MCGEOCH, MELODIE ALYCE

STRUCTURE AND FUNCTIONING OF THE LEPIDOPTERA COMMUNITY IN *RAVENELIA MACOWANIANA* PAZSCHKE FUNGUS GALLS ON *ACACIA KARROO* HAYNE: PROSPECTS FOR ENVIRONMENTAL MONITORING

PhD UP 1995

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Structure and functioning of the Lepidoptera community in *Ravenelia macowaniana* Pazschke fungus galls on *Acacia karroo* Hayne: prospects for environmental monitoring

by

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Submitted in partial fulfilment of the requirements for the degree Philosophiae Doctor
in the Faculty of Biological and Agricultural Sciences
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To my family,

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In the beginning...

" An intellect which at any given moment knew all the forces that animate Nature and the mutual positions of the beings that comprise it, if this intellect were vast enough to submit its data to analysis, could condense into a single formula the movement of the greatest bodies of the universe and that of the lightest atom: for such an intellect nothing could be uncertain; and the future just like the past would be present before its eyes."

Pierre Simon de Laplace, 19th century

and on the last day...

" However, if the sense of the individual is the only good, how will science succeed in recomposing the universal laws through which, and interpreting which, the good magic will become functional? Because if only the sense of the individual is just, the proposition that identical causes have identical effects is difficult to prove. A single body can be cold or hot, sweet or bitter, wet or dry, in one place - and not in another place. How can I discover the universal bond that orders all things if I cannot lift a finger without creating an infinity of new entities? For with such a movement all the relations of position between my finger and all other objects change. The relations are the ways in which my mind perceives the connections between single entities, but what is the guarantee that this is universal and stable?"

Umberto Eco, 1980

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ABSTRACT

Community patterns and processes operate within a hierarchy, and multiscale approaches to community studies are essential for understanding the role of local and regional processes in the structure and functioning of communities. This information enables viable management decisions to be made for the conservation of communities and ecosystems. In addition, monitoring terrestrial biotic communities to determine the impact of global climate and land-use changes has been highlighted as a priority.

Studies of herbivore insect communities are likely to contribute to the formulation of general principles of the structure and functioning of terrestrial communities, because insects and green plants together dominate most terrestrial ecosystems. Furthermore, communities living concealed in plant tissue structures, such as galls, are ideal for this purpose because they have quantifiable habitat boundaries, are multispecies and multitrophic level structures, and are easily sampled.

A community of phytophagous Lepidoptera larvae inhabit galls induced by the fungus *Ravenelia macowaniana* Pazschke on *Acacia karroo* Hayne. The objectives of this study were to examine the biology, structure and functioning of the community across South Africa, to contribute to understanding the community ecology of herbivore insects in discrete plant structures and, to evaluate the potential of this association for use as a bioindicator.

The community was sampled from nine localities (over a range of climates) in South Africa between 1991 and 1994. The galls were found to be seasonal, ephemeral, patchily distributed and of a high tissue quality. Twenty-two Lepidoptera species were recorded and parasitism of the larvae was low. A key to the larvae was compiled and diagnoses, illustrations, instar numbers and head-capsule sizes were determined for the dominant species. Gall occupancy and utilization was consistently high, and gall occupancy appears to provide the larvae with protective, nutritional and microenvironmental advantages. Positive aggregation, positive associations and abundance covariation and resource mediated competition occurred between individuals and species in the galls. The organization of this community had more in common with other communities associated with ephemeral, patchy resources, *i.e.* interactive and local processes were important, than with herbivore insect communities in general.

The value of community properties (evenness, diversity, larval density, species composition) were indicative of habitat quality differences (patch size and isolation, physical

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disturbance and proximity from agroecosystems). Climate variables best correlated with species richness, community structure and seasonality were total annual rainfall, rainfall variability and winter climate conditions. The community was spatially concordant, although the abundance rankings of rare species were variable. Typical and discriminant species were identified from the extent and constancy of their contribution to community structure. These species are sensitive indicators and potential pivotal species. Community properties were differentially sensitive to particular organizational processes and were identified as suitable for monitoring aspects of environmental change.

