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## Global patterns in local number of insect galling species

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**Abstract.** We evaluate a three-part hypothesis explaining why gall-inducing insect species richness is so high in scleromorphic vegetation: (1) persistence of low nutrient status scleromorphic leaves facilitates the galling habit in warm temperate latitudes; (2) favourable colonization sites for gallers result from reduced hygrothermal stress, high phenolics in the outer cortex of the gall, and reduced carnivore and fungal attack in the gall; and (3) in more mesic sites, mortality is high due to carnivore attack and invasion of galls by fungi. Over 280 samples of local species of galling herbivorous insects from fourteen countries on all continents except Antarctica revealed a strong pattern of highest richness in warm temperate latitudes, or their altitudinal equivalents. The peak of galling species richness on the latitudinal gradient from the equator into the Arctic was between 25 to 38° N or S. Galling species were particularly diverse in sclerophyllous vegetation, which commonly had greater than twelve species per local sample.

In mesic, non-sclerophyllous vegetation types the number of galling species was lower with twelve or fewer species present. Many sites in sclerophyllous vegetation supported between thirteen and forty-six galling species locally, including campina islands in Amazonia, cerrado savanna in central Brazil, the Sonoran Desert in Arizona and Mexico, shrubland in Israel, fynbos in South Africa and coastal scleromorphic vegetation in Australia. At the same latitude, or its elevational equivalent, galling species richness was significantly higher in relatively xeric sites when compared to riparian or otherwise mesic habitats, even when scleromorphic vegetation dominated the mesic sites. The results were consistent with the hypothesis and extend to a more general level the patterns and predictions on the biogeography of gall-inducing insects.

**Key words.** Biodiversity, galling insects, latitudinal gradients, local species richness, scleromorphic vegetation.

### INTRODUCTION

The discovery of broad patterns in nature stimulates the generation of factually based theory in biology. Hence, one of the preoccupations among ecologists has been the search for pattern and the mechanisms that shape pattern (e.g. MacArthur, 1972; Tilman, 1989; Brown, 1995). Phytosociologists and biogeographers have been particularly strong in employing broadly comparative studies.

Most of the faunal studies in global patterns have been based on comparisons of regional species richness, depending on compilations from many sources and diverse sampling techniques (e.g. Fischer, 1960; Williams, 1964; Wilson, 1992, and review by Stevens, 1989). Problems with direct comparisons arise because of different sampling intensities, sampling methods, unequal areas sampled, and lack of tests on how such methodological differences

influence the data base. (Alternatively, only one taxon of plants has been sampled, such as bracken fern by Lawton and colleagues [e.g. Lawton, Lewinsohn & Compton, 1993], providing less general views of pattern.)

For the past 12 years we have employed a broad and more directly comparable approach by sampling in standardized ways the local number of insect herbivore galling species around the world. The small number of people engaged in the sampling and the use of standardized methods, minimize sampling error and unwanted sources of bias. With over 280 samples completed from around the world, we are able to report on patterns of local species richness.

We are unaware of a similarly cosmopolitan data set for any other group of animals or plants. The small size of galling species, their abundance and ubiquity, the persistence of galls on plant parts, and their commonly conspicuous form, make them easy subjects for such a study. However, with issues of biodiversity and conservation becoming central concerns among naturalists, and given the long-standing debate on the causes of latitudinal gradients in species richness (e.g. Dobzhansky, 1950; Rohde, 1992),

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we feel that similar studies on other groups should be encouraged.

In the search for more general pattern and synthesis we extend previously reported results by more than doubling the number of previous samples, increasing the geographical range of samples, and testing the validity of ground-based samples in forest vegetation with tall canopy trees, especially those in tropical forests. We have also tested the comparability of the two sampling methods employed. Comparisons of galling species distribution in Arizona, U.S.A., and Minas Gerais, Brazil, were reported by Fernandes & Price (1988, 1991, 1992). Price (1991) provided additional data covering a latitudinal gradient from Amazonia into the Arctic. The mechanisms driving the pattern were investigated by Fernandes & Price (1991, 1992).

We based our questions on the following steps in the study of local galling species richness: (1) initially superficial observations in Arizona; (2) the subsequent research results reported by Fernandes & Price (1988); (3) a more global view in Price (1991); and (4) hypotheses on mechanisms driving the pattern suggested by Fernandes & Price (1991, 1992). Our studies in Arizona and Minas Gerais showed similar and strong increases in galling species richness with decreasing elevation and from more mesic to more xeric environments. Local samples at one elevation indicated the same kind of pattern with consistently more galling species in xeric than adjacent riparian and mesic sites. Correlated with increasing aridity and gall species numbers was a shift in vegetation from mesophytic woody plants to xerophytic, sclerophyllous shrubs and small trees. Further studies showed that gallers in mesic sites were exposed to significantly higher mortality from carnivores and fungal attack, suggesting a mechanistic explanation for the patterns. Based on general knowledge of galling insects and sclerophyllous plants we erected the following hypothesis (Fernandes & Price, 1991). Scleromorphic vegetation develops on nutrient-poor soils, and conservation of nutrients results from the evolution of long-lived and therefore tough leaves, with reduced probability of abscission. The high carbon gain from photosynthesis in low-nitrogen-status plants also results in carbon-based chemical defenses, notably phenolics and tannins. Nutrient concentration in the feeding zone for insects in galls is well documented (White, 1993), as are the increased concentrations of chemical defenses in the outer cortex (Fernandes & Price, 1991). Therefore, sclerophyllous plants provide favourable and safe sites for colonization because of reduced abscission, reduced hygro-thermal stress in xeric habitats, nutrient concentration, and increased chemical defense against other herbivores and fungal pathogens. Over evolutionary time galling species will tend to increase in richness in scleromorphic vegetation more rapidly than in mesophytic vegetation. A clear prediction from the hypothesis is that in warm-temperate, Mediterranean types of vegetation, dominated by woody scleromorphic species, galling species richness should reach a peak on latitudinal gradients. We were interested to discover if this prediction were evident over a much more extensive biogeographical range.

