: PSR ratio to remain constant with increasing PSR clearly indicates that in the plant species-rich fynbos samples, galler richness increased at a roughly constant rate with increasing 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. PSR appears to be of primary importance in fynbos. Xeric fynbos sites had higher GSR than karoo sites (semi-desert). This is further substantiated by a study done at adjacent fynbos and karroid-vegetation sites in the karoo (Wright and Samways 1996), where it was demonstrated that fynbos harboured twice as many gall species as karoo vegetation.

Plant richness in fynbos is considered to be largely the result of allopatric speciation in a topographically and edaphically complex region (Cowling and 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 and 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 to disturbances like fire, or may be the result of host shifts onto new plant species that 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 and Price 1991).

Elevation showed no significant effect on GSR, possibly because we sampled a relatively short gradient of 1100 m, in contrast with those analysed by Fernandes et al. (1994) and Fernandes and 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 and 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 and 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. A high degree of endemism may therefore be expected in many areas, considering the high level of host-fidelity exhibited by gall-insects.

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