The community was found to be a sensitive and practicable bioindicator, responding to habitat quality and climate gradients. A baseline for it's use in monitoring has been established, but the full value of such monitoring lies in an ongoing, long-term, regional programme.

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OPSOMMING

Gemeenskapspatrone en -prosesse funksioneer in 'n hiërargie en 'n veelskalige benadering tot gemeenskapstudies is noodsaaklik om die rol van plaaslike en streeks prosesse in die struktuering en werking van gemeenskappe te verstaan. Hierdie inligting stel mens in staat om lewensvatbare bestuursbesluite vir die bewaring van gemeenskappe en ekosisteme te kan maak. Monitering van terrestriële biotiese gemeenskappe om die impak van veranderinge in globale klimaat en landgebruik praktyke te bepaal, is as 'n prioriteit beklemtoon.

Omdat herbivoorinsekte en plante gesamentlik die meeste terrestriële gemeenskappe oorheers, kan herbivoorinsek gemeenskapstudies 'n bydrae maak tot die formulering van algemene beginsels oor die struktuur en werking van terrestriële gemeenskappe. Verder, omdat gemeenskappe wat versteek in plantweefsel strukture woon, byvoorbeeld in galle, meetbare habitatsgrense het, multispesies en multitrofiese strukture het, en ook maklik is om te monster, is sulke gemeenskappe ideaal vir hierdie studiedoeleindes.

Galle wat deur die swam *Ravenelia macowaniana* Pazschke op *Acacia karroo* Hayne veroorsaak word, word deur 'n gemeenskap van Lepidoptera larwes bewoon. Die doelstellings van hierdie studie was om die biologie, struktuur en werking van die gemeenskap oor Suid Afrika te bestudeer om eerstens, tot die kennis van herbivoorinsekte in afsonderlike plantstrukture by te dra en tweedens, om die potensieel van hierdie assosiasie as bioindikator te bepaal.

Die gemeenskap was op nege lokaliteite (oor 'n reeks klimaatstoestande) in Suid Afrika tussen 1991 en 1994 gemonster. Dit was bevind dat die galle seisonaal, kortlewend, gevlek verspreid en van 'n hoë weefselkwaliteit is. Twee en twintig Lepidoptera spesies is aangeteken en parasitisme van die larwes het selde voorgekom. 'n Sleutel tot die larwes is opgestel en diagnoses, illustrasies, getal larwale stadiums en kopkapsule groottes is vir die dominante spesies bepaal. Galbewoning en verbruik was deurlopend hoog, en dit blyk dat galbewoning, beskermings-, voedingswaarde- en mikroklimaatsvoordele vir die larwes inhou. Positiewe groepering, positiewe assosiasie en digtheids ko-variasie, sowel as hulpbronbemiddelde kompetiese het tussen individue en spesies in die galle plaasgevind. Die organisering van hierdie gemeenskap het meer in gemeen met ander gemeenskappe wat met kortlewende, vlekverspreide hulpbronne (d.w.s. interaktief met belangrike plaaslike prossese) geassosieer is, as met herbivoorinsekgemeenskappe in die algemeen.

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Die waardes van gemeenskapskenmerke (reëlmatigheid, diversiteit, larwale digtheid, spesie samestelling) dui habitats kwaliteit verskille aan (d.w.s. kol-grootte en afsondering, fisiese versteuring en nabyheid van landbou ekosisteme). Klimaatsveranderlikes wat met spesierykheid, gemeenskapstruktuur en seisoenaliteit gekorreleer was, was totale reënval, reënval variasie en winter klimaatstoestande. Die gemeenskap het ruimtelike ooreenstemming getoon, alhoewel die rangorde van die skaars spesies baie gevarieer het. Tipiese en diskriminerende spesies was deur die hoeveelheid en bestendigheid van hul bydrae tot gemeenskapstruktuur geidentifiseer. Hierdie spesies is sensitiewe indikators en potensiële draaipunt spesies. Gemeenskapeienskappe was ook differensieel sensitief vir spesifieke organiserende prosesse en is dus geskik vir die monitering van spesifieke aspekte van omgewingsveranderinge.

Dit is bevind dat die gemeenskap 'n sensitiewe en bruikbare bioindikator is wat op habitatskwaliteit en klimaatsgradiënte reageer. 'n Grondlyn vir die gemeenskap se gebruik in monitering is daar gestel, maar die volle waarde van sulke monitering lê in 'n voortgaande, langtermyn, streeksprogram.

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GENERAL INTRODUCTION: The structure and functioning of communities

It is generally appreciated that factors from all spatial and temporal scales are responsible for the present structure of biotic communities. The relative importance of historical, regional and local influences, and biotic and abiotic factors in community organization are, however, likely to vary between habitats and taxonomic groups (Ricklefs & Schluter 1993). Insects constitute the majority of all living species (excluding fungi, algae and 'microbes') and most terrestrial communities are dominated together by insects and green plants (Claridge 1987). The processes within and between trophic levels incorporating herbivore insects therefore constitute some of the major processes involved in the organization of terrestrial communities (Strong *et al.* 1984). Studies of herbivore insect communities are, thus, likely to contribute substantially to the formulation of general principles of the structure and functioning of terrestrial ecosystems. This is one of the primary goals of ecology. In addition, understanding whether, and if so how, organizational processes influence the number of species and individuals in communities has major implications for the conservation of ecosystem integrity and functioning. Elucidation of these processes may enable the prediction of medium and long-term consequences of global environmental change and could contribute to the maintenance of sustainable ecosystems.

A further challenge in ecology is to determine the mechanisms responsible for variation in community structure, because parameters of community structure show consistent trends over time (Strong *et al.* 1984) and across environmental gradients (Menge & Olson 1990; Ricklefs 1987). Community patterns and processes, therefore, exist within a hierarchical framework, and their spatial and temporal resolution can greatly influence the perception of community structure and function (Rahel 1990). A multiscale approach is, therefore, essential to elucidate the relative importance of local and regional processes in community organization.

One of the most commonly encountered problems with multiscale approaches to community studies is the inability to define and measure communities as discrete and self-contained (Cody 1989). Decisions concerning sampling effort and the delineation of spatial and temporal scales appropriate to the community under study are often difficult, particularly in vagile organisms with large or inconsistent home ranges (Cody 1989; Levin 1992). Phytophagous insect larvae living concealed within plant tissue structures, such as flower

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heads, leaf-mines, seed-pods or galls, however, have readily quantifiable habitat characteristics and temporal boundaries (Askew 1980; Zwölfer 1979). As a result they are not subject to the sampling and interpretation biases of communities with less well delineated habitats. They also generally have a multispecies structure, manifold interactions between their members, include several trophic levels, and, therefore, make valuable subjects for community studies.

In the light of the importance of plant-insect interactions in terrestrial ecosystems and the advantages associated with studies of herbivore insects inhabiting discrete plant structures, a multi-scale study of such a community is likely to yield results from which the relative importance of community structuring mechanisms can be determined, as well as from which management decisions for the conservation of the system or community can be made.

The procedures involved in a study such as this can be divided into three stages: the definition and description of the community, the elucidation of community structuring mechanisms, and the continued, long-term monitoring of the community.

Community definition and description

Because of the number of interpretations associated with the term community and the often loose sense in which it is used (Southwood 1987), a careful definition of the concept is essential at the start of a community study. This is particularly important when a multiscale approach is adopted.

The term community is applied, here, to three spatial levels of organization. First, the individual habitat unit, flower-head, seedpod or plant gall, within which individuals of a number of species (often in immature stages) of a single generation are located with the potential for interaction between them (Strong *et al.* 1984; Zwölfer 1979). Phytophagous insect larvae that inhabit discrete plant structures primarily constitute a guild, as they occupy the same structure and tend to feed in a similar manner (Simberloff & Dayan 1991). These guilds are, however, linked firstly with their host plant and secondly with a suite of insect parasitoids and predators. Such a group of species defined by its organizational properties (Elton 1927), rather than by its occupancy of a particular location (e.g. Diamond & Case 1986), implies the existence of linkages in the form of interactions between populations (Southwood 1987). Although the term community is commonly applied to large, taxonomically diverse associations (Southwood 1987), Strong *et al.* (1984) argue that a group

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of species living closely enough for the potential of interaction between its members, also constitutes a community. The association between an individual discrete plant structure and herbivorous insects, therefore, warrants community status. The interactions in these communities span a number of trophic levels, the communities have discrete spatial and temporal boundaries, and function as a unit with the phytophages at the core.

The second level to which the term community is applied is the local host plant population and associated herbivore species (Zwölfer 1979). This level is more inclusive in terms of species numbers in the community as a herbivore species may occupy the habitat-unit locally, but may not be present in each *individual* habitat unit. Once again, however, the potential for interaction between individuals exists at this community level, particularly between the reproductive and dispersal stages.

Last, the regional or global set of species associated with a particular host plant, or plant structure, may be referred to as the herbivore community of that particular host, *e.g.* the global or regional herbivore community of bracken (Strong *et al.* 1984; Lawton *et al.* 1993). This community level generally consists of local species subsets, partly to fully mutually exclusive, with no potential interaction between those species with mutually exclusive regional distributions (Southwood 1987).

A thorough description of community structure should, therefore, encompass three levels of organization and include all habitats and climate zones in which the association between the herbivore community and the host plant, or structure, is encountered. The regional distribution of phytophagous insect communities is largely dependent on the distribution range of their host plants, and may be restricted, or may extend over a large geographic range. The broader the range of the host plant and its associated herbivore insect community, the greater the heterogeneity of habitat and climatic conditions to which the community will be exposed and the greater the number of representative sampling habitats required. In addition, local communities either have discrete activity peaks in association with host plant phenology, or may be locally temporally continuous with overlapping generations and successional changes in species composition. The temporal patterns of local community functioning will, thus, determine the duration and timing of sampling procedures.

Community description, therefore, involves establishing the temporal and multiscale spatial boundaries, the species richness of the community, the identity of community members, and their absolute and relative abundances in the community at all levels. Diversity

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indices, rank abundance plots and multivariate techniques are used to compare community structure over time and along spatial gradients (Clarke & Warwick 1994). Structural community parameters can then be related to environmental variables and community structuring processes can be examined.

Community organization and structuring mechanisms

The first step in the process of determining whether mechanisms of assembly structure, or 'assembly rules', are operative is to show that the community is patterned to a greater degree than would be expected by chance (Drake 1990). Controversy concerning the presence of so-called assembly rules in communities has arisen as a result of the use of different null model tests with different assumptions (Wilson 1995). The concept of a structured community, nonetheless, remains the same, *i.e.* the species in a local community should be a non-random subset of those species that could possibly occur in it (Pimm 1991; Wilson 1995). High constancy, *i.e.* the variation in composition between localities, and high stability, *i.e.* the variation in composition over time, are two characteristics that indicate the non-random organization of communities (Southwood 1987; Pimm 1991; Wilson 1995). The regional species pool would thus be divided into stable and consistent local species subsets for the community to be considered non-random. This attempt to measure constancy in the community at local and regional levels is important because high constancy demonstrates the dominant role of deterministic organization processes in the community, whereas high variability implies that stochastic processes play a greater role (Rahel 1990). The degree of constancy and stability once again depends on the scale of resolution examined, and variation in community composition is often greatest at the smallest scale of the community studied (Levin 1992; Southwood 1987). Examining and quantifying this variation is one of the key elements in the process of understanding the mechanisms responsible for community organization (Hunter & Price 1992).

Among these mechanisms, geographical, evolutionary and historical factors contribute substantially to the present patterns of local community structure (Chown 1994; Ricklefs & Schluter 1993). However, comparisons of ecologically similar, yet geographically separated, communities demonstrate that regional and local processes also play a role in determining local community pattern (Ricklefs 1987). Establishing the evolutionary and historical factors that may have been responsible for present community patterns is often not possible, whereas

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the effects of regional and local processes can generally be discerned. Local determinants of community structure include 'top-down' processes (parasitism and predation), intra-trophic level interactions (*e.g.* competition, mutualism), 'bottom-up' factors (in the form of resource availability, distribution and quality) and abiotic weather conditions (Cornell & Lawton 1992; Matson & Hunter 1992; Ricklefs & Schluter 1993). Larger-scale processes that influence local community patterns include climatic conditions, long distance species dispersal and metapopulation patch dynamics (Cornell & Lawton 1992; Ricklefs & Schluter 1993).

i. Local processes

Bottom-up processes, in the form of resource characteristics, are important determinants of herbivore insect community structure. Plant tissue quality, particularly the nitrogen and moisture content of the tissue and the level of digestion inhibitors and secondary metabolic products, determine larval survival, development rate and adult fecundity (Bernays & Chapman 1994; Slansky 1993). Host plant phenology and interseasonal variation in resource availability and quality also play an important role in the demography and population dynamics of herbivorous insects (Connor *et al.* 1994; Dempster 1983; Strong *et al.* 1984). Host plant structures may provide the correct microclimatic conditions for insect development and mediate interactions between herbivores and natural enemies by providing concealment among foliage or within plant structures such as galls (Strong *et al.* 1984; Price 1988; Waring & Price 1989). In addition, the distribution of the host plant or plant structure, in terms of patch frequency and density within patches, affects the success of host plant location by a herbivore, the species richness within patches, population sizes of species in the patch and even the extent of interspecific and intraspecific interactions within the patch (Strong *et al.* 1984; Hanski 1983, 1994; Heard 1994; Shorrocks & Rosewell 1987).

Predation and parasitism, particularly parasitism by other arthropods, are known to have a significant 'top-down' impact on numerous herbivore insect communities (Hassell 1985; Strong *et al.* 1984). Natural enemies are capable of maintaining herbivore population levels, in a density dependent manner, below thresholds at which they may begin to compete, and are thus able to influence both the level and outcome of intraspecific and interspecific competitive interactions between herbivores (Minchella & Scott 1991). Natural enemies may also constitute density-independent mortality factors (Dempster 1983; Lessells 1985), in a similar manner to local weather events such as floods, droughts, and sporadic occurrences

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of temperature extremes (Dunson & Travis 1991).

In addition to bottom-up and top-down processes, communities tend to lie on a continuum from 'interactive' to 'non-interactive' (Cornell & Lawton 1992). In interactive communities, intra-trophic level processes play an important role in structuring the community, whereas in non-interactive communities intra-trophic interactions are weak (Cornell & Lawton 1992). Since the 1980's, the view of herbivore insect communities has been one of largely non-interactive, loosely associated guilds with the composition of local and regional communities dominated by accidents of evolutionary history and large-scale biogeographical processes (Denno *et al.* 1995; Lawton *et al.* 1993). One of the major proponents of this view is J.H. Lawton who conducted a comprehensive study of the insect herbivore diversity of the bracken fern (*Pteridium aquilinum*) (*e.g.* Lawton 1976, 1982, 1984, Lawton & Hassell 1981; Lawton & Strong 1981; Lawton *et al.* 1993). This ecological system is now considered one of the geographically best-studied in the world (Lawton *et al.* 1993). Bracken fern was seen as a model system for examining herbivore community patterns because it is cosmopolitan in distribution and generally locally abundant (considered a weed in some regions). It has been widespread since the Tertiary and its herbivore community has been studied on several continents for over two decades (Lawton *et al.* 1993). The most deterministic factors affecting the community of herbivores on bracken world-wide are geographical, in the form of species-area relationships and latitudinal gradients in species richness (Lawton *et al.* 1993). Species richness is, thus, not constrained by interspecific interactions, but "*accidents of evolutionary history and large-scale biogeographical processes dominate local community structure*" (Lawton *et al.* 1993). From the results of this work (see Lawton & Strong 1981), and two review publications on field experiments (Connell 1983; Schoener 1983), various authors have drawn the conclusion that local community interactions are too rare and weak to regularly structure herbivore insect communities (*e.g.* Bultman & Faeth 1985; Jermy 1985; Strong *et al.* 1984).

However, bracken fern may not be a good model species for understanding general patterns in herbivore insect communities. Although results from studies of bracken and its herbivores have provided valuable insights into community organization, the mechanisms responsible for the patterns have been inappropriately applied to herbivore insect communities in general. Bracken fern is a pteridophyte and lacks the structural and temporal complexity of the dominant order of terrestrial plants, the angiosperms. Ferns support a significantly

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different fauna to plants in general (Hendrix 1980), and highly subdivided leaf structures, such as fern pinnae, often have fewer leaf-feeding insects than plants with broad, soft leaves (Lawton & Price 1979). Bracken fern also has sophisticated defences against insects and is not easy to exploit (Cooper-Driver 1976). It contains a large number of chemical defence compounds (among the highest number of ecdysones found in a single plant species) and has a physical defence mechanism provided by ants attracted to the extrafloral nectaries (Cooper-Driver 1976; Lawton 1976). In addition, most plant species are not as cosmopolitan as bracken and many support far greater numbers of species than bracken fern (Schlettwein & Giliomee 1987; Stork 1988; Wright 1993). Angiosperms also possess the obviously unique feature of a variety of discrete, often comparatively large, structures such as fruits, seed-pods, seeds and flowers. These structures are characterized by high quantities of nutrients, high levels of allelochemicals and a tendency to be more ephemeral than the parent plant. In addition flowers, fruits and seed-pods are regularly present in terrestrial plant communities, provide a greater variety of high quality, exploitable resources to herbivore insects than do structurally more simple ferns, and are extensively exploited by herbivorous insects (Denno *et al.* 1995).

It has also recently been shown that interspecific competition is most frequent in phytophagous insect communities feeding on such discrete resources, and interspecific interactions have been resurrected as an important process in the structuring of herbivore insect communities (Damman 1993; Denno *et al.* 1995; Wootton 1994). Denno *et al.* 1995, in contrast to the reviews of Connell (1983) and Schoener (1983), found that interspecific competition occurred in 76 % of interactions between herbivore insects tested and was frequent in all guilds (particularly internal feeders) except free-living mandibulate folivores. Therefore, studies of herbivore insect communities should consider natural enemies, resource characteristics and intra-trophic interactions as potentially important local determinants of community structure.

In addition to these natural ecosystem processes, anthropogenic global landscape transformation, *i.e.* ongoing urbanization, industrialization and conversion of land to agriculture, that result in habitat destruction, fragmentation and simplification, has both major direct and indirect effects on the structure and function of local terrestrial herbivore communities (Scholtz & Chown 1993; Samways 1994). All studies of local herbivore communities and their organization, therefore, have to be addressed in the context of their

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location in an increasingly polluted and fragmented terrestrial landscape.

ii. Regional processes

The distribution and abundance of insects is closely linked to climate (Turner *et al.* 1987; Uvarov 1931). A combination of seasonal changes in temperature and total annual rainfall and its seasonality largely determine their activity times (although resource availability is also often an indirect causal agent of insect seasonality), and most species in temperate regions have short periods of reproductive activity (Wolda 1988). In fact, physiological tolerances, morphological and behavioural characteristics, and life-history plasticity, have been shown to be more important than host plant distributions in determining the distribution of British Lepidoptera (Dennis & Shreeve 1991). Species with the same ecological requirements in the same community often have different life history strategies in relation to seasonality (*i.e.* the temporal distribution of climatic factors and the degree to which they are predictable) (Wolda 1987). The potential species richness of local communities is, thus, determined by the number of species tolerant to the particular set of climate conditions in the given habitat (Wolda 1987). Community stability is also largely determined by climate (Wolda 1987). Climate, therefore, affects communities through differential effects on population abundances, and indirectly affects biotic interactions such as competition and parasitism (Menge & Sutherland 1987). In spite of these interspecific differences, community structures (including properties such as species richness and community stability) show consistent trends along environmental gradients (Menge & Olson 1990). Thus, at a regional level, differences between local communities are often explained best by climatic conditions, whereas interspecific interactions and other factors are often more important at the local community level (Menge & Olson 1990).

Changes in global climate are occurring as a result of enriched CO_2 atmospheres from deforestation and the burning of fossil fuels (Fajer *et al.* 1989; Gates 1993). In addition, the rate and extent of climate change is far higher than previous climate changes, and the main impact of the predicted changes will be from an increased frequency of extreme events such as floods and droughts (Dobson *et al.* 1989; Gates 1993). In response to these changes species may either adapt to the prevailing conditions, change their distribution ranges, or become extinct (Dennis & Shreeve 1991; Pitelka 1994).

The carbon to nitrogen ratio in plant tissues also increases as a result of high CO_2

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concentrations, thereby reducing the quality of host plants to herbivorous insects (Fajer *et al.* 1989; Cammel & Knight 1992). In Lepidoptera this may lead to higher larval mortalities, prolonged instar duration, and hence greater risks of predation and parasitism (Stamp 1993). It may also retard their ability to synchronize life-histories with seasonal changes and host plant availability (Fajer *et al.* 1989; Cammel & Knight 1992). The impact of global climate change on plant and animal communities is largely unknown (Dobson *et al.* 1989), and comparisons of the structure of similar communities occurring in different climate zones can provide useful information on the responses of communities to particular climatic conditions (Dennis & Shreeve 1991). Such studies may also contribute to answering questions on the impact of global warming on terrestrial ecosystems, and monitoring these communities may facilitate the detection of climate zone shifts (Dobson *et al.* 1989).

Community monitoring

If biotic diversity, community integrity and ecosystem functioning are to be maintained, knowledge of the ecological consequences of global environmental changes such as climate change and large scale changes in land use patterns will be required (Carpenter *et al.* 1993, Kingsolver *et al.* 1993; Kremen *et al.* 1994). Monitoring terrestrial biotic communities to determine the impact of these anthropogenic environmental changes has been highlighted as a priority ecological research field in order to evaluate the state of ecological resources, anticipate ecological change, and communicate the consequences of habitat destruction and degradation to decision makers and to the public (Kingsolver *et al.* 1993, Lubchenco *et al.* 1991). The aim of environmental monitoring is, therefore, to understand and predict the consequences of global environmental change. Monitoring must address the detection of stress in systems, relate this to the stressor/s, and allow predictions to be made of the possible effects of environmental changes on ecosystems.

Invertebrates are ubiquitous, diverse and an integral part of ecosystem functioning. They are often sensitive to environmental change and are therefore widely accepted as having the criteria necessary to be successful bioindicators (Samways 1994). A diverse array of invertebrate assemblages and communities, in a variety of habitats, have been monitored in South Africa over short and long periods of time (McGeoch 1994). