

**Structure and function of a Lepidoptera assemblage in a human-influenced
environment**

by

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A landscape is a mosaic of patches, the components of pattern

Urban *et al.* 1987

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Abstract

Natural habitat is under increasing pressure from urbanisation. Urban and suburban areas are therefore growing in significance as elements of the matrix within which conservation must be undertaken. The ability of such areas to maintain biodiversity may be assessed using biological indicators. However, annual variability in population and community parameters may alter the initially quantified relationship between habitat quality and the response of the bioindicator, rendering the bioindicator unreliable. Few studies have established the reliability of bioindicators over time, given this annual variability. In this study, the utility of a Lepidoptera assemblage inhabiting fungus induced galls, as a bioindicator of habitat quality in urban areas, is reassessed.

The Lepidoptera larvae inhabiting galls induced by the fungus *Ravenelia macowaniana* Pазschke on *Acacia karroo* Hayne were identified from galls collected from sites differing in their degree of urbanisation. The galls sampled in this study (1998) were older and weighed less than the galls sampled in 1995 and both gall age structure and gall mass (measures of resource quality and quantity) contributed significantly to explaining the variation in larval abundance. There was substantial variation in the absolute and relative

abundances of species between this study and the one conducted in 1995. Absolute abundance differences were attributed to the variation in gall mass between studies, while changes in resource quality as a result of gall age were hypothesised to be the main factor influencing relative abundance patterns. The Lepidoptera assemblages at roadside sites and at sites closest to the city centre were significantly different from those found elsewhere. In both studies, species richness, larval density and larval abundance were generally lower at sites closest to the city centre than at those further away. Also, distance to city centre explained a significant proportion of variation in larval abundance in this study. Thus, despite the resource differences (gall age and mass) between the two studies, assemblage patterns relative to the degree of urbanisation were similar. Consequently, this Lepidoptera assemblage may reliably be used to evaluate the impact of urbanisation on invertebrate communities. However, if phenological matching in sampling dates cannot be achieved, species abundances and species richness measured across sites are more suitable monitoring parameters than species composition and abundance ranking.

The spatial distribution and abundance structure of species and populations are determined both by biotic factors, for example resource quality, and abiotic factors, such as habitat quality. These factors are known to change as a result of the impact of urbanisation. Local scale variability (at the level of the gall, tree and site) in the above-mentioned moth assemblage, and the resource with which it is associated, was examined. The moth assemblage and its resource were found to be aggregated (positively autocorrelated) at the smallest scale, both across and within rural and urban areas. This small scale aggregation pattern in the moth assemblage may be attributed to the availability and quality of the habitat and gall resource that the assemblage occupies. Furthermore, most of the variation in the system was explained at the level of the individual

gall. Microscale factors at the level of the gall are thus the most important factors structuring this system. These microscale factors include variations in microclimate, gall mass, gall age and exploitation competition.

Species spatial distribution patterns may follow resource distribution patterns if 'bottom-up' processes are governing a system. The zone of influence (the size of the area over which the full range of values for the variable are expressed) was found to be smaller for the assemblage and species than for the resource. Also, patch diameters (the area within which the values of a variable are more similar to one another than expected by chance) were similar for resource and assemblage variables. Furthermore, parasitism (a 'top-down' process) in this assemblage was extremely low. Thus the spatial structure of the resource and assemblage variables provides support for the importance of 'bottom-up' processes in structuring this Lepidoptera assemblage.

Both the assemblage and the resource variables were positively autocorrelated at the smallest scale however, positive autocorrelation across rural sites was significantly stronger than across urban sites. Greater variability in disturbance factors over smaller spatial scales in urban than rural areas contribute to the dilution of spatial autocorrelation values in urban areas. This urbanisation influence however, is not observed across the extent of the study area as no clear spatial gradient was identified to which the assemblage or resource responded.

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General introduction

It is estimated that around 25% of the total land area in South Africa is transformed by anthropogenic activities (Macdonald 1989). Urbanisation contributes significantly to this transformation (Macdonald 1989). Furthermore, the continued expansion of urban areas in South Africa will cause a larger proportion of the environment to be influenced by urbanisation (Scholtz & Chown 1993). With the increasing interest in managing "off-reserve" areas for the maintenance of biodiversity, urban areas are therefore growing in significance as elements of the matrix within which conservation must be undertaken (McNeely 1994; Pressey & Logan 1997). However, the construction of man-made features, such as roads, in urban environments causes new habitat boundaries to be established that are often impermeable to species dispersal (Urban *et al.* 1987; Duelli *et al.* 1990; Mader *et al.* 1990). Furthermore, the impact of habitat quality changes, as a result of urbanisation, has been shown to influence the structure of invertebrate communities (Kuschel 1990; Miyashita *et al.* 1998). Although urban environments usually have lowered species diversity and abundance (Bolger *et al.* 1997; Suarez *et al.* 1998), 'green areas' within urban environments have been shown to play an important role in preserving biotic diversity (Frankie & Ehler 1978; Owen 1991; McGeoch & Chown 1997; Blair 1999). These green areas may therefore contribute to conservation within the regional matrix.

The impact of urbanisation on communities may be assessed using bioindicator taxa (McGeoch 1998). Terrestrial arthropods, with their high diversity and abundances, are ideally suited as bioindicator taxa (Pearson & Cassola 1992; Kremen *et al.* 1993; also see McGeoch 1998). For example, insects in urban habitat patches have been used as indicators of the consequences of anthropogenic disturbance, both for insects and other taxa (Kuschel 1990; Blair 1999). Although bioindicators may be used to demonstrate the effects of environmental change on biotic systems, annual variability in both resource

quality and quantity and community structure (Cappuccino & Price 1995; Price 1997) may alter the observed values of the bioindicator (McGeoch 1998). However, few studies have examined the reliability with which bioindicators of habitat quality can be used, given this inevitable variability. Confirming the operational reliability of such biological indicators is essential if they are to be of value in ongoing monitoring and assessment (see McGeoch 1998). If year to year variation in population and community parameters were to alter the initially quantified relationship between habitat quality and the response of the biological indicator, the value of such a bioindicator would be low.

In addition to altering assemblage structure, human-induced fragmentation within the distribution ranges of species and assemblages is likely to increase the patchiness of species distributions, and to disrupt gradients in species abundances. As a result of increased patchiness of natural habitats in urban environments, organisms inhabiting urban areas may be expected to display greater variability in their distribution patterns over small to medium spatial scales compared to the same species found in unfragmented rural or undeveloped areas. Furthermore, a disturbance gradient across developed areas, from urbanised to less developed rural habitats, may exist to which species respond. The spatial distribution patterns of species and assemblages in urban environments may therefore be expected to be very different from those found in rural environments. In the event that species spatial distribution patterns and their resources are altered across an urban-rural gradient, an understanding of these changes in spatial distribution patterns would yield useful results to apply to long-term species conservation and habitat management.

The spatial structure of organisms in an environment may be elucidated using spatial autocorrelation (Sokal & Oden 1978; Koenig & Knops 1998; Kuuluvainen *et al.* 1998; Legendre & Legendre 1998; Koenig 1999). Structure functions, such as correlograms, may be used to view changes in the spatial structure of a variable, such as species abundance, with distance (Sokal & Oden 1978; Koenig & Knops 1998; Legendre &

Legendre 1998). Evaluating how spatial structure changes, for example, across a disturbance gradient will reveal the influence that this disturbance has on the variable under consideration.

In this thesis, the utility of a Lepidoptera assemblage inhabiting fungus induced galls that was identified by McGeoch & Chown (1997) in 1995 as a biological indicator of habitat quality in urban areas is re-assessed (Chapter 1). If the assemblage is a reliable indicator of the effects of urbanisation on insect communities, as was suggested by McGeoch & Chown (1997), then interannual differences in, for example, weather conditions should not change the response of this assemblage to urbanisation effects. Furthermore, the spatial structure of the assemblage and the resource that it inhabits across a city-urban-rural development gradient is determined (Chapter 2). In addition to possible variation in the spatial structure of this assemblage across urban and rural habitats, numerous factors may influence this Lepidoptera assemblage and its resource at three hierarchical scales (gall, tree and site) (Chapter 2). Assessing the relative importance of these scales to the Lepidoptera assemblage and its resource provides insight into establishing the scales at which different ecological processes that generate these patterns operate (Borcard *et al.* 1992; Underwood & Chapman 1996).

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CHAPTER 1

Testing a bioindicator assemblage: gall inhabiting moths and urbanisation

Introduction

Urbanisation leads to habitat quality changes. These include decreased patch size, increased isolation, decreased landscape connectivity due to habitat fragmentation, the invasion of alien flora and an increase in air pollution and physical disturbance (Frankie & Ehler 1978; McDonnell & Pickett 1990; Blair 1996; Mökkönen & Reunanen 1999; Rottenborn 1999). Such modifications in habitat quality are known to significantly influence the species composition and abundance of natural communities. In the urban environment, disturbance effects on biota often decrease with an increase in the distance from the city centre (McDonnell & Pickett 1990). Bird species composition, for example, has been shown to shift from indigenous species in undisturbed areas to exotic species in more developed urban areas (Blair 1996), and arthropod assemblage structure has been shown to vary between sites in urban areas with different habitat qualities (Duelli *et al.* 1990; Kuschel 1990; Miyashita *et al.* 1998).

An organism's ability to utilise a resource patch in an otherwise developed environment will not only depend on the size and condition of the patch, but also on the distance from colonisation sites, the nature of the area between the patches and on the biology and behaviour of the organism (den Boer 1990; Mader *et al.* 1990; Taylor *et al.* 1993; Thomas & Jones 1993; Halley & Dempster 1996). The more hostile the environment, and the greater the distance between resource patches, the less likely the patch is to be colonised (Duelli *et al.* 1990; Taylor *et al.* 1993; Thomas & Jones 1993; Halley & Dempster 1996; Mökkönen & Reunanen 1999). Because this is also particularly true for insects in urban environments, the presence and diversity of insects in urban habitat patches may be

used as indicators of the consequences of anthropogenic disturbance, both for insects and other taxa (e.g. Kuschel 1990; Kremen *et al.* 1993; Blair 1999).

With urban and suburban areas increasing as a proportion of the landscape in both developed and developing countries (Soulé 1991; Scholtz & Chown 1993), they are growing in significance as elements of the matrix within which conservation must be undertaken (McNeely 1994). The maintenance of 'green areas' of relatively undisturbed natural vegetation in urban and agricultural environments has been shown to play an important role in preserving biotic diversity (Frankie & Ehler 1978; Samways 1989; Duelli *et al.* 1990; Owen 1991; Feber *et al.* 1996; McGeoch & Chown 1997a; Blair 1999; Fleishman *et al.* 1999). How well such areas are performing can be assessed in a variety of ways. One such method is the use of bioindicators. Assessing trends in taxa identified as biological indicators, i.e. establishing the robustness of these bioindicators, is, however, first necessary before they can be used with a measurable degree of confidence to monitor changes in biodiversity in urban environments (Kremen *et al.* 1993; McGeoch 1998).

Thus, while the impact of habitat quality changes due to urbanisation have been shown to influence the structure of insect communities (Duelli *et al.* 1990; Kuschel 1990; Miyashita *et al.* 1998), no studies have examined the reliability with which bioindicators of such change can be used (i.e. ecological bioindicators, *sensu* McGeoch 1998), given inevitable annual variability in both resource quality and quantity, species abundances and interactions (Cappuccino & Price 1995; Price 1997). Confirming the operational reliability of such biological indicators is essential if they are to be of value in ongoing monitoring and assessment (see McGeoch 1998). If year to year variation in population and community parameters were to alter the initially quantified relationship between habitat quality and the response of the biological indicator, the value of such a bioindicator would be low. Hence they would be inappropriate for assessing the value of urban areas for conservation. To

date no tests have evaluated the repeatability of bioindicators, an essential procedure if they are to be of any utility (McGeoch 1998).

In this study we therefore re-assess the utility of a Lepidoptera assemblage that was identified by McGeoch & Chown (1997a) in 1995 as a biological indicator of habitat quality in urban areas. If the assemblage is a reliable indicator of the effects of urbanisation on insect communities, as was suggested by McGeoch & Chown (1997a), then interannual differences in, for example, weather conditions should not change the response of this assemblage to urbanisation effects.

The Lepidoptera assemblage

The larvae of the Lepidoptera assemblage, identified as a potential indicator of urbanisation, inhabit galls induced by the rust-fungus (*Ravenelia macowaniana* (Pazschke)) on *Acacia karroo* (Hayne). The resource that these fungus galls provide for the Lepidoptera larvae is seasonal, ephemeral and patchily distributed (McGeoch 1993). However, the galls have high nutritional value, provide protection from natural enemies and are a favourable environment for larval development (McGeoch 1995).

McGeoch & Chown (1997a) showed that assemblage diversity varied within and between urban and rural habitat patches in Pretoria (South Africa). Gall occupancy, larval density and species richness were lowest at the most disturbed city sites, whereas the high diversity of urban reserves contributed to the local persistence of the assemblage. Assemblage structure at the suburban sites was variable, and appeared to be transitional in structure between the city assemblage and the rural and urban-reserve assemblages (McGeoch & Chown 1997a). In total, seven Lepidoptera species were recorded in the assemblage.

Although these results were obtained for the assemblage in 1995, the consistency of this apparent response to habitat quality has not been determined. In addition to normal

weather and resource fluctuations, habitat quality may have declined in the interim as a result of increased pressure from urbanisation. To establish the reliability of a bioindicator, such as this Lepidoptera assemblage, sampling of the same, and different, localities over time to quantify trends in diversity and its response to environmental change (natural and anthropogenic), are thus needed (Philippi *et al.* 1998).

In this paper we examine whether the same relationships between habitat quality and assemblage characteristics (species richness, composition and abundance) that were found in 1995 (McGeoch & Chown 1997a) are apparent three years later. Specifically, we test for differences in assemblage structure between habitat quality categories, and whether assemblage structure changes with distance from the city centre. We further examine the effect of gall resource characteristics on assemblage structure, and control for these when examining assemblage-habitat quality relationships.