The questions we addressed in our research were as follows. (1) Are the patterns found in Arizona and Minas Gerais general on a more global basis? (2) Is the peak in galling species richness in warm temperature climates a general pattern? (3) Is high richness in insect galling species associated with sclerophyllous vegetation? (4) At the same latitude, are mesic sites generally depauperate relative to drier sites in galling species richness? (5) Does this broad-based sampling approach provide clues to the mechanisms that shape the pattern? (6) Can galling species richness be predicted for an unsampled region?

## METHODS

Sampling was conducted between 1984 and 1994, intensively in Arizona and Minas Gerais, and intermittently elsewhere as opportunities materialized. Basic assumptions have been that each gall morph is unique to a galling species and that gall species are specific to a single plant species. Small errors may have resulted from dimorphism of galls within species of aphids, cynipids and eriococcids, but few sites contained many species in these taxa. The taxonomy of galling species is in a state of flux, and changes in taxonomy increasingly reflect support for host specificity of gallers and gall morphology as an indicator of a morphospecies of insect (cf. Price & Roininen, 1993; Roininen *et al.*, 1993; Kopelke, 1989). Galls were opened to determine if they had been induced by an insect species.

There is no doubt that after much sampling experience observers could anticipate the kind of galler species richness to be found at a particular latitude and in a certain vegetation type. Thus, potential biases may be of concern. However, the range in richness at one latitude and even within one geographical region was considerable, as will be seen in the results, so there was a persistent challenge to find as many species as possible. Therefore, any subjective bias was probably very small, and certainly diminutive relative to the strength of the patterns revealed.

### Sampling Method I—architectural census

At each site a 10-m-wide transect was staked out and all plants were searched for galls above ground until 1000 herbs, 100 shrubs, and forty-five trees had been sampled, representing the three major architectural types of plants. Previous tests on the adequacy of this sampling intensity showed that an asymptotic species richness was always reached before the total sample was completed (Fernandes & Price, 1988). The different number of plants sampled in each structural category was necessary to compensate for size differences and the frequency of galling insects on each type. Generally, galling species are far more common and abundant on woody plants than on herbs (Fernandes & Price, 1988, 1991). In both the tropics and in the temperate regions, 99% of all galling species discovered per site were included when the following sizes were used:  $461.2 \pm 288.9$  for herbs,  $58.5 \pm 22.1$  for shrubs, and  $25.9 \pm 12.4$  for trees (Fernandes & Price, 1988).

### Sampling Method 2—60-min census

An alternative sampling procedure was much less time consuming and more practical when extensive travelling was underway. At each site a 60-min census was taken by examining all plants carefully while moving slowly through an area. Paths and roads were commonly used as census routes because foliage was lower in the canopy at their edges, and they provided access through dense vegetation. A record was kept on morphospecies of plants and gall types and the total number of galling species was recorded. Disturbance of vegetation, including trimming, increases the chances of finding galls because many species attack rapidly growing shoots. Therefore, use of paths and roads no doubt increased the rate of discovery of galling species, although the total species richness in a locale would be little affected because all species were usually discovered well within the 1-h sample time.

### Comparison of methods

In Arizona both methods were employed on the same elevational gradient at the same sites, for a total of eleven sites from 984 to 3843 m at intervals of 305 m, plus one sample at 3843 m. Pearson's product-moment correlation analysis was employed to test for the similarity between sampling methods (Sokal & Rohlf, 1969).

### Comparison of ground-based and canopy samples

The potential for erroneous estimates derived only from ground-based sampling in tall vegetation was evaluated in two tropical forest locations.

In Panama, in September 1993, method 2, the 60-min census, was used to sample from the ground, and compared with paired samples in the canopy taken from a gondola hanging from a crane. The site was in the Parque Natural Metropolitano in Panama City with the crane erected and operated by the Smithsonian Tropical Research Institute in Ancon. A total of 8 h sampling the canopy from the crane and 8 h sampling the understory from the ground covered most of the area available within the 45 m radius of the crane's boom. Each 30-min sample in the canopy was matched with a 30-min sample below, providing sixteen matched pairs for comparison.

In Amazonia, a similar test was conducted near Porto Velho, Rondonia, in February 1994. Thirty-one ground-based samples were matched with thirty-one samples in the canopy of trees which had been lowered to the ground. We used sampling method 2 again. In the young second-growth forest, each tree could be bent over by several people and sampled.

For both sets of samples, the Wilcoxon matched-pairs signed-ranks test was employed to test the null hypothesis that no significant differences existed between canopy and understory samples (Siegel, 1956). Two-tailed tests were used because we had no prediction on how the canopy and ground samples would compare.

### Choice of sampling sites

Two approaches were employed in designating sampling sites. A formal design was used in Arizona and Mexico and Minas Gerais, with one or two samples taken at every 305-m elevational interval above sea level, from 0 m in Mexico to 3843 m in Arizona, and from 650 to 1350 m in Minas Gerais (Fernandes & Price, 1988, 1991). Sampling method 1, the architectural census, was used. Informal, opportunistic sampling using method 2, the 60-min census, was conducted during travels principally for other purposes. Samples were taken whenever time allowed when more or less natural vegetation was available. When opportunities permitted, diverse vegetation types within an area were sampled.

### Comparison between sampling personnel

We were interested in detecting any personal bias in sampling, so whenever two samplers took independent samples in the same locality, in closely associated sites, these matched samples were compared with Pearson's product-moment correlation analysis (Sokal & Rohlf, 1969).

### Conversion of altitude to latitudinal equivalents

As elevation above sea level increases at any one latitude, the climate cools to an equivalent climate at sea level but further from the equator north or south (Merriam, 1894, 1898; Holdridge *et al.*, 1971). The altitudinal effect on temperature can be converted to the latitudinal equivalent by using an increase in 4° latitude for every 305 m increase in elevation. We used this conversion to express all data on a latitudinal gradient as if samples were taken at sea level, even though samples were taken at many altitudes from sea level to a maximum of 3843 m above.

### Testing predictions based on pattern

After sampling in most biogeographic realms, we predicted that fynbos vegetation in South Africa should have high galling species number. We were aware of no such samples taken in this vegetation type. Subsequent sampling by MGW, following methods similar to Sampling Method 1, the architectural census, yielded an independent test of the predictability of the patterns discovered in other biogeographic realms. Fynbos is a heathland and shrubland vegetation growing on low-nutrient soils and is somewhat representative of the types found in Mediterranean kinds of ecosystems, such as chaparral, matorral, and Kwongan (Wright, 1993; Richardson *et al.*, 1995). The similarity and differences among these Mediterranean-type ecosystems are considered by Hobbs, Richardson & Davis (1995).

Once sampling in fynbos commenced, our direct comparison was rendered more difficult and tentative by the very high diversity of plant species in fynbos, accompanied by the small stature of the mainly shrubby species. Species density in the Cape Floristic Region reaches close to that in tropical rain forest, with 94,400 species per 10<sup>6</sup> km<sup>2</sup> in South Africa compared to 103,300 species in

Panamanian rain forest (Wright, 1993). Asymptotic richness of galling species in fynbos was reached only between 400 and 600 individual plants per sample. This is a much larger number of shrubs sampled than in other regions but less than the total plant individuals sampled when herbs, shrubs and trees were present at a sample size. Therefore, we suggest that samples in fynbos provide an interesting comparison with other regions, although they proved to be less directly comparable than expected.

## RESULTS

### Sample site locations

Samples were taken in fourteen countries: Australia, Brazil, Canada, Costa Rica, England, Fiji, Finland, Israel, Japan, Mexico, Panama, Russia (Siberia), South Africa, and the United States (mainly Alaska, Arizona, Florida, and Hawaii). The only continent without representation was Antarctica, and the only biogeographic realm unsampled was the Oriental. A map provides the approximate locations of samples (Fig. 1).

### General patterns in galling species richness

#### *The latitudinal gradient*

In response to question 1 on the generality of patterns initially discovered in Arizona and Minas Gerais, the answer is generally positive, but with important qualifiers. Between adjusted latitudes of 23° and 45° N or S in warm temperate climates galling species richness was very high (Fig. 2). The pattern included climates with cool dry winters and warm wet summers (Minas Gerais) and cool moist winters and hot dry summers with little rain (Arizona). Samples taken in these latitudinal equivalents included Australia (galling species richness from eight to fourteen species, six samples), Brazil (richness from zero to forty-six, forty-three samples), Israel (richness from six to twenty, two samples), Mexico (richness from fourteen to fifteen, two samples) and U.S.A. in Arizona (richness from six to twelve, four samples). Samples from South Africa were consistent with the pattern (richness from three to twenty-four, ten samples). Clearly, there is a large range in species richness in these latitudes, but a common feature is high values in the warm temperate zone relative to general values outside the warm temperate zone. This broad generalization needs qualifying on two counts.

In Arizona at elevations equivalent to 45° to 60° North, diversity is high in dry sites reaching up to eighteen galling species per sample. Many elements of the richly galled Sonoran Desert flora each up to 1000 m above sea level and higher and these are the plants that retain a high galling species diversity at latitudinal equivalents of 45 to 60° N.

A major departure from low richness in tropical latitudes was seen in campina vegetation along the Rio Negro in Amazonia. Campina and caatinga are terms referring to similar vegetation types in Amazonia, according to Pires and Prance (1985). Developing on nutrient-poor leached white sand, the campina vegetation has a xeromorphic

aspect with thick sclerophylly and bark. After walking for many kilometres in extensive wet tropical forest with low galling richness one can suddenly enter a small island of campina vegetation and find many galls; nine to twenty-six species in the three patches sampled in this study.

Note that high gall species richness, at twenty or more species per sample, was observed in three biogeographic realms: the Palearctic (Jordan Valley, Israel), the Ethiopian (southern Cape Province, South Africa), and the Neotropical (Campina, Amazonas; Serro de Cipo, Minas Gerais, Brazil). The exceptional case from the tropics in campina vegetation leads us into the subsequent questions raised in the introduction.

### Warm temperate climates

Our second question addressed the generality of high galling richness in climates just outside the tropics. Mediterranean climates with hot dry summers and warm wet winters are common at latitudes from 23° to 45° N and S. However, hot wet summers and cool dry winters are also found in these latitudes where typhoons bring summer rains, for example, in Japan. Also, in tropical latitudes such as in Minas Gerais, the summers are very wet and the winters are very dry (Hueck, 1972). The altitude at which samples were taken in Minas Gerais moved these tropical locations at 19° S into the equivalent of the warm temperate belt.

Therefore, the answer to question 2 is that galling species richness in warm temperate latitudes and equivalents is commonly high so long as there are distinct dry and wet seasons each year.

### Galling species richness in scleromorphic vegetation

We asked in question 3 if galling species richness is related to sclerophyllous vegetation. In warm temperate climates and their equivalents, typical climatic types have hot dry summers and warm wet winters, or warm wet summers and warm dry winters. Both climatic regimes result in scleromorphic elements in the vegetation. Whether or not phytosociologists accept the term sclerophyllous for a particular type, scleromorphy is a common denominator for many species in truly Mediterranean climates, and in climates with wet summers, as in savannas in Brazil (cerrado, with grasses and herbs intermixed with low, tortuous, sclerophyllous trees with thick bark), and the evergreen forest types in southern Japan.

Scleromorphic vegetation is defined as a flora dominated by plants with persistent and tough leaves (Schulze, 1982). In fact, a combination of the terms scleromorphy and xeromorphy covers the range of plant types on which galls become most abundant. Features of xeromorphic plants include 'reduced stature, reduction in internode lengths, perennality' (Schulze, 1982, p. 649), and small leaves with thick cuticles (Small, 1973). Scleromorphic plants may have large leaves, but leaves are so hardened that they retain their mature shape while drying. At the upper extreme of this leaf type in the cerrado is *Palicourea rigida* (Rubiaceae) with some leaves the size of those on a large cabbage

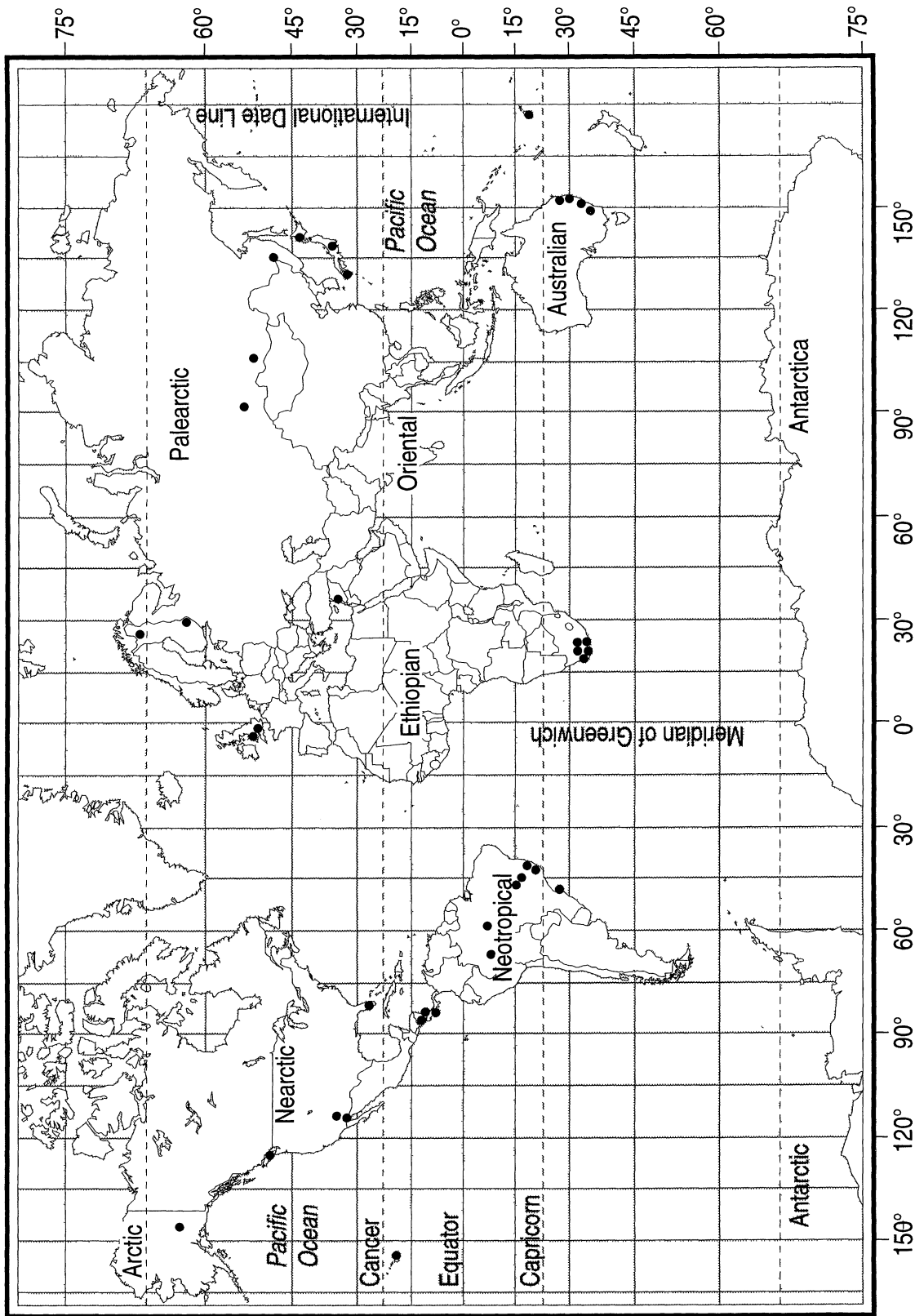


FIG. 1. Map of the World showing the approximate distribution of local sample sites estimating insect herbivore galling species richness. The map uses the Mercator projection, as if longitude is represented by a set of parallel lines north and south, grossly overrepresenting land and sea areas in northern and southern latitudes. The tropics, temperate and arctic regions are indicated by dashed lines of latitude. Biogeographic realms are indicated. The International Date Line at 180° longitude is the general case and is not accurate for all specific regions.

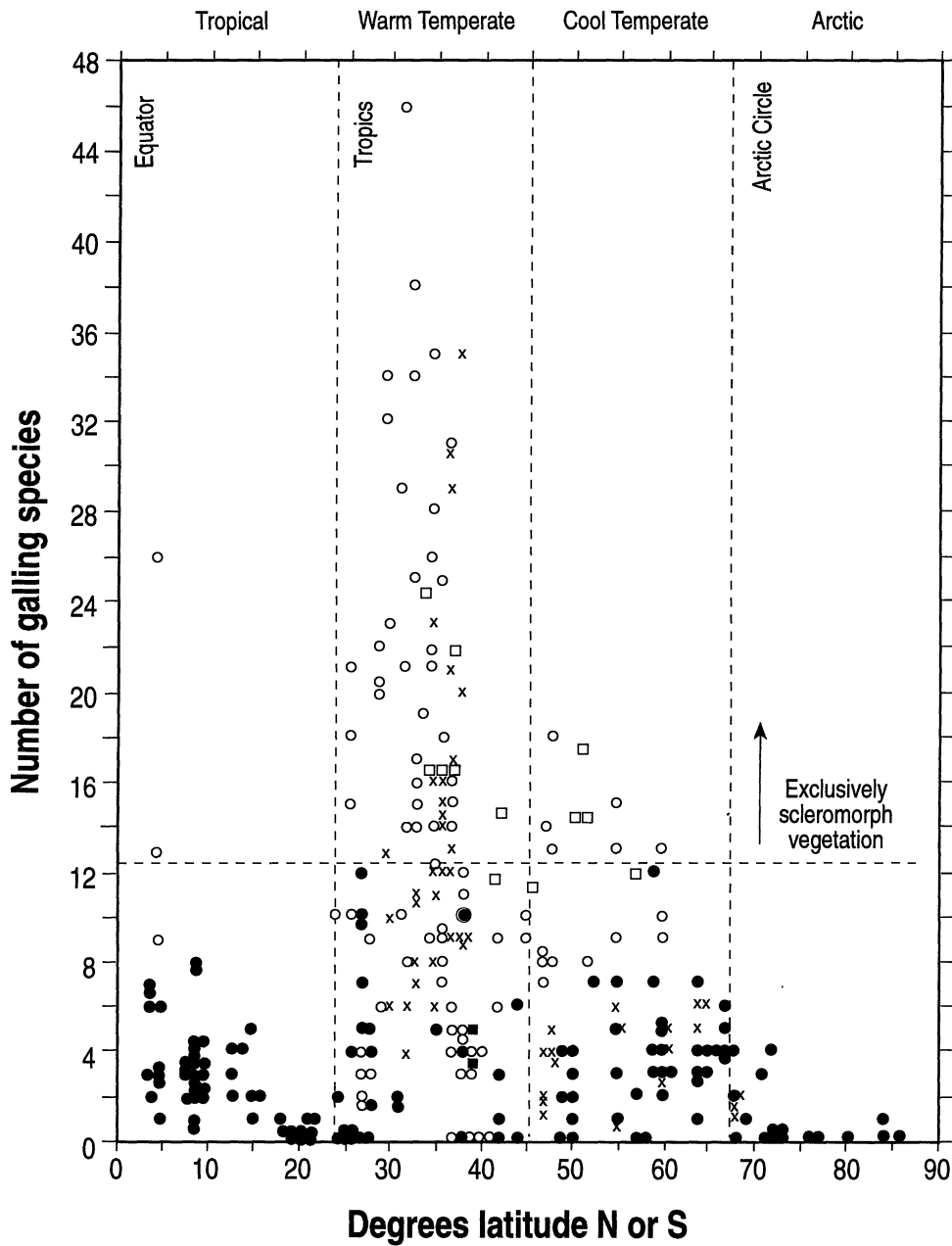


FIG. 2. Distribution of samples measuring galling species richness on a latitudinal gradient north or south of the equator. The gradient is divided into tropical, warm temperate, cool temperate and arctic zones, and shows a strong peak in richness in warm temperate regions or their equivalents, based on latitude and altitude. Open circles represent samples on scleromorph vegetation and closed circles are samples in mesic sites on nonscleromorph vegetation. Samples taken on scleromorph vegetation in relatively mesic sites are indicated by an x. Squares indicate samples from fynbos vegetation in South Africa which acted as an independent test of the pattern. Twelve xeric sclerophyll (open squares) and two mesic sites (closed squares) in riparian woodland are given. Note that all samples with a richness greater than twelve species are from scleromorph vegetation types. This apparent limit on species richness in mesic sites is indicated by the broken line horizontal to the X axis.

and almost the toughness of a cyclist's plastic safety helmet!

The highest estimates of galling species richness around the world are all associated with scleromorph and xeromorph vegetation (Fig. 2). In the warm temperate zone and its equivalents, richness reaches a strong peak based on samples in Australia, United States (Arizona),

Israel, Brazil (Minas Gerais, Amazonia) and South Africa. Scleromorph and xeromorph vegetations in these areas support commonly local galling species of thirteen and more, above any vegetation types that are not sclero- or xero-morph (Fig. 2). We address the mechanisms driving this strong pattern when discussing Question 5 on mechanisms.

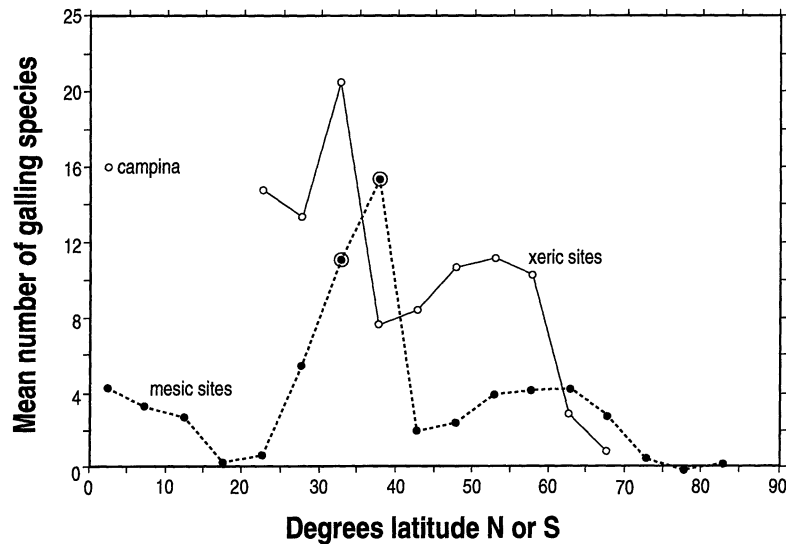


FIG. 3. Distribution of galling species richness on a latitudinal gradient north or south of the equator with a distinction made between relatively xeric sites and relatively mesic sites at the same latitude. Estimates are based on the empirical data presented in Fig. 2 categorized into 5° latitudinal classes (N or S). Mesic sites include scleromorphic vegetation, commonly found in riparian habitats in the tropics and temperate regions, (x in Fig. 2), and mesic sites with nonscleromorphic vegetation indicated by solid circles in Fig. 2. No scleromorphic vegetation was sampled in the range of 6–20° N and S, and the two circled points result exclusively from data collected in sclerophyll vegetation in riparian habitats. North of latitudes in the 66–70° N and S or their equivalents, no scleromorph vegetation was sampled. Open circles and solid lines indicate data for xeric sites, and solid circles and broken lines indicate data for mesic sites.

### Galling species in relatively dry and wet sites

If galling species are strongly associated with scleromorphy in their host plants, are drier (xeric) sites more favourable than wetter (mesic) sites for gallers? (Question 4). Using data in Fig. 2 we have categorized sites as either xeric with scleromorphic plant species or more mesic sites with scleromorphic and nonscleromorphic plant species. If a mesic site was sampled with scleromorph vegetation it was usually matched with a drier site at the same elevation and latitude, unless no equivalent was available, as for *campina* vegetation.

The pattern shows a clear preponderance of galling species in xeric sites (Fig. 3). In all but three of the pairwise comparisons per 5° latitudinal range class, out of the eleven comparisons, xeric sites supported more species than mesic sites, a significantly different species richness in general (Wilcoxon's signed-ranks paired-comparisons test:  $n=11$ ;  $T=9$ ,  $P<0.025$  one-tailed test). We anticipated this result based on studies by Fernandes & Price (1988, 1991, 1992) on pairwise tests of xeric and riparian habitats in Arizona and Minas Gerais at the same altitude. In the range of latitudes from 60° to 70° the contrast between mesic and xeric sites diminishes and numbers of galling species per habitat type tend to converge. Mechanisms driving the general pattern are considered next.

### The mechanisms driving the patterns

In question 5 we asked if clues on mechanisms were provided by the sampling adopted for this global view on galling insect species richness. In general, the patterns are

consistent with the hypothesis developed by Fernandes & Price (1991). Galling species richness increases on scleromorphic vegetation, more so in xeric than mesic sites in the same locality, and a scleromorphic flora is typically associated with nutrient or water limitations in warm temperate regions or equivalents (Loveless, 1962). Each region is likely to have different critical factors associated with the scleromorphic habit: very poor soils, low available water, high concentrations of elements such as aluminium, or a combination of these factors (cf. Haradisan, 1982). Depauperate volcanic deposits (e.g. Kagoshima, Japan), ancient soils on old continents like Australia (Barlow, 1981), white alluvial sands (e.g. Rio Negro, Amazonia), weathered limestones producing white sands (e.g. Pirinópolis limestone hills, near Brasilia, Brazil) sandy and rocky deserts (e.g. Sonoran Desert, Arizona, U.S.A.), saline soils (e.g. Israel), high concentration of aluminium in soils (e.g. cerrado vegetation in Minas Gerais, Mato Grosso and Goias states and the Federal District of Brasilia, Brazil), all result in a scleromorphic vegetation (cf. Kruger, Mitchell & Jarvis, 1983). Galling insect species respond positively to many of the plant species growing on these less than hospitable soils.

We have not tested mechanisms driving the pattern of galling species richness in the present study. All we can claim is that this large sample from many areas of the world is consistent with the pattern. Nevertheless, we remain optimistic that the hypothesis will prove to be correct because the correlated traits of scleromorphy, poor soil conditions or water shortage, and high galling species richness, persist as a central result in this study.



### A test of predictions

In question 6 we asked if it is possible to predict a pattern of gall species richness in a previously unsampled biogeographic realm. Samples in the Western Cape Region of South Africa included twelve from xeric sites with fynbos vegetation and two from mesic woodland without the fynbos components represented. Estimates of species numbers fell within the values from the rest of the world, and are indicated with square symbols in Fig. 2. Outside warm-temperature-latitude equivalents, five samples in fynbos vegetation were consistent with those from Arizona between the latitudes of 45–57° N or S. The results indicate that crude predictions on galling species richness can be made and supported, although deviations from the general sampling methods because of the unique flora diminish the power of our test.

### Gall-inducing taxa in the study

The gall midges (Diptera: Cecidomyiidae), a cosmopolitan family, were largely responsible for the patterns detected. They are known to be associated with a wide range of host plant taxa in both tropical and temperate latitudes (cf. Gagné, 1989, 1994). Other taxa with galling insects were much more restricted in the host-plant range and geographic distributions in our samples. Tenthredinid sawfly and aphid gallers were found only in north-temperate latitudes or their Northern Hemisphere elevational equivalents. Cynipids were sampled on oaks and roses providing relatively high local species numbers in adjusted latitudes between 35° and 60° N. However, a small number of samples was dominated by the Cynipidae. Gall-forming Eriococcidae were found in Australia alone, representing a small component of the samples. Galling insects in the Lepidoptera, the Tephritidae (Diptera) and the Psyllidae (Homoptera) were not common enough to influence the pattern significantly.

### Comparison of sampling methods

#### *Comparison of methods*

Method 1, the architectural census, was employed by G.W.F. on the San Francisco Peaks in Arizona down into the Verde Valley at 984 m and beyond and reported in Fernandes & Price (1991). Method 2, the 60-min census, was used by P.W.P. covering the same eleven sites for direct comparison. The correlation between sampling methods was highly significant ( $Y = 1.58 + 0.80X$ ,  $n = 11$ ,  $r = 0.93$ ,  $P < 0.01$ ). The intercept of 1.58 resulted from a slightly higher number of galling species in Method 2 at higher elevations because of the more extensive area searched. This effect also lowered the slope of the correlation to 0.80. However, the relationship predicted differences in galling species richness of 1.38 species per sample as a maximum, if any galls were found by sample method 1 ( $X = 1$ ,  $Y = 2.38$ ), providing confidence in the direct comparison in sampling methods.

#### *Comparison of ground and canopy samples*

In Panama, ground-based sampling yielded significantly higher estimates of galling species richness than matched

canopy samples (ground mean = 1.88 galling species per 30 min; range 0 to 3; canopy mean = 1.31 galling species per 30 min; range 0 to 2; Wilcoxon  $T = 23.5$ ,  $n = 16$ ,  $P < 0.05$ , 2-tailed test). When ground and canopy samples were combined to simulate a total sample taken throughout the under- and over-story an intermediate richness was estimated with a mean of 1.75 galling species per 30-min sample (range 1 to 3). The total samples were not significantly different from the ground-based samples alone (Wilcoxon  $T = 39$ ,  $n = 16$ , N.S.).

In general, in the wet season in dry tropical forest, sampling from the ground provided a small overestimate of galling species richness in samples combining under- and over-story vegetation. However, in this vegetation with low richness of gallers, the ground samples provided a mean estimate within one species of the combined canopy and ground samples. For a 1-h sample this would translate to an overestimate of two species per sample on average. Given the wide range in galling species richness around the world this is a small and acceptable overestimate.

Sampling the canopies of lowered trees in Amazonia provided results similar to those obtained in Panama. Ground samples identified significantly higher gall species numbers than matched canopy samples (ground mean = 1.32 galling species below a canopy; range 0–6; canopy mean = 0.48 galling species in a canopy; range 0–4; Wilcoxon  $T = 58.92$ ,  $n = 26$ ,  $P < 0.01$ , 2-tailed test). We then combined samples from ground and tree canopy for a composite sample. This provided a mean of 1.71 galling species per tree canopy plus ground sample (range 0–10). In contrast to the samples in Panama, the total samples were significantly higher than ground samples (Wilcoxon  $T = 0$ ,  $n = 9$ ,  $P < 0.01$ ), although in only nine cases were differences observed, and the mean difference was 0.48 galling species. Hence, the ground samples provided an acceptable estimate of total galling species richness.

#### *Comparison among sampling personnel*

Two tests were conducted on the correlation between pairs of samples conducted simultaneously by different samplers in at least nine locations. The paired samples were not in identical sites, but displaced by a few metres, enough to introduce the probability that real differences in gall species number would be expected, in addition to biases introduced by the researchers themselves.

At locations with low galling species richness PWP and GWF sampled nine paired sites, each using method 2, and the correlation between samples was significant ( $r = 0.54$ ,  $P < 0.05$ , slope = 1.00, intercept = 1.00). All samples were taken before a direct comparison of results was planned. In sampled richness ranging from 0 to 6 galling species per hour, there was a consistent bias in which GWF would find on average one gall more than PWP per sample. Such a generally small difference in results between personnel could not alter the general patterns discussed in the next section.

The second test was conducted in the richest galling species habitats we have discovered to date, using method 1, on Serra do Cipó in Minas Gerais, Brazil, near Belo Horizonte. In 1991, samples were spread among wet and dry sites at elevations from 900 to 1400 m a.s.l., with paired

data collected by GWF and ACFL. All samples yielded richness estimates between eleven and thirty-eight galling species per sample, except one pair at the highest elevation with estimates of four and five galling species. Samples were significantly correlated ( $n=13$ ,  $r=0.33$ ,  $P<0.05$ , slope = 0.59, intercept 10.66). However, the correlation was not as strong as we expected. The extent to which the differences were due to personnel or to real differences in the field needs more study. However, all samples fell within the range, or exceeded the richness of samples taken at equivalent sites by GWF in 1984 and 1986 on Serra do Cipó (Fernandes & Price, 1988). These results indicated that samples were correlated, and strong patterns could be detected repeatedly, even though different people sampled.

## DISCUSSION

Opportunity and adversity take different forms in the adaptive radiation of insect groups. Tenthredinid sawflies are poorly represented in the tropics as if the cool temperate climates in which they radiated and the important families of plants that they utilize, such as the Salicaceae, have constrained exploitation outside their primordial latitudes (Smith, 1979). Aphids are also depauperate in the tropics, perhaps because their method of finding hosts by trial and error is inefficient in floristically diverse vegetation (Dixon *et al.*, 1987). The galling insects are represented by several families, although the pattern we describe is driven undoubtedly by the abundance of the gall midges (Diptera: Cecidomyiidae). For the gallers, opportunities for adaptive radiation obviously have been very extensive in scleromorphic vegetation and the wet tropics present mostly adverse conditions.

Galling insects such as the gall midges appear to be excellent colonizing species. Even though adults are short lived, galls can be found in isolated patches of vegetation after disturbance. They can be rare in a landscape, but common very locally, as we have found for two tenthredinid gallers (e.g. Roininen *et al.*, 1993). They colonize newly sprouting host plants rapidly after fire in the cerrado as we have noted around Brasília and Belo Horizonte (e.g. Vieira, Andrade & Price, 1996). Therefore, the richness of tropical rainforest floras does not seem to pose a significant barrier to colonization by galling species as hypothesized for aphids. Nor do gall midges have evident broad phylogenetic associations with cool temperate climates and host plants, even though specific genera are associated with northern plant taxa. Indeed there may be very ancient links between gallers and cerrado vegetation, for this savanna system may be very old, some 30 million years perhaps (Cole, 1986). Without doubt localities with dry climates have been centres of adaptive radiation, especially for cecidomyiids, with very rich communities in deserts, shrublands and savannas.

The prolonged debate about the adaptive significance of the galling habit, at least since 1889, was discussed by Price *et al.* (1986, 1987). We argued that the most cogent thesis implicated hygrothermal stress as the selective factor. Sampling in Arizona and Minas Gerais reinforced this argument (Fernandes & Price, 1988, 1991), and the data presented in this paper add further support. The pattern of

galling species richness on the latitudinal gradient is clear enough, but the underlying explanation for the pattern is unresolved.

Strong association of galler species richness with scleromorphic vegetation, lower richness in moist sites relative to dry sites at the same latitude, and reduced richness in the wet tropics and cool temperate climates, focused our concern on the special features of scleromorphic vegetation. We argued that scleromorphic hosts provide commonly persistent leaves of low nutrient status and high phenolic concentrations, but gallers could concentrate nutrients and overcome low nutritional status (Fernandes & Price, 1991; White, 1993). Nutrients would be concentrated in the feeding zone of the insect (White, 1993) while phenolics acting as chemical defenses against other herbivores are concentrated in the outer cortex of the gall. In moist sites activity of endophytic fungi, fungal pathogens, and parasitoids would be detrimental to gallers and reduce species richness (Fernandes & Price, 1992). The net result is higher richness in relatively dry sites and in dry latitudes. 'Dryness' in these cases must be viewed as physiologically relevant stresses on the host plants, rather than the amount of precipitation, for campina vegetation receives about 2200 mm rainfall per year and cerrado about 1500 mm per year (Hueck, 1972). Such 'physiological drought' was recognized as important in xeromorphic and scleromorphic plants a century ago by Schimper (1898).

An interesting consideration concerns the mechanisms by which gall species richness develops in scleromorphic vegetation. Does such richness derive from multiple independent colonizations, or are a small number of initial colonizations followed by extensive speciation in closely related taxa? Focusing on the cecidomyiids as the richest taxon of gall inducers, we favour the latter scenario. With the caution advised by Gagné (1989), that generic categories are subjective, and in the Cecidomyiidae genera may not be monophyletic, we offer the following tentative argument. Several genera of cecidomyiids are large, indicating extensive host-plant shifting without major change in morphology. *Rabdophaga* contains about seventy species globally, *Rhopalomyia* over 120 species, and *Asphondylia* contains 247 described species (Gagné, 1989, 1994). On a local scale we know that one genus may radiate into several different ecological niches on the same host plant, with the best examples from deserts in the SW United States and Kenya. Creosote bush, *Larrea tridentata* (DC.) Coville is host in Arizona to sixteen species in the cecidomyiid genus *Asphondylia* (Gagné, 1989; Waring, 1986, 1987; Waring & Price, 1990). *Asphondylia* is also represented by eight species on *Atriplex canescens* (Pursh) Nuttall and *A. polycarpa* (Torrey) Watson in southern California (Hawkins & Goeden, 1984; Hawkins, Goeden & Gagné, 1986). In Kenya, the genera *Acacidiplosis* (13 spp.) and *Aposchizomyia* (6 spp.) have radiated across *Acacia* host plant species (Gagné & Marohasy, 1993). One host plant species, *Acacia tortillis* (Forssk.) Hayne, has a total of eighteen cecidomyiid gall-forming species recorded, with eleven *Acacidiplosis* and three *Aposchizomyia* included. Therefore, it is conceivable that ecological opportunities for host shifting in xeric habitats, once cecidomyiids became adapted to such dry

sites, provided the basis for extensive adaptive radiation from a small number of phylogenetic lineages. Knowing that most gall midges attack and utilize only one plant species (Gagné, 1989) suggests that the details of the interaction between host and parasitic galler necessitate extreme specialization, as argued by Price (1980). Nevertheless, Gagné (1989) noted that females may lay eggs on plants related to the normal host, with such 'accidents' providing the basis for host shifting and ultimately speciation, in our opinion.

Latitudinal gradients in species richness of plants and animals are more complex than is usually acknowledged in the literature (cf. Pianka, 1966; Price, 1991). Each taxon is under specific constraints in its adaptive radiation, with associated opportunistic outlets for resource exploitation. We have shown that a strong peak in galling species richness is associated with edaphic and climatic conditions resulting in scleromorphic vegetation. We have not invoked any of the forces commonly considered in discussions of latitudinal gradients in diversity, such as competition, species packing, or niche width, and the importance of natural enemies in gall-forming communities is very different from that invoked in general debates. Indeed, in forthcoming papers we will show for galling species assemblages in the wet tropics and at peak richness in the cerrado, that any kind of community organization is very hard to discover, and may well be absent. Gallers in local, favourable environments appear to be radiating opportunistically, in loose assemblages, seemingly unconstrained in evolutionary time. The data on galling insects do not support any of the conventional views of the tropics regarding community organization which date back to the great naturalists of the nineteenth century, and which were summarized by Dobzhansky (1950). As Vandermeer (1989) noted, much of our current ecological 'theory' relies on arguments unfounded in empirical facts.

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