Materials and methods

Sampling procedure and data analysis

Galls were sampled between 6-9 February 1998 (precisely the same days on which sampling took place in the 1995 study (McGeoch & Chown 1997a)) from 17 sites in and around Pretoria ($25^{\circ}45'S$ $28^{\circ}10'E$) (Fig. 1.1). Five of the 17 sites sampled here were the same as those sampled in 1995. The sites were classified visually, i.e. into habitat categories, as rural, suburban garden or roadside (McGeoch & Chown 1997a). Roadside sites were located on pavements bordering busy suburban roads. One rural site (R6) was located in a rural reserve, and suburban site 5 (SG5) was located in an urban reserve. The following site and environmental variables were quantified, as in the 1995 study, to distinguish between the habitat quality of sites: (a) patch size (m^2), (b) *A. karroo* abundance at the site, (c) distance to nearest road (m), (d) distance to city centre (km) and (e) vegetation structure. Vegetation structure was scored as a value from 1-5 depending on the dominant plant cover present: (1) graminaceous ground cover, (2) non-graminaceous herbaceous ground cover, (3) woody shrubs, (4) *Acacia karroo* trees and (5) non-*Acacia karroo* trees. Cluster analysis using Euclidean distances with group average linking was then used to determine if the *a priori* habitat categories (rural, suburban garden and roadside groups) clustered together based on the quantified habitat quality variables.

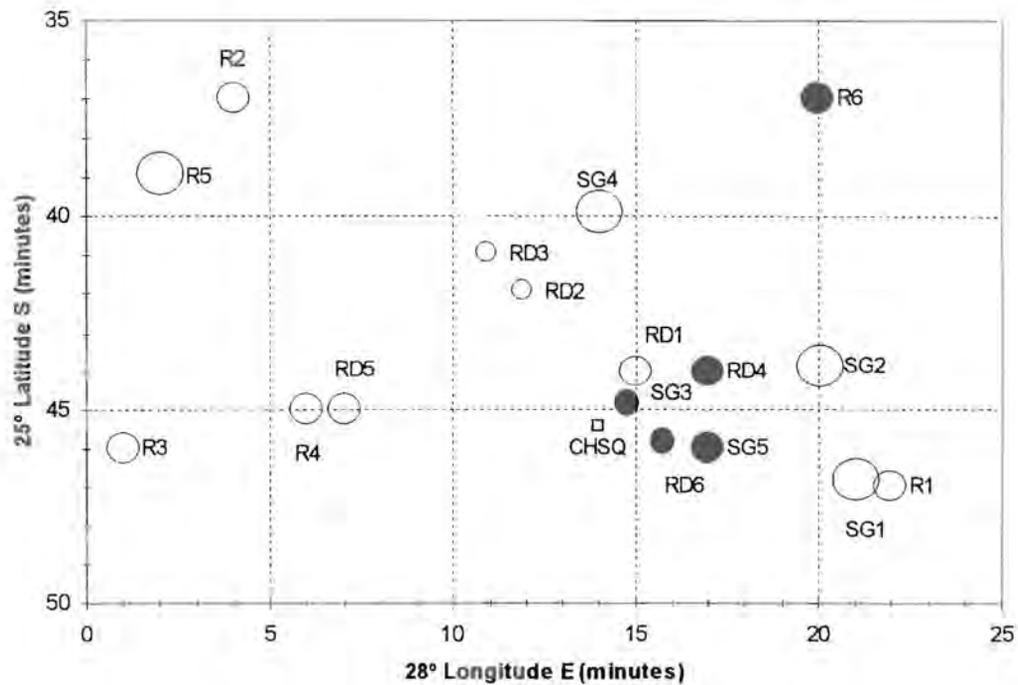


Fig. 1.1. Map depicting the positions of the sampling sites in and around Pretoria (CH SQ = Church Square, the city centre; R1-R6 = rural sites; SG1-SG5 = suburban garden sites; RD1-RD6 = roadside sites). Circle size represents number of Lepidoptera species present at site (○ = five species; ○ = six species; ○ = seven species; ○ = eight species). Solid circles represent sites sampled in 1995 and 1998.

Ten galls per tree and five trees per site were sampled (except for one site where only four trees were sampled). This has been shown to be an adequate sample size to reflect species richness and abundance at a site, and was the same as sampling conducted in 1995 (McGeoch & Chown 1997a). Gall prevalence per tree was estimated to the nearest ten galls by standing 5m from the base of the tree and first counting the galls on one half of the tree and then moving to the opposite side of the tree and counting the number of galls present on the second half. The position of each tree was determined using a Garmin 12XL Global Positioning System (GPS).

Galls were weighed and dissected. Larvae were removed and preserved in a glacial acetic acid (8%), 10% formaldehyde (3%), 96% ethyl alcohol (30%) and distilled water (59%) solution. Gall age was determined according to McGeoch (1995) and fell into one of four categories: (1) growing galls, (2) post-growth galls, (3) lignifying galls and (4) dead galls.

Although gall mass was rendered normal after log-transformation, variances were not homogenous (Zar 1984) and Kruskal-Wallis analyses of variance by ranks and Dunn's distribution free multiple comparison tests were therefore used to compare gall mass between sites, between habitat categories and between gall ages. The mean number of Lepidoptera larvae per gall and density of larvae per gall (number of larvae per 1.0 g of gall tissue) could not be rendered normal with transformation ($n = 840$), and Kruskal-Wallis analyses of variance by ranks and Dunn's distribution free multiple comparison tests were used to compare these variables between sites and between habitat categories (rural, suburban garden and roadside) (Zar 1984). Significant differences in larval abundance and density between gall ages were assessed using the same procedures.

Spearman's rank correlation coefficient was used to evaluate the relationship between gall occupancy (number of galls occupied per tree) and gall mass. The composition of gall

ages sampled in 1995 and 1998 were compared. The mean relative abundances of the species in the assemblage in 1998 were also compared with those found in 1995.

PRIMER v4.0, 1994 (Plymouth Routines in Multivariate Ecological Research) was used to conduct multivariate analyses on the assemblage data. A double square-root transformation was used on the species abundance data to weight common and rare species equally (Clarke & Warwick 1994). Bray-Curtis similarity coefficients were used because of their robustness and wide use in ecology (Faith *et al.* 1987). Similarity matrices were calculated between trees and between sites. The data from all the trees were then pooled and non-metric multidimensional scaling (MDS) was used to map the biotic sample interrelationships for all sites in a two-dimensional ordination. This was done to determine if the moth assemblage clustered according to the *a priori* habitat groupings. Analyses of similarity (ANOSIM) were then used to test if the assemblage structure differed significantly between a) these habitat groupings, and b) between groups of sites differing in their distance from the city centre. For the latter, Church Square (CH SQ) (25°45'S, 28°14'E) was taken to be the city centre (Fig. 1.1). The distance categories used were as follows: 0-5 km; 5.5-10 km; 10.5-15 km and 15.5-20 km.

The relationship between gall mass and larval abundance was examined using Spearman's rank correlation coefficient. To estimate the effect of independent habitat quality variables on larval abundance, categorical and continuous variables were analysed separately because there were insufficient degrees of freedom to include all of these in a single model. Analyses of covariance were used to analyse categorical variables, while multiple regression models were constructed for the continuous variables. Analyses of covariance were used to evaluate differences in average (across all galls at a site, $n = 17$ sites) larval abundance between i) modal gall ages and vegetation structure categories and between ii) modal gall ages and habitat categories, each with gall mass as covariate (Sokal & Rohlf 1995). Multiple regression models (Sokal & Rohlf 1995) were constructed to

determine the contribution of the environmental (patch size, *A. karroo* abundance, distance to road and distance to city centre) and resource (gall mass and gall prevalence at a site) variables to variation in larval abundance (\log_{10}) between the 17 sites at which galls were sampled. Species richness was assumed to have a poisson error structure and a generalised linear model with a log-link function was thus constructed to evaluate the contribution of the environmental (patch size, *A. karroo* abundance, distance to road and distance to city centre) and resource (gall mass and gall prevalence at a site) variables to variation in species richness at the sites (McCullagh & Nelder 1998).

Results

Gall age and mass

Although the two studies (1995 and this) were conducted at precisely the same time of year, most of the galls sampled in this study were of gall age category four (dead galls) (Table 1.1), while the modal gall age for the 1995 study was two (post-growth galls) (Fig. 1.2). Gall age structure was clearly different, and the galls older in this study compared with galls sampled at the same time in 1995. The mean (\pm S.E.) gall mass for this study was 6.39 ± 0.24 g and the oldest galls (age category four) weighed less than galls in the other age categories (Table 1.2). The galls at roadside sites had significantly lower masses than galls at the rural and suburban garden sites (Table 1.3). There is clearly large variation in gall age structure, both within and between habitat categories, and between years (i.e. the two studies, 1995 and this study conducted in 1998).

Comparison of Lepidoptera assemblage between 1995 and this study

Eight species was the maximum recorded at a single site here, whereas only seven were recorded at any single site in 1995 (McGeoch 1993; McGeoch & Chown 1997a). *Eublemma gayneri* was not recorded in 1995, although it has previously been recorded in

galls in the Pretoria area (McGeoch 1995). Furthermore, the relative abundance ranks of the species differed markedly between the two studies (Fig. 1.3). In this study, *Euzophera cullinanensis*, *Cydia* (*Cydia*) *victrix* and the Phycitinae complex occurred at all the sites and in combination these three species accounted for between 37 % to 78% of all individuals occurring at the sites. In contrast, in 1995 *E. cullinanensis* was found at one site only, and in very low numbers (Fig. 1.3) (McGeoch & Chown 1997a). Furthermore, *Ascalenia pulverata* and *Anarsia gravata* together constituted over 80% of the larvae found in the galls (Fig. 1.3).

Gall resource characteristics and larval abundance and occupancy

In this study significantly higher larval abundances ($H = 173.429$; $p < 0.05$) and larval densities ($H = 110.92$; $p < 0.05$) were found in gall age 3 (lignifying galls) than in the other gall ages, with the exception of gall age 1 (growing galls) (Table 1.2). There was also a significantly positive relationship between larval abundance and gall mass ($n = 840$, $r_s = 0.593$, $p < 0.01$). Gall age, gall mass and larval abundance were therefore interrelated. Because gall mass changes with gall age categories (Table 1.2), differences in larval abundance between gall ages were examined controlling for gall mass (Table 1.4). This was done at the level of the site rather than at the level of the individual gall, because larval abundance could not be rendered close to normal in the latter case and variances were not homogeneous. Larval abundance was shown to vary significantly between modal gall ages with gall mass held constant (Table 1.4). Gall resource characteristics therefore contribute significantly to explaining larval abundance at any site.

Significant differences in larval abundance were found between sites (Table 1.1) and between habitat categories (Table 1.3). The highest mean larval abundances were found at the urban reserve (SG5), two rural sites (R4, R5) and a suburban garden site (SG1) (Table 1.1). Larval abundance and larval density were significantly lower at the

roadside sites than at the rural and suburban garden sites (Table 1.2).

The number of galls occupied varied between 18% and 98% (Table 1.1). Roadside sites again had the lowest occupancy levels, while rural site gall occupancy was highest (78-98%) (Table 1.1). The number of galls occupied per tree also increased with an increase in gall mass ($n = 84$; $r_s = 0.58$; $p < 0.001$), and in addition to larval abundance, gall occupancy at sites with different habitat qualities was thus also not independent of the gall mass at those sites.

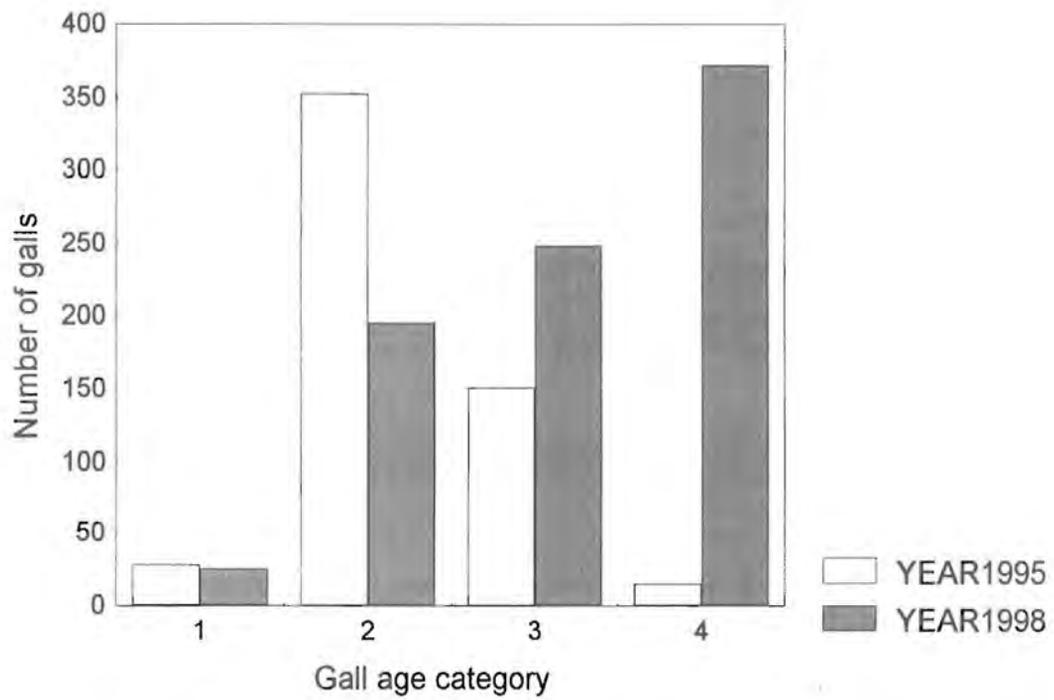


Fig. 1.2. Number of galls in each age category for 1995 and this study (1998).

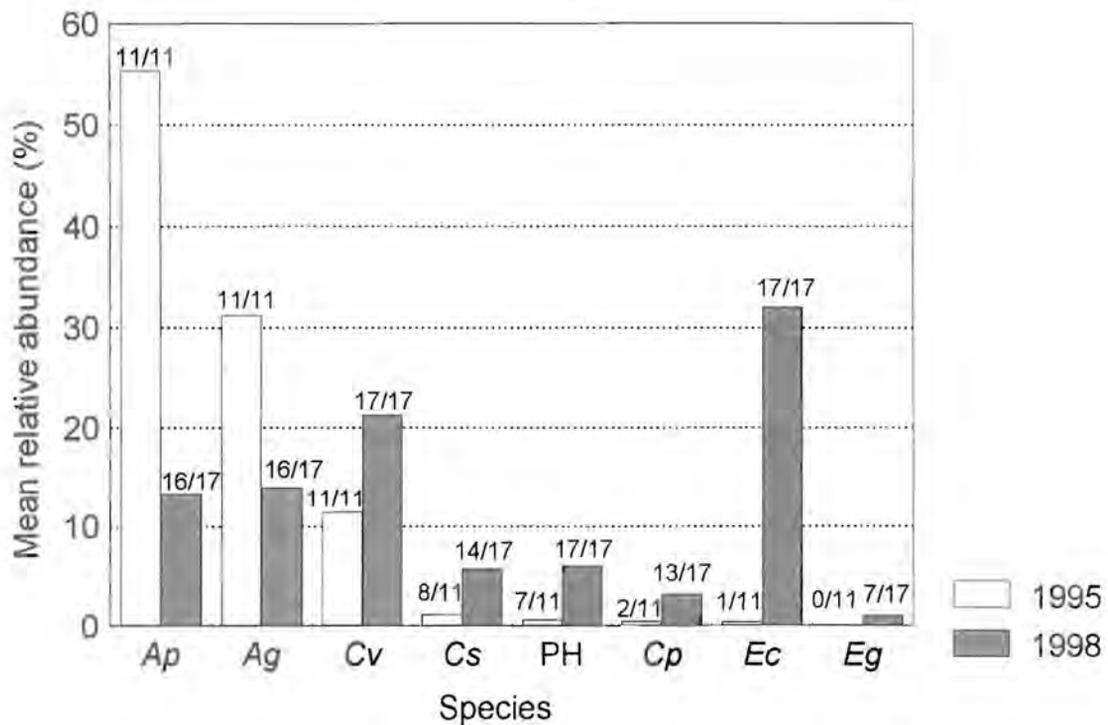


Fig. 1.3. Average relative abundance's of species for the 1995 and 1998 studies. Species ranked according to the 1995 study. Values above bars represent number of sites at which the species was present out of the total number of sites sampled (*Euzophera cullinanensis* = *Ec* (listed by McGeoch & Krüger (1994) as *Euzophera* sp. near *verrucicola* Hampson.); *Cydia* (*Cydia*) *victrix* = *Cv*; *Cryptophlebia peltastica* = *Cp*; *Characoma submediana* = *Cs*; undetermined Phycitinae species = *PH*; *Ascalenia pulverata* = *As*; *Anarsia gravata* = *Ag*; *Eublemma gayneri* = *Eg* (listed by McGeoch & Chown (1997c) as *E. brachygonia*)).

Table 1.1. Mean (\pm S.D.) of gall mass (g) (Kruskal-Wallis $H = 239.34$; $p < 0.05$), larval abundance (number of larvae per gall) (Kruskal-Wallis $H = 261.99$; $p < 0.05$), larval density (number of larvae per 1.0 g gall mass) (Kruskal-Wallis $H = 201.32$; $p < 0.05$) and species richness (S), modal gall age and percentage galls occupied by the Lepidoptera larvae at each site. (R1-R6 = rural sites; SG1-SG5 = suburban garden sites; RD1-RD6 = roadside sites).

Site	n	Mean \pm S.D. gall mass	Mean \pm S.D. Larval abundance	Mean \pm S.D. Larval density	S	Modal gall age	% galls occupied
R1	50	4.12 \pm 3.09	2.62 \pm 2.45	0.71 \pm 0.63	7	3	78
R2	50	8.96 \pm 6.72	4.12 \pm 3.32	0.60 \pm 0.59	7	4	92
R3	50	5.96 \pm 4.34	3.02 \pm 3.26	0.53 \pm 0.51	7	4	84
R4	50	13.01 \pm 10.72	5.38 \pm 5.15	0.45 \pm 0.32	7	2	98
R5	50	13.80 \pm 10.15	5.76 \pm 6.97	0.39 \pm 0.33	8	3	84
R6	50	3.82 \pm 2.79	3.00 \pm 4.98	0.68 \pm 0.93	7	4	64
SG1	40	9.07 \pm 7.86	7.60 \pm 6.43	0.99 \pm 0.76	8	3	90
SG2	50	6.52 \pm 7.18	2.96 \pm 3.17	0.57 \pm 0.55	8	4	78
SG3	50	4.71 \pm 4.17	1.12 \pm 1.21	0.34 \pm 0.48	6	4	60
SG4	50	6.02 \pm 4.68	1.66 \pm 1.77	0.36 \pm 0.43	8	2	76
SG5	50	5.08 \pm 5.17	5.98 \pm 7.26	1.24 \pm 1.04	7	3	84
RD1	50	2.69 \pm 2.74	0.64 \pm 1.32	0.24 \pm 0.44	7	4	30
RD2	50	2.25 \pm 1.11	0.36 \pm 0.72	0.15 \pm 0.32	5	4	24
RD3	50	3.09 \pm 2.84	0.44 \pm 1.15	0.06 \pm 0.15	5	4	18
RD4	50	2.94 \pm 3.98	1.04 \pm 2.31	0.73 \pm 2.84	7	4	42
RD5	50	11.69 \pm 8.27	1.92 \pm 2.04	0.17 \pm 0.20	7	2	64
RD6	50	5.36 \pm 6.23	2.42 \pm 4.31	0.49 \pm 0.71	6	4	62

Table 1.2. Kruskal-Wallis one-way analyses of variance by ranks and Dunn's multiple comparison test of gall mass ($H = 103.90$), larval abundance ($H = 173.429$) and density ($H = 110.92$) between gall ages. No letters in common denote significant differences at $p < 0.05$.

Gall age	n	Mean \pm S.E.	Mean \pm S.E.	Mean \pm S.E.
		gall mass	larval abundance	larval density
3	248	7.94 \pm 0.48 ^a	4.82 \pm 0.36 ^a	0.75 \pm 0.05 ^a
1	25	6.56 \pm 0.90 ^a	3.36 \pm 0.71 ^{ab}	0.55 \pm 0.11 ^{ab}
2	195	9.40 \pm 0.65 ^a	3.63 \pm 0.33 ^b	0.46 \pm 0.04 ^b
4	372	3.76 \pm 0.18 ^b	1.18 \pm 0.11 ^c	0.36 \pm 0.06 ^c

Table 1.3. Mean (\pm S.E.) of gall mass (g) (Kruskal-Wallis $H = 86.71$; $p < 0.001$), larval abundance ($H = 157.64$; $p < 0.001$) and larval density (Kruskal-Wallis $H = 125.70$; $p < 0.001$) between habitat categories. Means with no letters in common denote significant differences between galls of $p < 0.001$.

Site	n	Mean \pm S.E. gall mass	Mean \pm S.E. larval abundance	Mean \pm S.E. larval density
Rural	300	9.19 \pm 0.50 ^a	4.30 \pm 0.29 ^a	0.54 \pm 0.03 ^a
Suburban garden	240	6.16 \pm 0.39 ^b	3.71 \pm 0.33 ^a	0.69 \pm 0.05 ^a
Suburban roadside	300	4.67 \pm 0.34 ^c	0.90 \pm 0.10 ^b	0.19 \pm 0.02 ^b

Table 1.4. Results of one-way analysis of covariance across sites for larval abundance between gall ages, with gall mass as covariate ($R^2 = 0.75$, $F_{3,13} = 12.75$, $p < 0.001$). No letters in common denote significant differences in least squares means for larval abundance (\log_{10}) at $p < 0.05$.

Covariate and factor	d.f.	Type III Sum of Squares	F	p<
Gall mass (\log_{10}) g	1	0.977	19.71	0.001
Gall age	2	0.393	3.97	0.05
	<u>n (sites)</u>	<u>Larval abundance \pm S.E.</u>		
	2	2.99 \pm 0.31 ^{ab}		
	3	5.38 \pm 0.46 ^a		
	4	1.91 \pm 0.14 ^b		

Assemblage structure and habitat quality

Species richness (S) was highest at one of the rural sites (R5) and at three suburban garden sites (SG1, SG2, SG4) (with eight species), and lowest at two roadside sites (RD2, RD3) (five species) (Table 1.1).

Habitat quality varied greatly between sites as well as within the *a priori* habitat classification groupings (Table 1.5). Roadside sites were expected to cluster together because of their small patch size, low *A. karroo* abundance and proximity to the nearest road and city centre. Rural sites were expected to constitute larger patches with higher *A. karroo* abundance and greater distance from the nearest road and from the city centre, while suburban garden sites were expected to be transitional between roadside and rural sites in terms of habitat quality. The sites did however not cluster clearly according to these habitat quality variables (Fig. 1.4).

Although in terms of moth assemblage structure, the rural sites were mostly clustered together, there was little clear grouping of the assemblages according to the *a priori* habitat quality categories (Fig. 1.5). The Lepidoptera assemblage at rural sites was however found to be significantly different from the assemblage at roadside sites, but not from suburban garden sites (ANOSIM Global R = 0.089; $p < 0.001$) (Table 1.6). In addition, the Lepidoptera assemblage structure of sites 0-5 km from the city centre was significantly different from the assemblage structure at all sites further than 5 km from the city centre (ANOSIM Global R = 0.145; $p < 0.001$) (Table 1.7).

Although no significant differences were found in assemblage structure between the roadside and garden sites, in general the garden sites (i.e. on average further from the city centre (Table 1.5) and lower traffic volume (pers. obs.)) had more species than the roadside sites (Table 1.1). Larval abundance was significantly lower at the roadside sites than at sites in the other habitat categories. Larval density was also significantly lower at

roadside than garden sites (Table 1.3). Thus the Lepidoptera assemblage characteristics at roadside sites are significantly different from the other habitat quality categories.

Interactions between resource, assemblage and habitat quality variables

Although the analyses of covariance for larval abundance with gall age and habitat category, as well as with gall age and vegetation structure, as factors were significant and explained a high proportion of the variation, only gall mass as the covariate contributed significantly to the models (Table 1.8). Therefore, as measures of habitat quality, neither habitat category nor vegetation structure appear to explain between site differences in larval abundance.

All six continuous environmental and resource variables provided the best-fit model for larval abundance, explaining 93% of the variation (Table 1.9). Gall mass and distance to the city centre contributed significantly (positive relationship) to explaining larval abundance (Table 1.9). Patch size and gall prevalence also contributed significantly to explaining larval abundance, although in the latter case this relationship was negative (Table 1.9). None of the variables in the generalised linear model contributed significantly to explaining species richness ($p > 0.05$ for all variables in model; d.f. = 10, deviance = 0.79).

Table 1.5. Habitat quality variables and average (\pm S.E.) gall prevalence at each site (R1-R6 = rural sites; SG1-SG5 = suburban garden sites; RD1-RD6 = roadside sites). Vegetation structure was a scored value from 1-5 depending on the dominant plant cover present: (1) graminaceous ground cover, (2) non-graminaceous herbaceous ground cover, (3) woody shrubs, (4) *Acacia karroo* trees and (5) non-*Acacia karroo* trees.

Site	Patch size (m ²)	<i>A. karroo</i> abundance	Distance to road (m)	Distance to city centre (km)	Vegetation Structure	Gall prevalence (\pm S.E.)
R1	121000	300	1.00	18.75	4	62 \pm 7.10
R2	103130	20	9.36	18.00	4	76 \pm 6.90
R3	78700	100	10.00	17.50	4	58 \pm 4.05
R4	593750	80	49.00	8.00	4	78 \pm 3.07
R5	6000	18	5.04	17.00	4	62 \pm 7.10
R6	2898000	400	10.00	19.75	4	126 \pm 11.07
SG1	125000	30	2.00	17.75	3	42.5 \pm 6.24
SG2	230740	40	1.00	15.00	3	70 \pm 14.25
SG3	213000	16	2.16	6.75	2	86 \pm 6.68
SG4	3900	200	4.38	9.50	5	104 \pm 5.62
SG5	1014000	150	150.00	8.50	2	46 \pm 1.26
RD1	15000	28	10.80	6.75	1	56 \pm 6.21
RD2	20000	17	10.08	4.75	5	128 \pm 9.51
RD3	37500	7	4.32	4.50	4	64 \pm 4.07
RD4	104700	22	5.76	10.50	5	62 \pm 4.63
RD5	8750	80	7.70	6.25	5	70 \pm 2.65
RD6	17500	10	3.00	8.75	5	24 \pm 1.61

Table 1.6. Probability values of analyses of similarity (ANOSIM) of the Lepidoptera assemblage between habitat categories (***) = $p < 0.001$). n = number of trees.

	Rural	Suburban garden	Roadside	n
Rural	–			30
Suburban garden	ns	–		24
Roadside	***	ns	–	27

Table 1.7. Probability values of analyses of similarity (ANOSIM) of the Lepidoptera assemblage between sites differing in their distance from the city centre (* = $p < 0.05$, *** = $p < 0.001$). n = number of trees.

	0-5 km	5.5-10 km	10.5-15 km	15.5-20 km	n
0-5 km	–				10
5.5-10 km	***	–			35
10.5-15 km	*	ns	–		10
15.5-20 km	***	ns	ns	–	29

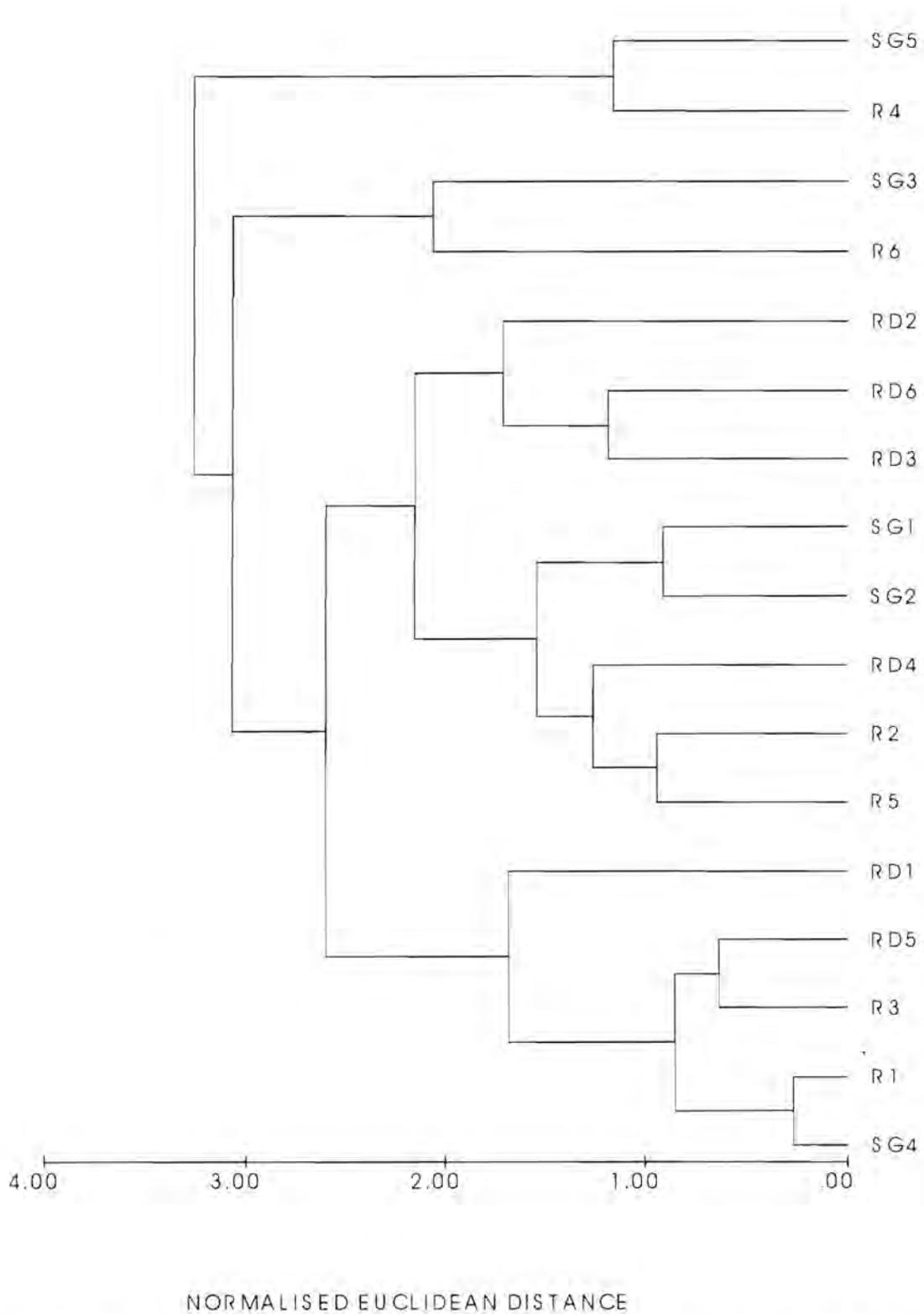


Fig. 1.4. Dendrogram of normalised Euclidean Distances between the 17 sites for the habitat quality variables (R1-R6 = rural sites; SG1-SG5 = suburban garden sites; RD1-RD6 = roadside sites).

Table 1.8. Results of one-way analyses of covariance between sites for \log_{10} (larval abundance) a) between gall ages and habitat categories ($R^2 = 0.82$; $F_{5,11} = 10.32$; $p < 0.001$), and b) between gall ages and vegetation structure ($R^2 = 0.70$; $F_{6,10} = 3.87$; $p < 0.05$) with gall mass as covariate.

Covariate and factor	d.f.	Type III Sum of Squares	F	p<
a. Gall mass (\log_{10}) g	1	0.446	11.00	0.01
Gall age	2	0.179	2.20	0.16
Habitat category	2	0.198	2.44	0.13
b. Gall mass (\log_{10}) g	1	0.424	5.55	0.05
Gall age	1	0.002	0.03	0.87
Vegetation structure	4	0.250	0.82	0.54

Table 1.9. Best-fit multiple regression model to determine the contribution of environmental and gall resource variables to explaining variation in larval abundance (\log_{10}) for 17 sites (adjusted $R^2 = 0.93$; $F_{6,10} = 34.82$; $p < 0.001$).

Variable	Coefficient estimate	t(10)	p
Intercept	0.39	1.18	0.267
\log_{10} gall mass	0.98	7.76	< 0.001
\log_{10} patch size	0.11	2.75	0.021
\log_{10} <i>A. karma</i> abundance	0.12	1.85	0.094
\log_{10} distance to road	0.10	1.66	0.129
distance to city centre	0.02	3.76	0.004
\log_{10} gall prevalence	-0.68	-4.08	0.002

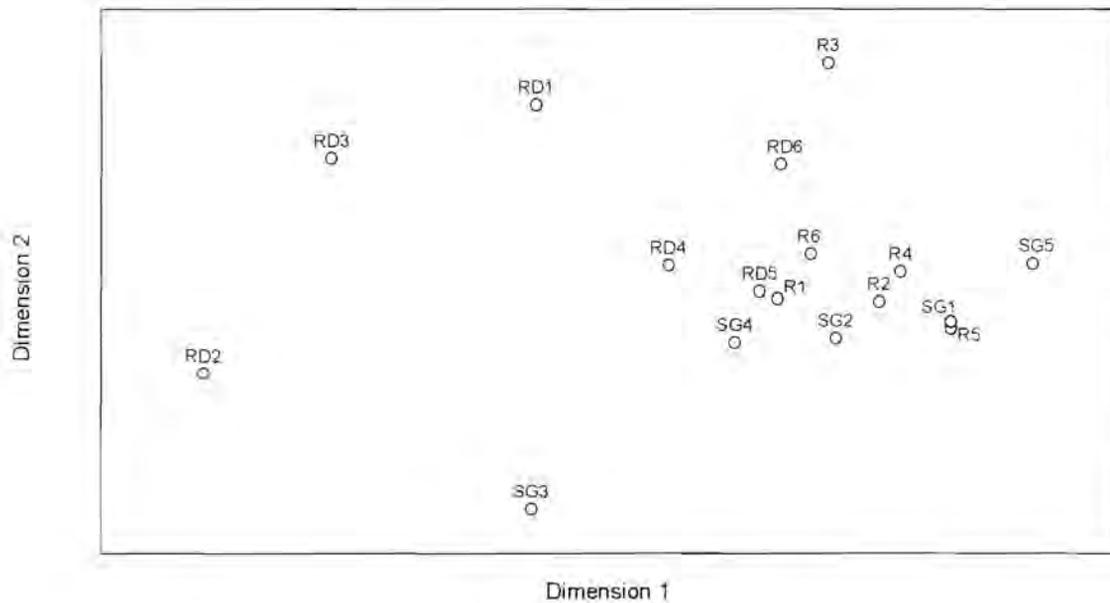


Fig. 1.5. Non-metric multidimensional scaling ordination of abundance's of species in the Lepidoptera assemblage at 17 sites, stress = 0.09. The absolute distance between every pair of points on the ordination is a relative measure of their similarity (R1-R6 = rural sites; SG1-SG5 = suburban garden sites; RD1-RD6 = roadside sites).

Discussion

Despite substantial differences in gall age structure, absolute larval abundance, and species relative abundances between this study and the one undertaken in 1995, habitat-associated differences in the lepidopteran assemblages were consistent across years. That is, both in this study, and the one undertaken by McGeoch & Chown (1997a), assemblages closest to the city centre and those occupying galls in roadside sites differed significantly from those found elsewhere. In both studies, species richness, larval density and larval abundance were generally lower at sites closest to the city centre than at those further away, and in this study distance to the city centre explained a significant proportion of the variation in larval abundance. Likewise, in both 1995 and 1998 the urban reserve had the highest larval density (McGeoch & Chown 1997a), and there were pronounced differences between roadside and suburban garden sites. Larval abundance was significantly lower at roadside sites than at sites in other habitat categories (rural and suburban garden), and garden sites tended to have both higher species richness and larval densities compared with roadside sites.

Therefore urbanisation, represented by distance to the city centre, and the influence of roadside disturbance had similar effects on the assemblage, in both years, notwithstanding seasonal variation in the quality and quantity of the gall resource available, and successional changes in the Lepidoptera assemblage (see also McGeoch 1993; McGeoch & Chown 1997c). By providing such an independent, post-identification test of the assemblage as an ecological bioindicator (McGeoch 1998; McGeoch *et al.* submitted), we have demonstrated that this moth assemblage is a robust biological indicator of the impact of urbanisation on an insect assemblage.

The most pronounced effects of urbanisation on the lepidopteran assemblage took the form of a significant decrease in larval densities and abundances, and a somewhat less consistent reduction in species richness, both here and in the 1995 study (McGeoch &

Chown 1997a). Such decreases in abundances and/or densities with disturbance, and/or proximity to central city areas (often business districts), are common features of both insect and avian assemblages studies along urban and/or disturbance gradients (Duelli *et al.* 1990; Blair 1996, 1999; Rottenborn 1999; see also Ruszezyk 1996). In this respect, our results are similar to those undertaken elsewhere.

Nonetheless, there was substantial variation in the absolute and relative abundances of species between years. For example, in 1995, *Ascalenia pulverata* had the highest relative abundance of all the species present, while *Euzophera cullinanensis* had the lowest. In contrast, the latter species had the highest relative abundance in 1998, while the former ranked fourth. This variation was undoubtedly due largely to differences in gall age structure in the two sampling periods, despite the fact that sampling dates were identical across years. Galls sampled in 1995 were mostly in age category two, while those sampled in 1998 were mostly in age category four. Such phenological variation is perhaps not surprising because *Acacia karroo* flowering phenology, and hence gall development, is highly dependent on annual rainfall patterns, tree water status and the age of the tree, and these factors generally vary between galling seasons (McGeoch 1995). Nonetheless, this variation has a substantial effect on gall mass because of the relationship between gall age and mass (see above and McGeoch 1993, 1995). Galls sampled in 1995 (mean (g) \pm S.E. = 14.07 ± 0.53 , data from McGeoch & Chown 1997a) were significantly heavier (Mann-Whitney U test $Z = -3.95$, $p < 0.001$) than those sampled in 1998 (mean (g) \pm S.E. = 6.39 ± 0.24). In turn, gall mass has a substantial influence on larval abundance (see Table 1.4 and McGeoch & Chown 1997c), hence accounting for the differences in absolute abundance found between years. In contrast, the different relative abundance patterns are likely to be a consequence of differences in succession in the moth assemblage associated with gall age (McGeoch 1993, 1995; McGeoch & Chown 1997c), a characteristic common

to assemblages that occupy discrete and ephemeral habitats (Mitchell & Arthur 1990; Hirschberger 1998).

Thus species composition, species abundance ranking, and species abundances across years are unlikely to be best-suited to monitoring the impact of urbanisation on this assemblage because of the difficulty of achieving close phenological matching. Rather, species abundances and densities, and species richness compared across sites, provide more suitable parameters for monitoring if phenological matching cannot be achieved. This is also likely to be the case for monitoring in disparate sites because species relative abundances are generally not concordant (McGeoch & Chown 1997b). Species richness and larval abundances measured across sites within a given year are therefore likely to be most useful for long-term monitoring of this assemblage across urban-rural gradients. These parameters have been found to be useful for measuring the effects of urbanisation on other invertebrate assemblages (Miyashita *et al.* 1998), but this may not be the case when the goals of indication concern the early detection of habitat change (see discussion McGeoch 1998; McGeoch *et al.* submitted).

In conclusion, our study has verified the findings of an earlier one undertaken by McGeoch & Chown (1997a), that urban reserves are important for conserving diversity in cities, that otherwise have a negative influence on biodiversity (see also Blair 1996, 1999; Miyashita *et al.* 1998; Rottenborn 1999). Of course the utility of these reserves, or green areas, will depend on the extent to which this diversity remains largely unchanged through time, which in turn depends on the size and condition of the urban reserve patch, changing distances from colonisation sites as urban areas expand, and the nature of the area between the patches (den Boer 1990; Mader *et al.* 1990; Taylor *et al.* 1993; Halley & Dempster 1996). Such long term monitoring is seldom undertaken for urban reserves, and particularly not in South Africa. We have provided a verified means of so doing, at least for

urban areas located in the grassland and savanna biomes of South Africa where *Acacia karroo* and its gall-associated lepidopteran assemblage are abundant.

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CHAPTER 2

Spatial patterns in a Lepidoptera assemblage across an urban-rural gradient.

Introduction

The spatial distribution and abundance structure of species are determined by a complex of biotic and abiotic factors, and are likely to vary across the ranges of species and assemblages. Species abundances may be spatially structured as a result of, for example, climate and topography (Brown 1984; Brussard 1984; Coxwell & Bock 1995; Thomson *et al.* 1996; Koenig 1999), metapopulation dynamics (Hanski 1982; Hanski & Gyllenberg 1993), the distribution of available resources and habitats (Dempster & Pollard 1981; Dempster 1983; Underwood & Chapman 1996; Logerwell *et al.* 1998) and stochastic processes (Rossi & Quénéhervé 1998). Despite the multiple mechanisms likely to structure species abundances, there is some evidence to show that abundance tends to be highest near the centre of species distribution ranges, decreasing towards their boundaries (Andrewartha & Birch 1954; Hengeveld & Haeck 1982; Brown 1984; Brussard 1984; Bock 1987; Brown *et al.* 1995). This may also be true, and is perhaps more so, of populations within the distribution ranges of species (Lennon *et al.* 1997; Thomas & Kunin 1999). Changes in the abundance and density of individuals across their range are usually associated with one or more environmental gradients, such as moisture or elevation, or as a result of biotic factors, such as resource quality and competition (Brown 1984; Brussard 1984; Lennon *et al.* 1997; Kuuluvainen *et al.* 1998; Stiling *et al.* 1999). Therefore, because there is generally a positive relationship between abundance and occupancy (Bock & Ricklefs 1983; Brown 1984; Bock 1987; Brown & Maurer 1987; Gotelli & Simberloff 1987;

Collins & Glenn 1990; Bolger *et al.* 1997), when sampling across the distribution range, or populations, of an organism, a species will be found to occur at most of the sampling sites in the centre of the range or population, while its distribution will be more patchy towards the boundaries (Brown 1984; Lennon *et al.* 1997). Likewise, distributions of species may end abruptly as a result of sharp environmental changes, or the abundance (or the number of sites occupied) of a species may decline gradually across an environmental gradient without showing an abrupt distribution edge (Lennon *et al.* 1997).

In addition to this variability in the distribution and abundance of species, fragmentation within the distribution ranges of species and assemblages is likely to increase the patchiness of species distributions, and to disrupt spatial gradients in species abundances. For example, urbanisation divides the landscape into fragments of natural vegetation surrounded by, for example, buildings, roads and alien vegetation (McDonnell & Pickett 1990). The effect of such fragmentation includes a reduction in total natural habitat available to organisms, a reduction in habitat fragment size, an increase in isolation of the habitat fragments, and an increase in pollution and the invasion of alien flora (Bolger *et al.* 1997; Gordon 1998; Suarez *et al.* 1998; Rottenborn 1999). The effects of this human-induced disturbance on biotic communities are known to include a reduction in species richness and abundance, and the invasion of alien fauna and subsequent reduction in both species richness and abundance of native fauna (Bolger *et al.* 1997; Suarez *et al.* 1998; Zabel & Tschardtke 1998; Rottenborn 1999). Increased fragmentation of natural habitats in urban environments may therefore result in the organisms inhabiting these urban areas having more patchy distributions than the same species found in unfragmented rural or undeveloped areas. In addition, a disturbance gradient across developed areas, from urbanised to less developed rural habitats, may exist to which species respond. The spatial distribution patterns of species and assemblages may thus differ substantially between urban and rural environments.

However, spatial patterns in biotic variables are also influenced by the scale of (extent and grain) investigation of a study (Wiens 1989; Koricheva & Haukioja 1994; MacNally & Quinn 1998). For example, if the grain (the size of individual units of observation) of the study is kept constant and the extent (the overall area encompassed) of the study is reduced, fewer landscape elements will be included in the study area (Wiens 1989). This will affect the observed spatial structure (Wiens 1989; Erasmus *et al.* 1999). Different processes are likely to have an influence on observed patterns in species distributions and abundances at these different spatial scales (Levin 1992; Koricheva & Haukioja 1994; Sale 1998; Huston 1999). There is therefore no “correct” scale at which spatial patterns should be investigated; instead a scale relevant to the organism(s) and processes of interest should be chosen (Levin 1992; Huston 1999).

Few studies have however examined spatial patterns in the distribution of insect populations or assemblages across either undeveloped or developed landscapes (Underwood & Chapman 1996; Legendre & Legendre 1998). Consequently, information on the spatial structure of species abundances and other variables is seldom available for insect species and assemblages. Pattern analysis, such as the documentation of spatial patterns in species distributions, is the first fundamental step towards the formulation of hypotheses and predictions of the mechanisms and processes that are likely to underlie these patterns (Levin 1992; Blackburn & Gaston 1998). Thus, quantifying spatial distribution patterns in species abundances and the resources that they utilise, provides the groundwork for establishing the scales at which different ecological processes that generate these patterns operate (Borcard *et al.* 1992; Underwood & Chapman 1996; Koenig 1999).

The Lepidoptera assemblage

The Lepidoptera larvae examined in this study inhabit galls induced by a rust fungus (*Ravenelia macowaniana* (Pazschke)) on *Acacia karroo* (Hayne) trees. The resource that these fungus galls provide is seasonal, ephemeral and their distribution and abundance is highly variable (McGeoch 1993). Nonetheless, the galls provide protection from natural enemies and are a high quality food source to the Lepidoptera larvae inhabiting the galls (McGeoch 1995). A previous study by McGeoch (1995) showed that eight Lepidoptera species inhabit these galls in the Pretoria area. These include the following families: Gelechiidae (*Anarsia gravata* Meyrick), Cosmopterigidae (*Ascalenia pulverata* (Meyrick)), Tortricidae (*Cryptophlebia peltastica* (Meyrick), *Cydia* (*Cydia*) *victirx* (Meyrick)), Noctuidae (*Characoma submediana* Wiltshire, *Eublemma gayneri* Rothschild), Pyralidae (*Euzophera verrucicola* (Balinsky) and an undetermined Phycitinae species). Gall occupancy has been shown to be extremely high; between 52-100 % of the galls at any site are generally occupied (McGeoch & Chown 1997a) (18-98 % in this study).

Numerous factors may influence this Lepidoptera assemblage and its resource at the scale of the gall (microscale), tree (mesoscale) and site (local scale). Assessing the variability of resource and assemblage parameters at these three scales provides insight into the likely relative importance of mechanisms affecting the assemblage and its resource within the local scale of a patch of *A. karroo* trees.

(i) Local scale factors

Local scale factors are those factors operating at and across the scale of the individual patch of *A. karroo* trees. The association between the fungus and the Lepidoptera larvae inhabiting the fungus galls has a widespread distribution in South Africa (McGeoch 1995). Species richness, abundance and composition have been shown to vary within a region (McGeoch & Chown 1997a, b). In this study, galls were sampled across an urban-rural

gradient. Lepidoptera assemblage structure at sites closer to the city centre was shown to be significantly different from assemblage structure at sites further away (Chapter 1). Furthermore, larval abundance, larval density and species richness were lower at two sites closest to the city centre (Chapter 1). As habitat quality changes in urban areas have been shown to alter the structure of other arthropod assemblages (Duelli *et al.* 1990; McGeoch & Chown 1997a; Miyashita *et al.* 1998), it is thus likely that the species composition and abundance of the gall inhabiting Lepidoptera assemblage will change along this urban gradient. Climate has also been shown to influence species geographical distributions (Rogers & Randolph 1991; Ayres & Scriber 1994; Davis *et al.* 1998; Hill *et al.* 1999). However, a climatic gradient across a finer scale, such as an east-west moisture gradient in and around Pretoria, may be present in this system which may influence fungus spore germination. Processes at the level of the tree and gall may however influence these local scale patterns (Sale 1998).

(ii) *Mesoscale factors*

These are processes operating at the scale of the tree. The galls develop from the flowers and seed pods of *A. karroo* (McGeoch 1995). Annual rainfall patterns, tree water status and the age of the individual tree influence *A. karroo* flowering. Thus rainfall, tree water status and tree age may thus directly affect gall development (McGeoch 1995).

(iii) *Microscale factors*

The finest scale processes operating in this system would be at the scale of the gall. Galls are affected by environmental conditions, such as temperature (Layne 1991; Layne 1993). Microclimatic conditions such as humidity, time of exposure to sunlight and gall water content may cause individual galls to be more suitable as a resource than others. Although gall occupancy increases with an increase in gall mass (Chapter 1), a positive

relationship between gall mass and larval density has previously been found for this assemblage (McGeoch & Chown 1997b), demonstrating some level of resource limitation. Thus, heavier galls may be more suitable to oviposition than galls that weigh less. Furthermore, as the galls age, the gall tissue becomes drier and less suitable for consumption by the larvae that feed on the live gall tissue (McGeoch 1995). Thus gall age may also influence the abundance and composition of the Lepidoptera assemblage found within the galls. The abundance and species of larvae present in the galls may also influence the spatial patterns found due to exploitation competition (McGeoch & Chown 1997b). A threshold density of 13 individuals per gall has been recorded for this assemblage as the limited tissue within a single gall causes mass compensation between individuals at densities higher than this (McGeoch & Chown 1997b).

Thus numerous factors, from the widespread influence of urbanisation to the small-scale suitability of the individual gall as a resource, influence this Lepidoptera assemblage, and are likely to affect observed spatial patterns in the system.

This paper therefore examines spatial patterns in the distribution and abundance of a fungus-gall inhabiting Lepidoptera assemblage across a city-urban-rural development gradient. First, the spatial structure of the gall resource inhabited by the assemblage is compared with the spatial structure of species and assemblage characteristics. Second, the spatial structure of resource (vegetation structure, gall mass, density and age) and assemblage (larval abundance, species richness and individual species abundances) variables are compared between urban and rural sites. Using spatial autocorrelation we compare the patch diameters, zones of influence, general correlogram structure and individual autocorrelation statistics (see explanation below) of resource and assemblage variables across the study area.

Materials and Methods

Sampling procedures

Galls were collected from 17 sites in and around Pretoria, South Africa (25°45'S 28°10'E) from 6-9 February 1998 (Fig. 2.1). The sites were sampled across an urban-rural gradient. Urban sites constituted trees sampled in suburban areas. Rural sites were situated on the outskirts of Pretoria in less developed areas (Fig. 2.1). Rural sites were expected to be larger and further from the city centre, with Church Square (CH SQ) (25°45'S, 28°14'E) taken as the city centre (Fig. 2.1). Ten galls per tree and five trees per site were sampled (this has been shown to be an adequate sample size according to McGeoch & Chown (1997a)), except for one site where only four trees could be sampled. Vegetation structure at a site was scored as a value from 1-5 depending on the dominant plant cover present: (1) graminaceous ground cover, (2) non-graminaceous herbaceous ground cover, (3) woody shrubs, (4) *Acacia karroo* trees and (5) non-*Acacia karroo* trees. Gall density per tree was estimated to the nearest 10 galls by standing 5m from the base of the tree and first counting the galls on the one half of the tree and then moving to the opposite side of the tree and counting the number of galls present on the second half. The position of each tree was determined using a Garmin 12XL Global Positioning System (GPS). The GPS coordinates for the trees were converted to decimal degrees before analysis.

Galls were weighed, dissected and the larvae were removed and preserved in a glacial acetic acid (8%), 10% formaldehyde (3%), 96% ethyl alcohol (30%) and distilled water (59%) solution. Larvae were identified according to the key developed by McGeoch (1995). Gall age was determined according to McGeoch (1995) and fell into one of four categories: (1) growing galls, (2) post-growth galls, (3) lignifying galls and (4) dead galls.

Spatial autocorrelation

One means of quantifying and comparing patterns in spatial structure is the use of measures of spatial autocorrelation (Koenig & Knops 1998; Legendre & Legendre 1998; Koenig 1999). Biotic or abiotic variables are said to exhibit positive spatial autocorrelation when observations from neighbouring areas are more similar than expected for randomly, spatially-associated pairs of observations (Legendre & Fortin 1989; Legendre 1993; Legendre & Legendre 1998). Pairs of sites, a given distance apart, that are less similar than expected for randomly, spatially-associated pairs of observations are negatively autocorrelated (Legendre & Legendre 1998).

Structure functions, such as correlograms, may then be used to graphically represent changes in the autocorrelation coefficient with physical distance between pairs of observations or sites (Sokal & Oden 1978a; Legendre & Legendre 1998) (Fig. 2.2). Positive autocorrelation in the first distance class of a correlogram, for example for a variable such as species abundance, indicates that the variable is clumped or patchy at that scale of examination (represented by the size of the distance class) (Legendre & Fortin 1989; Legendre & Legendre 1998; Rossi & Quénéhervé 1998). The patch diameter of a variable was taken here as approximately equal to the midpoint distance between the first positive or last positive value (if more than one positive autocorrelation value occurs before the first negative value) (b in Fig. 2.2) and the first negative autocorrelation value in each correlogram (c in Fig. 2.2). Patch diameter therefore represents the area within which the values of a particular variable are more similar to one another than expected by chance.

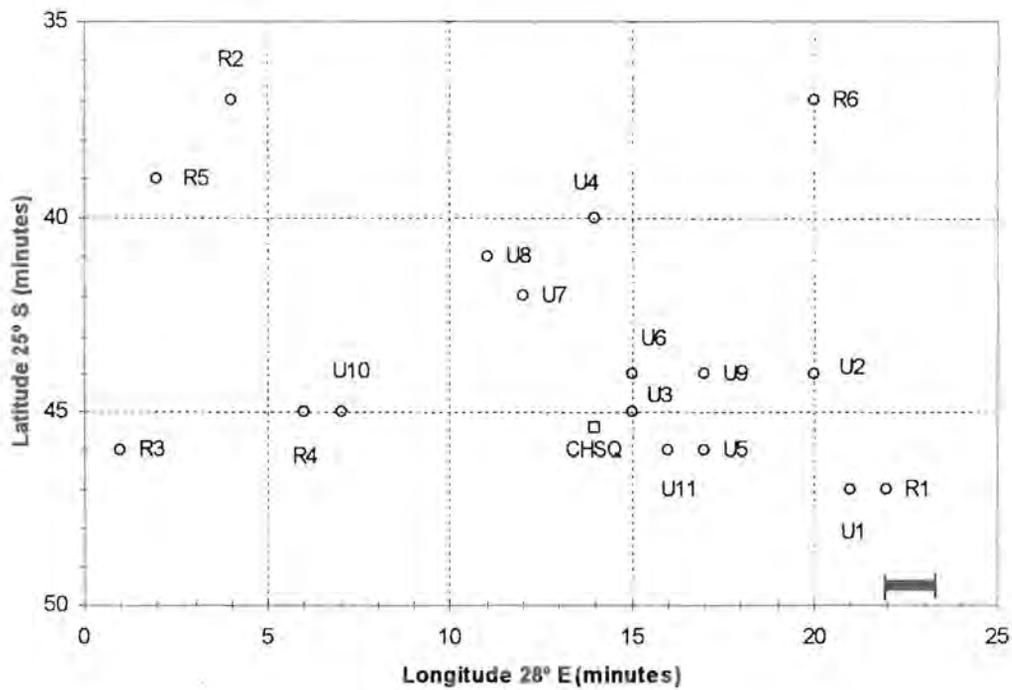


Fig. 2.1. Positions of the 17 sites used in the spatial analyses (R1-R6 = rural sites; U1-U11 = urban sites; CH SQ = Church Square, the city centre). Scale bar represents 2 km.

A further aspect of the spatial structure of the variables that was examined was the 'zone of influence' (Legendre & Legendre 1998). The distance at which the first maximum negative autocorrelation value is found delimits the distance between zones of maximum and minimum values of the variable under consideration, and is termed the zone of influence (Fig. 2.2) (Legendre & Legendre 1998). The zone of influence therefore depicts the size of the area over which the full range of values for the biotic variable are expressed, although the change in the value of the variable across this area may not be monotonic. The correlogram of a biotic variable (such as species abundance) responding to a linear environmental gradient, will decrease monotonically with an increase in spatial scale (Sokal & Oden 1978b; Legendre & Fortin 1989; Legendre & Legendre 1998) (Fig. 2.2a-e). If species abundance's are structured by such a gradient, the zone of influence will be represented by a monotonically decreasing correlogram (Fig. 2.2a-e). The zone of influence will approximate patch diameter if the maximum negative autocorrelation value is also the first negative value on the correlogram.

The final correlogram characteristic examined was the presence of repeated patterns across distance classes. For example, positive autocorrelation at both small and large distances reflects the reoccurrence of an aggregated structure through space (Legendre & Fortin 1989).

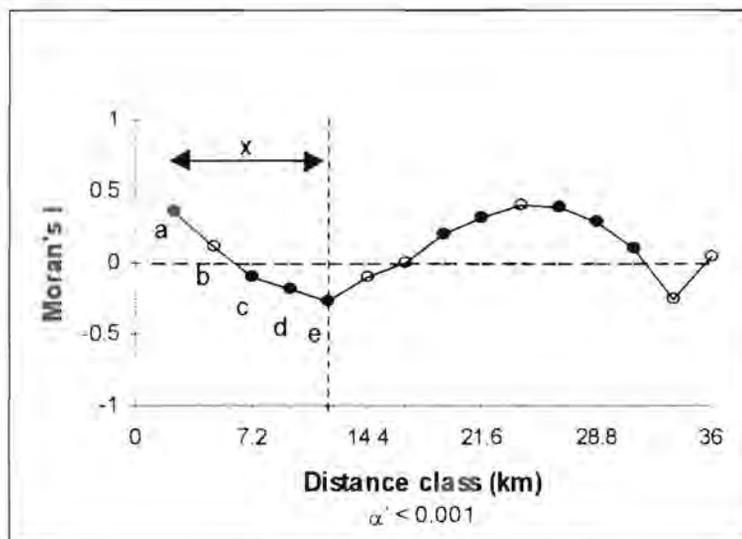


Fig. 2.2. Illustrative correlogram (structure function) representing changes in the autocorrelation coefficient with distance. Doubled-headed arrow (x) depicts the zone of influence of a variable. a-e represent a monotonic decrease in a component of the correlogram. a: first significant positive autocorrelation value; b: second positive autocorrelation value (non-significant); c: first significant negative autocorrelation value; d: second significant negative autocorrelation value; e: first maximum negative autocorrelation value; patch size is taken as the midpoint distance between b and c (approximately 6 km). Closed circles represent significant autocorrelation (I) values. In this example, each distance class represents 2.4 km. 36 km = maximum distance between any two pairs of points (localities) for which value of represented variable is known. α' = Bonferroni corrected overall correlogram significance level for multiple comparisons.

Spatial data analysis

Nested analysis of variance (Sokal & Rohlf 1995) was performed for \log_{10} gall mass, larval abundance and larval density (number of larvae per 1.0 g gall tissue) ($n = 800$) (excluding the site where only four trees were sampled). After log transformation, gall mass was the only variable of the three that approximated normality. However, no non-parametric equivalent to a nested ANOVA is available, and the above results were therefore retained. The results for larval abundance and density for this analysis should therefore be interpreted with caution. Nested analysis of variance (Sokal & Rohlf 1995) was also performed for \log_{10} gall mass, \log_{10} larval abundance and \log_{10} larval density after removing all zero abundance's and densities ($n = 555$) in a further attempt to render the data normally distributed. The design was therefore unbalanced and Satterthwaite's approximation was applied to the analyses (Sokal & Rohlf 1995). For Satterthwaite's approximation a new denominator mean square is synthesized against which the mean square of the groups is tested (Sokal & Rohlf 1995). The significance of the variance ratio that is obtained (F') is then evaluated against a critical value of F (Sokal & Rohlf 1995). After log transformation, gall mass and larval density approximated normality however, larval abundance was still not normally distributed. All nested analyses were computed using PROC NESTED in SAS 6.12 (SAS®).

Spatial patterns were investigated using spatial autocorrelation analysis (Legendre & Fortin 1989; Legendre 1993) (SAAP-PC Version 4.3, Exeter Software). Moran's I was used as the coefficient of autocorrelation as it is more robust than Geary's c (Geary's c is sensitive to outliers) (Wartenberg 1989). This coefficient varies between -1.0 and $+1.0$.

For this study, spatial patterns were investigated across all sites combined, as well as for urban and rural sites separately. All directional correlograms were drawn from the results of the spatial analyses across sites (all sampled trees, $n = 84$; 0.0 km – 36.0 km) to evaluate changes in the autocorrelation coefficients with distance (Sokal & Oden 1978a;

Legendre & Legendre 1998). Correlograms were compiled for resource variables, i.e. vegetation structure, gall density, gall mass and modal gall age, as well as for assemblage variables, i.e. total larval abundance, species richness and for the abundances of each of the eight species in the assemblage (where these species were sampled at sufficient trees for the analysis to be meaningful) (Legendre & Fortin 1989). Correlograms for *Eublemma gayneri* and *Cryptophlebia peltastica* were not compiled because the abundances of these species were very low (Table 2.1). The correlograms were compiled using equal distance intervals (2.4 km), therefore the number of point pairs in each distance class varied. Distance classes with fewer than 1 % of the total number of point pairs were considered to be unreliable and were not interpreted throughout this study (Legendre & Fortin 1989). Thus when analysing spatial patterns across sites the number of point pairs required to interpret Moran's I in each distance class was 35 (Table 2.2). Fifteen distance classes were used in the correlograms constructed using all 17 sites (i.e. 84 trees). Each distance class represented 2.4 km with the fifteenth distance class corresponding to 33.6 km – 36.0 km (the distance between the two furthest sites). Spearman's rank correlation coefficient was used to evaluate changes in the relationship between I values for the first distance class across all sites and the larval abundance of individual species. Bonferroni approximation (correcting for multiple comparisons) was used to evaluate the overall significance of each correlogram (Legendre & Fortin 1989). Only the correlograms that proved significant at the Bonferroni corrected level are reported.

The same distance interval (2.4 km) was used for the calculation of I values across rural sites (0 km - 36 km) however, for the urban sites (0 km - 22.8 km) each distance class represented 2.28 km, rather than 2.4 km because nine and a half distance classes would have been required to represent 2.4 km. This was done to maximise the power of the test used to compute the autocorrelation coefficients (more power when there are more pairs in a distance class) (Legendre & Legendre 1998). The autocorrelation values of the first and

third distance classes for urban (54 trees; 10 distance classes each representing 2.28 km) and rural (six sites, 30 trees; 15 distance classes each representing 2.4 km) sites were determined and were compared using the Mann-Whitney U test (Zar 1984). When the data were subdivided into urban and rural sites, these were the only distance classes that allowed comparison as the other distance classes had insufficient point pairs for the comparison to be meaningful (Table 2.2).

Table 2.1. Total number of larvae (N) present of each species, parasitised larvae (paras) and unidentifiable larvae (unid), number of trees and number of sites at which the species was collected and total number of larvae of all species present at a site (Total N). (*Euzophera cullinanensis* = Ec†; *Cydia (Cydia) victrix* = Cv; *Ascalenia pulverata* = Ap; *Anarsia gravata* = Ag; *Characoma submediana* = Cs; *Cryptophlebia peltastica* = Cp; undetermined Phycitinae species = PH; *Eublemma gayneri* = Eg# (‡ indicates site where only four trees were sampled) (R1-R6 = rural sites; U1-U11 = urban sites).

Species	N	No. trees	No. sites	Site	Total N
Ec†	794	63	17	R1	104
Cv	463	69	17	R2	181
Ap	313	61	16	R3	155
Ag	304	56	16	R4	263
Cs	149	47	14	R5	284
Cp	48	26	13	R6	119
PH	81	39	17	U1‡	279
Eg#	13	8	7	U2	124
paras	43	25	10	U3	37
unid	2	2	2	U4	71
				U5	292
				U6	18
				U7	13
				U8	19
				U9	57
				U10	96
				U11	98
TOTAL					2210

†listed by McGeoch & Krüger, 1994 as *Euzophera* sp. near *verrucicola* Hampson.

#listed by McGeoch & Chown, 1997c as *Eublemma brachygonia*

Table 2.2. Number of trees sampled, total number of point pairs across distance classes (N_T), number of point pairs required for the interpretation of Moran's "I" within a distance class (N_{MIN}) and distance classes with sufficient point pairs ($> N_{MIN}$) for analysis. See text for full explanation of scales.

Scale	No. of trees	N_T	N_{MIN}	Distance classes with point pairs $> N_{MIN}$
0 - 36 km (all sites)	84	3486	35	1-7; 15
0 - 36 km (rural sites)	30	435	5	1; 3-8; 11-13; 15
0 - 22.8 km (urban sites)	54	1431	15	1-3; 10

Results

Micro-, meso- and local scale factors

Although the results of the nested analysis of variance for all the data ($n = 800$; site with only four trees removed) revealed that gall mass, larval abundance and larval density varied significantly between trees and sites (Tables 2.3 - 2.5), the results of the nested analysis of variance for the galls with zero larval abundance removed ($n = 555$) revealed that gall mass, larval abundance and larval density did not vary significantly between sites (Tables 2.6 - 2.8). Satterwaithe's approximation can only be calculated for the site level and hence determining whether variation at the level of the tree is significant, is impossible (Sokal & Rohlf 1995). However, most of the variation in \log_{10} gall mass was explained at the level of the gall for both analyses (approximately 58 %) (Tables 2.3 & 2.6). Less than half of the variation in gall mass was explained at the level of the site and tree combined (Tables 2.3 & 2.6). Five times more variation in larval abundance and three times more variation in larval density was also explained at the level of the gall (Tables 2.4 & 2.7, 2.5 & 2.8). However, the percentage of variation explained at the level of the gall, was higher for

the assemblage, i.e. larval abundance and density, than for gall mass (Tables 2.3 - 2.5 & 2.6 - 2.8). Although the variation at the level of the gall includes the error variation (Sokal & Rohlf 1995), a much greater percentage of variation is explained at this level than at the level of either the site or tree. Thus factors operating at the level of the gall (the finest scale) appear to be most important in determining gall mass, larval abundance and larval density.

Table 2.3. Nested analysis of variance of \log_{10} gall mass for three levels (site, tree and gall) (all data, $n = 800$) and the percentage of variation explained at each level.

Variance Source	d.f.	SS	MS	F	% of variation	p <
Site	15	50.97	3.40	8.11	28.09	0.001
Tree	64	26.83	0.42	3.41	13.97	0.001
Gall	720	88.46	0.12		57.94	
Total	799	166.25	0.21		100	

Table 2.4. Nested analysis of variance of larval abundance for three levels (site, tree and gall) (all data, n = 800) and the percentage of variation explained at each level

Variance Source	d.f.	SS	MS	F	% of variation	p <
Site	15	2474.94	165.00	8.12	17.6	0.001
Tree	64	1301.16	20.33	1.59	4.58	0.01
Gall	720	9213.10	12.80		77.82	
Total	799	12989	16.26		100	

Table 2.5. Nested analysis of variance of larval density for three levels (site, tree and gall) (all data, n = 800) and the percentage of variation explained at each level.

Variance Source	d.f.	SS	MS	F	% of variation	p <
Site	15	55.85	3.72	7.21	17.28	0.001
Tree	64	33.05	0.52	1.82	6.27	0.001
Gall	720	204.24	0.28		76.44	
Total	799	293.14	0.37		100	

Table 2.6. Nested analysis of variance of gall mass (\log_{10}) for three levels (site, tree and gall) (galls with no larvae present removed) (F' = Satterwaithe's approximation for unequal sample sizes) ($n = 555$) and the percentage of variation explained at each level.

Variance Source	d.f.	SS	MS	F or (F')	% of variation	p <
Site	16	22.68	1.42	4.37 (0.06)	20.43	0.001 (ns)
Tree	67	21.75	0.32	3.45	21.81	0.001
Gall	471	44.24	0.09		57.75	
Total	554	88.67			100	

Table 2.7. Nested analysis of variance of larval abundance (\log_{10}) for three levels (site, tree and gall) (galls with no larvae present removed) (F' = Satterwaithe's approximation for unequal sample sizes) ($n = 555$) and the percentage of variation explained at each level.

Variance Source	d.f.	SS	MS	F or (F')	% of variation	p <
Site	16	15.80	0.99	4.90 (0.11)	16.09	0.001 (ns)
Tree	67	13.51	0.20	1.81	9.27	ns
Gall	471	52.55	0.11		74.63	
Total	554	81.87			100	

Table 2.8. Nested analysis of variance of larval density (\log_{10}) for three levels (site, tree and gall) (galls with no larvae present removed) (F' = Satterwaithe's approximation for unequal sample sizes) ($n = 555$) and the percentage of variation explained at each level.

Variance Source	d.f.	SS	MS	F or (F')	% of variation	p <
Site	16	18.72	1.17	5.78 (0.11)	20.65	0.001 (ns)
Tree	67	13.55	0.20	2.07	11.18	ns
Gall	471	46.10	0.10		68.17	
Total	554	78.37			100	

Comparison of across site correlograms

(i) Patch diameters

The correlograms including data for all the sites in the study area revealed that both vegetation structure and gall mass were significant and positively autocorrelated in the first distance class only (areas with a radius of approximately 2.4 km) (Fig. 2.3a, b). Within this first distance class, gall mass was the most strongly autocorrelated of all the variables (highest I value), and larval abundance and species richness (assemblage variables) had higher I values than those of the individual species (Table 2.9). The size of I in the first distance class was however not significantly related to the abundance of the individual species ($n = 6$, $r_s = 0.66$, $p = 0.16$) (Table 2.1).

Vegetation structure and gall mass patch diameters (the midpoint between the first positive value and first negative autocorrelation value) were both approximately 3.6 km

(Fig. 2.3a, b). Gall density and modal gall age were not significantly autocorrelated across the study area and may thus be viewed as randomly distributed at the scale examined.

Correlograms drawn for total larval abundance and species richness, as well as for five of the six sufficiently abundant species (the correlogram for the Phycitinae species complex was not significant), displayed a spatial pattern similar to that of gall mass and vegetation structure. First, these variables were all significant and positively autocorrelated in the first distance class (areas with a radius of approximately 2.4 km) (Fig. 2.3c-i). In addition, patch diameters for species richness, *Ascalenia pulverata* and *Anarsia gravata* were also approximately 3.6 km (Fig. 2.3d, g, h). Patch diameters were, however, larger for larval abundance, *Euzophera cullinanensis*, *Cydia (C.) victrix* and *Characoma submediana*, and were approximately 6.0 km in diameter (Fig. 2.3c, e, f, i). The patch diameters of the resource variables and a number of the assemblage variables were thus similar, and the patches for the remaining assemblage variables were larger than those of the resource variables.

(ii) Zone of influence

The zones of influence (distance between high and low values of the variables) for vegetation structure and gall mass were approximately 9.6 km – 12.0 km, i.e. the area over which the autocorrelation coefficients for vegetation structure and gall mass decreased to a minimum (Fig. 2.3a, b).

The zones of influence for larval abundance, species richness and individual species were somewhat smaller and all fell between 4.8 km - 9.6 km (Fig. 2.3c-i). Therefore, the zones of influence for assemblage variables were smaller than the zones of influence for the resource variables.

(iii) Overall correlogram structure

In six of the nine correlograms, the autocorrelation coefficient became significantly positive again at larger distance classes (from approximately distance class five onwards), after the initial decline from positive to negative I values described above (Fig. 2.3 a-i). This was most pronounced for total larval abundance and species richness (Fig. 2.3c, d). After a monotonic decrease across the first three to four distance classes (2.4 km – 12.0 km), I increased to a maximum at 12.0 km - 14.4 km (Fig. 2.3c, d). The patchiness of these variables was thus nested at at least two spatial scales. At greater distances, between 19.2 km - 33.6 km, there were insufficient pairs of trees for these classes to be interpreted on the correlograms (Table 2.2). The possibility of multiple levels of patchiness can thus not be excluded for these variables.

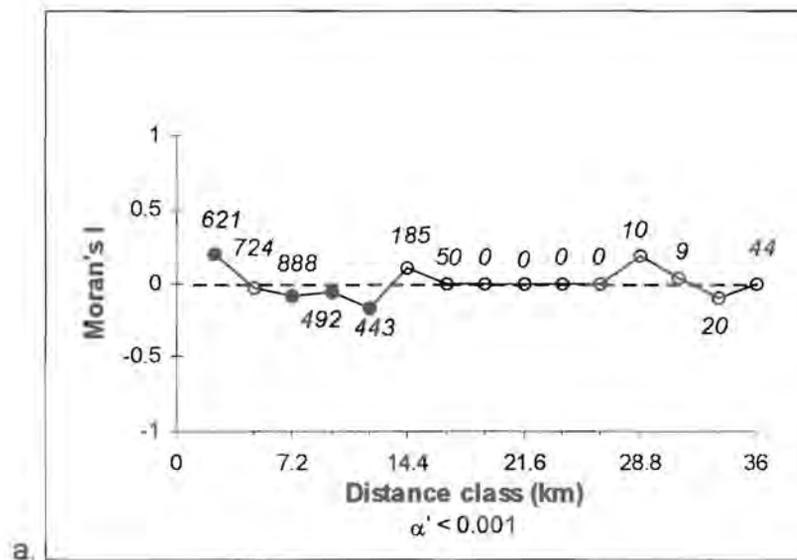


Fig. 2.3a. Spatial correlograms of the distance 0 km – 36 km (all sites included) for vegetation structure. Closed circles represent significant I values at $p < 0.05$. The number of point pairs in each distance class appears in Italics. $\alpha' =$ Bonferroni corrected overall correlogram significance level.

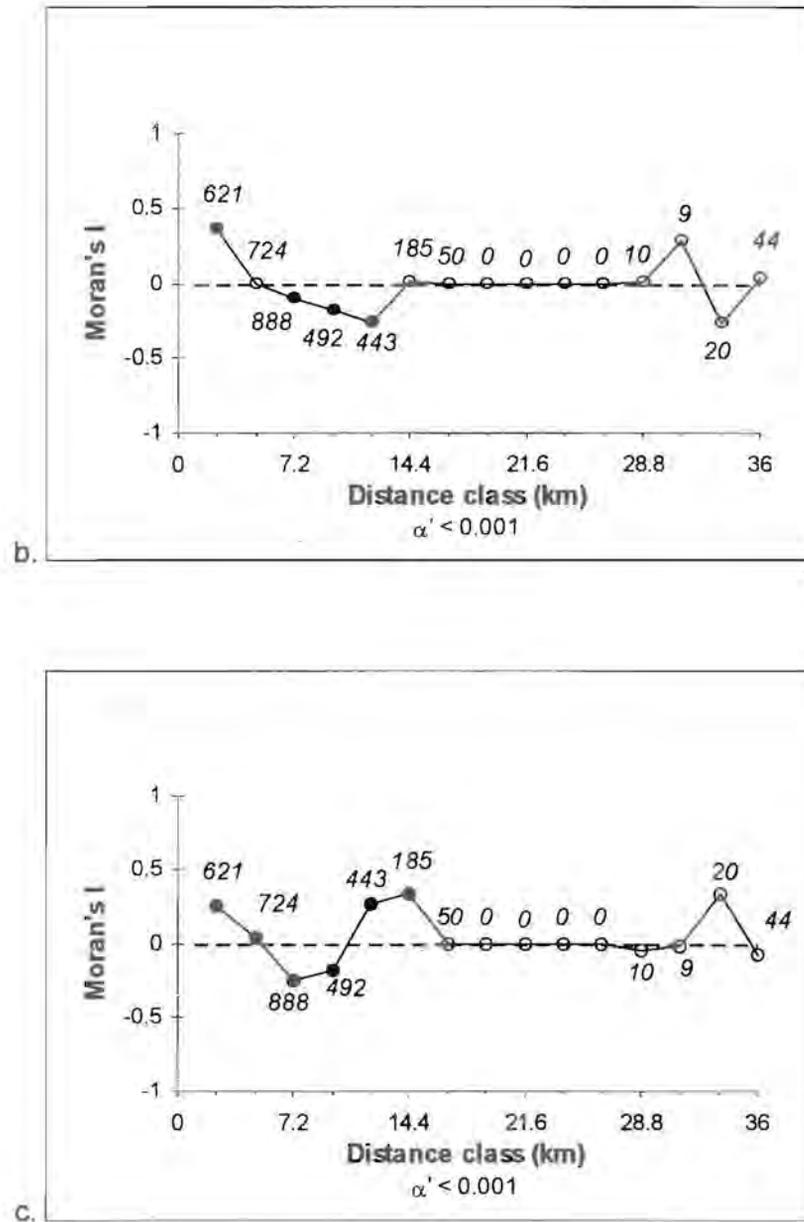


Fig. 2.3. Spatial correlograms of the distance 0 km – 36 km (all sites included) for b) gall mass and c) total larval abundance. Closed circles represent significant I values at $p < 0.05$. The number of point pairs in each distance class appears in Italics. α' = Bonferroni corrected overall correlogram significance level.

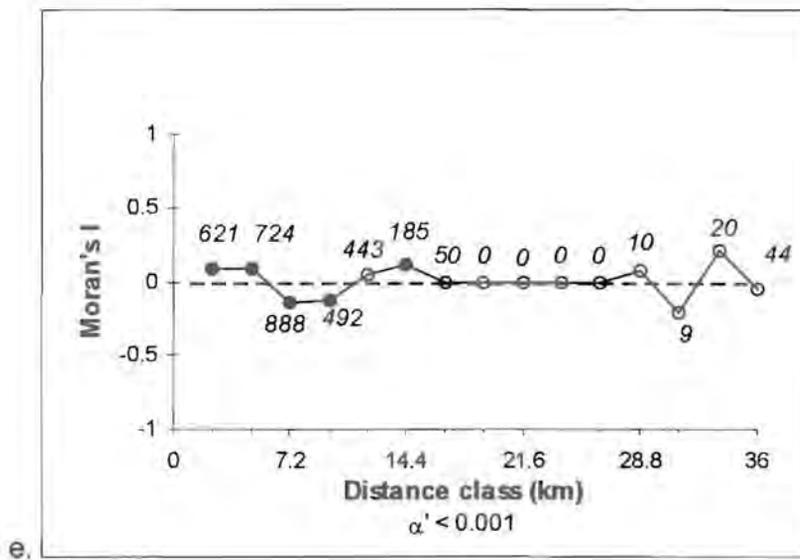
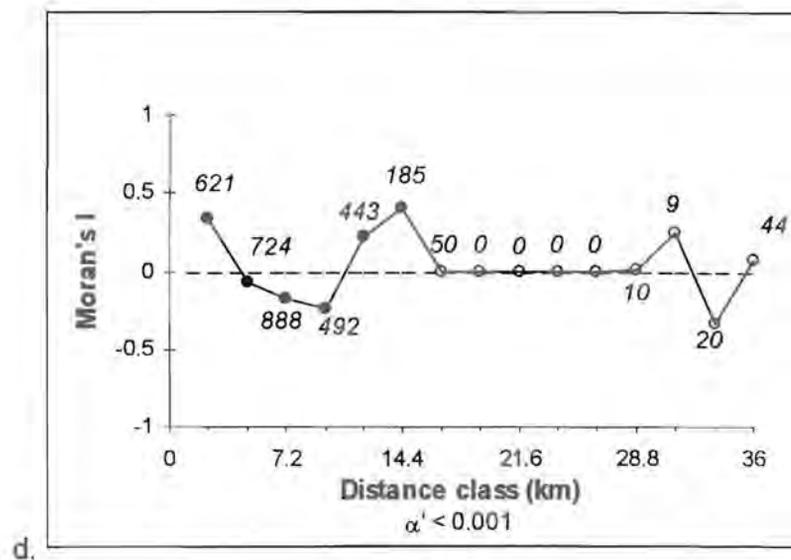


Fig. 2.3. Spatial correlograms of the distance 0 km – 36 km (all sites included) for d) species richness and e) *Euzophera cullinanensis* = *Ec* (listed by McGeoch & Krüger, 1994 as *Euzophera* sp. near *verrucicola* Hampson). Closed circles represent significant I values at $p < 0.05$. The number of point pairs in each distance class appears in Italics. α' = Bonferroni corrected overall correlogram significance level.

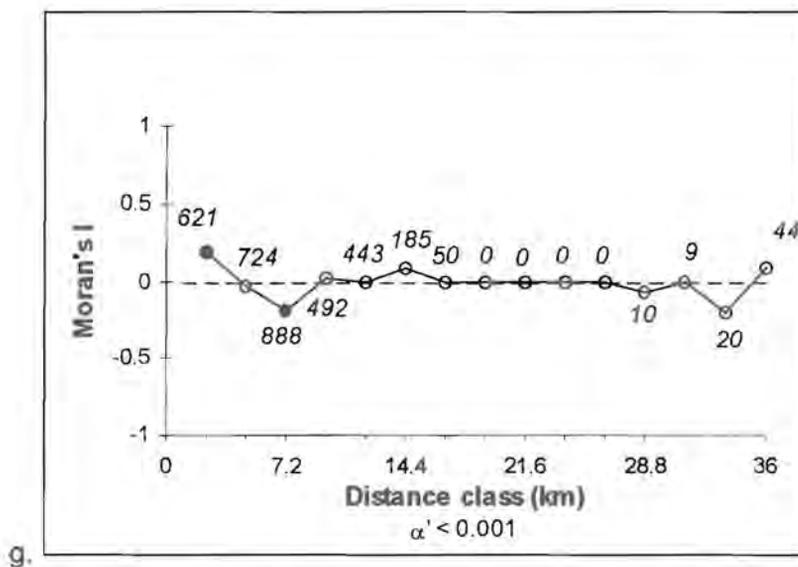
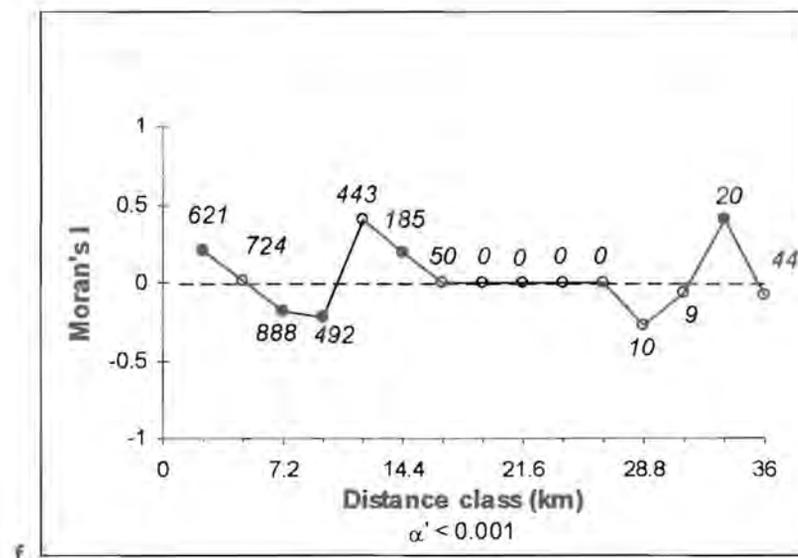


Fig. 2.3. Spatial correlograms of the distance 0 km – 36 km (all sites included) for f) *Cydia (C.) victrix (Cv)* and g) *Ascalenia pulverata (Ap)*. Closed circles represent significant I values at $p < 0.05$. The number of point pairs in each distance class appears in Italics. α' = Bonferroni corrected overall correlogram significance level.

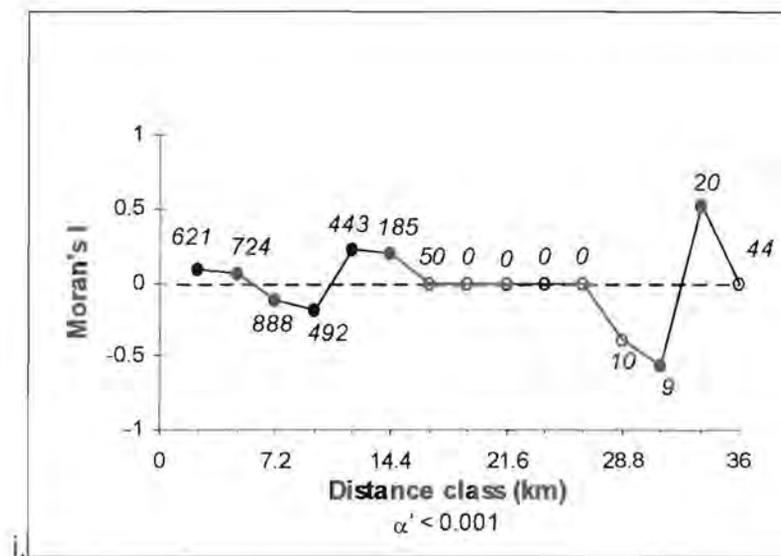
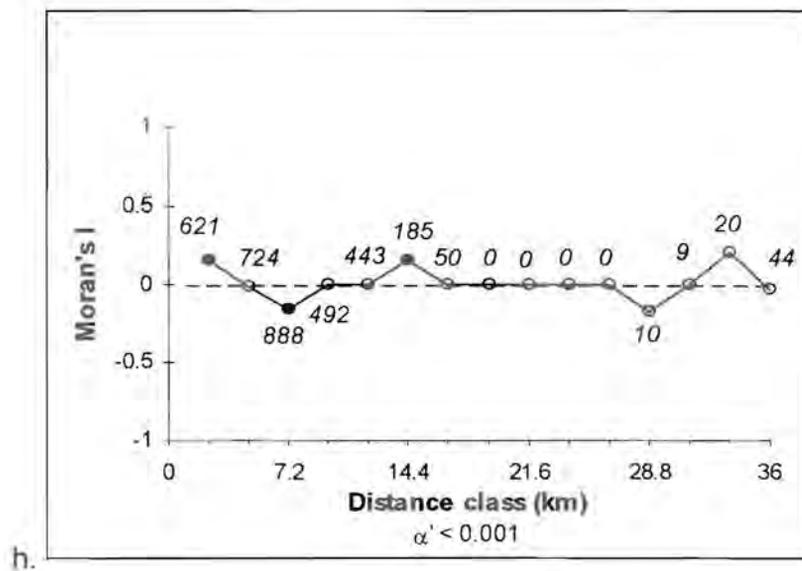


Fig. 2.3. Spatial correlograms of the distance 0 km – 36 km (all sites included) for h) *Anarsia gravata* (*Ag*) and i) *Characoma submediana* (*Cs*). Closed circles represent significant *I* values at $p < 0.05$. The number of point pairs in each distance class appears in Italics. α' = Bonferroni corrected overall correlogram significance level.

Table 2.9. I values for the first distance class for resource and assemblage variables across all sites, and for the first (D1) and third (D3) distance class I values for resource and assemblage variables across urban and rural sites. Species for which no values are provided were present on < 30 trees. * represent $p < 0.05$ at the table-wide alpha level (sequential Bonferroni adjusted significance level, Rice 1989) for the I value. n = number of point pairs. *Euzophera cullinanensis* = Ec†; *Cydia (Cydia) victrix* = Cv; *Ascalenia pulverata* = Ap; *Anarsia gravata* = Ag; *Characoma submediana* = Cs; undetermined Phycitinae species = PH.

Variable	All sites (D1) n = 621	Rural (D1) n = 60	Urban (D1) n = 752	Rural (D3) n = 25	Urban (D3) n = 72
Resource					
Vegetation structure	0.203*	0.280*	0.008	-0.620*	-0.296*
Gall mass	0.363*	0.544*	0.075*	0.150	0.448*
Gall age	-0.040	0.022	-0.018	-0.217	-0.002
Gall density	0.061*	0.016	0.054*	0.006	-0.048
Assemblage					
Larval abundance	0.256*	0.236	0.197*	-0.041	-0.500*
Species richness	0.339*	0.322*	0.128*	0.217	-0.033
Ec†	0.095*	0.338*	0.104*	-0.615*	-0.401*
Cv	0.207*	0.177	0.106*	0.225	-0.022
Ap	0.188*	0.284*	0.126*	-0.224	-0.158
Ag	0.154*	-	-	-	-
Cs	0.092*	-	-	-	-
PH	0.026	-	-	-	-

† listed by McGeoch & Krüger, 1994 as *Euzophera* sp. near *verrucicola* Hampson.

Urban-rural site comparisons

Comparisons were made between rural and urban autocorrelation values for vegetation structure, gall mass, age and density, larval abundance, species richness and three of the lepidopteran species in the assemblage (the remaining species were not present on sufficient trees at both rural and urban sites for comparison). All these resource and assemblage variables were positively autocorrelated in the first distance class (areas with a radius of approximately 2.4 km) for both rural and urban sites (the only exception was gall age across urban sites) (Table 2.9). In contrast, the I values for these variables were mostly negative in the third distance class (areas with a radius of approximately 7.2 km) across both urban and rural sites (with the only significant exception being gall mass) (Table 2.9). Therefore, for both rural and urban sites the autocorrelation coefficients changed from positive to negative between the first and third distance classes.

The sizes of the I values in the first distance class (areas with a radius of approximately 2.4 km) were significantly greater across rural (mean (\pm S.E.) = 0.25 ± 0.05) than across urban (mean (\pm S.E.) = 0.09 ± 0.02) sites ($U = 15.00$, $n = 9$, $p = 0.024$). There was however no significant difference between rural (mean (\pm S.E.) = -0.12 ± 0.11) and urban (mean (\pm S.E.) = -0.11 ± 0.09) sites in the size of the I values in the third distance class (areas with a radius of approximately 7.2 km) ($U = 38.00$, $n = 9$, $p = 0.83$). In some instances the I values were more strongly negative across rural sites, and in others I values were positive across rural and negative across urban sites and there were therefore no general differences between urban and rural sites in this distance class (Table 2.9).

Discussion

The Lepidoptera assemblage and its resource examined here displayed an aggregated spatial structure at the smallest spatial scale examined, both across and within rural and urban areas. Furthermore, spatial patterns of larval abundance and species richness were similar to the spatial patterns of abundances of individual species. Neither resource nor assemblage variables were found to be structured by any strong environmental gradient across the extent of the study area (36 km), although a number appeared to respond to a shorter gradient of approximately 7.2 to 14.4 km. The small scale pattern of aggregation may be attributed to the availability and quality of the habitat and gall resource (vegetation structure and gall mass) that the assemblage occupies. Furthermore, factors operating at the scale of the gall will influence the Lepidoptera assemblage, examined at this scale, to a greater extent than other factors which may be operating at higher levels. In addition, both the habitat and gall resource, as well as the lepidopteran assemblage, are apparently structured as a result of other biotic and abiotic factors, including the effect of urbanisation. Although both resource and assemblage variables were positively autocorrelated within areas with a radius of approximately 2.4 km, this autocorrelation was significantly weaker in urban than in rural environments. Both resource and urbanisation effects should therefore be examined more closely in an attempt to explain the spatial patterns in the assemblage that were found at the scales examined.

After correcting for unequal sample sizes, larval abundance, larval density and gall mass did not vary significantly at the level of the site. Most of the variation in larval abundance and density, and gall mass was explained at the level of the gall. Thus those factors operating at the scale of the gall (e.g. microclimate, gall mass, gall age, competitive interactions) will influence the Lepidoptera assemblage, examined at this scale, to a greater extent than other factors which may be operating at higher levels.

The fungus galls, that form both food and habitat resource for the Lepidoptera larvae in the assemblage examined here, are ephemeral and only develop on the seedpods or flowers of *Acacia karroo* trees (McGeoch 1993; McGeoch 1995). Thus the distribution of the resource is dependent on the distribution of *A. karroo* trees across the landscape. Although *A. karroo* is widespread in and around Pretoria (McGeoch 1995), within the urban matrix, *A. karroo* trees are usually confined to small pockets of natural vegetation (< 1 km²) along roadsides, or individual trees are occasionally found on pavements or in gardens in suburban areas (pers. obs.). Thus the distribution of the gall resource (with trees as the unit of comparison) may be expected to be spatially aggregated (positively autocorrelated) between trees and sites, with trees exposed to, for example, very different moisture and disturbance regimes. New (1982) found that the gall density of another gall forming rust fungus species varied between sites, and even between individual trees in the same habitat patch. This was not found to be the case for this study. Both gall density and age were randomly distributed, while gall mass and vegetation structure were the only resource variables that displayed a non-random spatial structure and were found to be positively autocorrelated at the smallest scale (0 km – 2.4 km). This distance was greater than within site inter-tree distances and corresponded approximately to the distance between pairs of urban sites (see Fig. 2.1). Thus gall mass and vegetation structure appear to be responding to some underlying spatially determined variable that is present at a scale larger than within site inter-tree distances.

Although patch diameters were similar for most autocorrelated resource and assemblage variables, the zones of influence were larger for resource than assemblage variables. Furthermore, the nested analyses also revealed that more variation was explained for the assemblage (larval abundance and density) (68%-78%) than for the resource (gall mass) (58%). When 'bottom up' processes (resources) govern a system (Hunter & Price 1992), species distribution patterns may be expected to follow the spatial

distribution patterns of their resources (see Brown 1984; Hill *et al.* 1998). Because the zone of influence covers the full range of values of a variable (e.g. from maximum to minimum gall mass values), the resource may not be suitable to the species in the assemblage across the entire range of this zone of influence. In this instance the zone of influence of the assemblage or species may be expected to be smaller than the zone of influence of the resource, as was found here. The Lepidoptera assemblage examined has been shown to be resource limited (McGeoch & Chown 1997b), and it is therefore perhaps not surprising that the patch diameter of the assemblage mimics the resource patch diameter (gall mass). Such a relationship has also been demonstrated for seabirds and their prey (Logerwell *et al.* 1998). Thus if the species are responding to resource distribution patterns, gall mass is likely to be the most important resource variable responsible for assemblage distribution patterns. Indeed, gall mass has been shown to explain a significant proportion of the variation in larval abundance in this assemblage (Rösch *et al.* submitted). Furthermore, parasitism in this assemblage has been shown, both here and previously, to be extremely low (2% in this study, Table 2.1; 0.6 %, McGeoch & Chown 1997b) in comparison to other studies (Cameron 1939, Heads & Lawton 1983). The spatial structure of the resource and assemblage variables found here thus provides further support for the importance of 'bottom up' processes in structuring this Lepidoptera assemblage (see McGeoch & Chown 1997b; Rösch *et al.* submitted).

When examining all the sites together, the patch diameters (as defined on the correlograms for this study) of the two most abundant species were larger than the patch diameters for the other species and for gall mass (although there was no significant relationship between species abundance and the I value in the first distance class). Although the abundance of seeds has been shown to influence the observed spatial pattern in a seedbank (Dessaint *et al.* 1991), no documented cases exist of the influence of abundance on patch diameter (as defined on the correlograms for this study). Species

with higher abundances have however been shown to occupy more sites (Bock & Ricklefs 1983; Bock 1987; Gaston & Lawton 1988; Venier & Fahrig 1998). This may cause correlogram patch diameters for the abundant species to be larger. This explanation is however unsatisfactory for *Characoma submediana* as this species was present in low abundances at fourteen of the seventeen sites. *C. submediana* is known not to be an obligate inhabitant of these fungus galls (Krüger 1998), and is probably utilising other resources present in the environment. This may result in the patch diameter for this species being larger than patch diameters for more obligate gall inhabitants even though its frequency of occurrence is low.

In the urban-rural comparison, both resource and assemblage variables changed from being positively to negatively autocorrelated between 2.4 km and 7.2 km (first and third distance classes). Nonetheless, the positive autocorrelation across rural sites was significantly stronger than across urban sites. Fragmentation and disturbance effects in urban areas may be responsible for this finding. For example, many urban gardens contain exotic plant species that change the vertical structure, and increase the diversity and heterogeneity of vegetation across small scales (< 2.4 km) in urban, in comparison with rural, environments (Lövei 1997; Gordon 1998). The density of humans occupying urban areas is also larger than in rural areas, and this is likely to result in greater variability of disturbance factors over smaller spatial scales in urban than rural areas. This may contribute to the dilution of spatial autocorrelation values in urban areas observed here. Indeed, the structure of this assemblage has been shown to be significantly different within 5 km of the city centre, in comparison with more outlying areas (McGeoch & Chown 1997a; Rösch *et al.* submitted). Koenig (1997) also shows that the strength of autocorrelation values is related to the dispersal behaviour of species. However, no information is available on the dispersal abilities of the species in the Lepidoptera assemblage studied.

Although a mensurative approach to documenting spatial structure in a species assemblage was adopted here, such studies are limited by the natural distribution of the organisms of interest. Correlograms can only be constructed and meaningful comparisons made between similar distance classes, when sufficient point pairs exist that are the given distance apart for all variables to be compared. In spite of this limitation, this study demonstrated that such comparisons can be made between species distributions and the resources that they utilise, as well as between areas with different habitat or disturbance characteristics. A comparative approach such as this is likely to contribute to a better understanding of the spatial structure of species populations and assemblages, and ultimately to the processes that determine this structure.

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General Conclusion

The increasing pressure from anthropogenic disturbances worldwide places many natural communities under threat (Soulé 1991; Scholtz & Chown 1993). As a result of their ubiquitous nature, insects are often utilised as indicators of such environmental changes (Kuschel 1990; McGeoch 1998; Blair 1999). The Lepidoptera assemblage inhabiting fungus induced galls on *Acacia karroo* has been identified as such a potential bioindicator (McGeoch & Chown 1997a). However, the consistency with which a bioindicator responds to habitat quality changes, determines the bioindicator's ability to monitor the impact of such habitat quality changes (McGeoch 1998).

Although the fungus galls sampled in this study were sampled at precisely the same time of year as the 1995 study, gall resource conditions (quality and quantity) between these two years were different. These resource differences had an effect on the Lepidoptera assemblage characteristics found, namely, an additional species was recorded and the relative abundance structure of the assemblages in the two years were very different. Nonetheless, the relationship between moth assemblage structure and habitat quality in this and the 1995 study were similar. Larval abundance, larval density and species richness were lowest at the sites closest to the city centre in both studies. Furthermore, larval abundance and density were shown to be consistently higher at suburban garden than city centre or roadside sites. The degree of urbanisation (distance to the city centre) therefore appears to affect this moth assemblage in the same way as three years ago. Thus this assemblage may reliably be used as a biological indicator of habitat quality, notwithstanding the seasonal variation in the quality and quantity of the gall resource. Furthermore, as the moth–rust fungus association has been shown to be widespread across South Africa (McGeoch 1995), this assemblage would be a useful bioindicator of anthropogenic disturbance at a larger scale, namely across South Africa.

Although the spatial distribution and abundance structure of species are determined by numerous biotic and abiotic factors (Hanski 1982; Dempster & Pollard 1981; Dempster 1983; Brown 1984; Thomson *et al.* 1996; Logerwell *et al.* 1998), resource and habitat quality were found to impact on the spatial structure of the Lepidoptera assemblage examined here. Both the assemblage and the resource were aggregated (positively autocorrelated) at the smallest scale. Gall mass and vegetation structure were the only variables to display a non-random spatial structure. Also, the use of a multiscale approach in this study, revealed that microscale factors are more important in structuring this assemblage than other factors that may be operating at higher levels. Furthermore, parasitism in this assemblage was very low. This Lepidoptera assemblage has also been shown to be resource limited (McGeoch & Chown 1997b). Consequently, 'bottom up' processes (resources) (Hunter & Price 1992) are likely to strongly influence this system. Numerous studies have demonstrated that both 'top down' and 'bottom up' processes are important in structuring insect communities, however, this study has demonstrated that the role of resource and habitat quality are important in this assemblage (Dempster & Pollard 1981; Hunter & Price 1992; Cappuccino & Price 1995; McGeoch & Chown 1997b; Dyer & Letoumeau 1999).

Although neither the resource nor assemblage variables were structured by a strong environmental gradient across the extent of the study area, a shorter gradient was observed. Habitat quality changes due to urbanisation are possibly causing this spatial gradient. Changes in habitat quality across an area have been shown to alter the spatial structure of the organisms found in that area (Brown 1984; Brussard 1984; Thomson *et al.* 1996) however, the resource and urbanisation effects identified in this study should be examined more closely to elucidate their relative roles in structuring this assemblage.

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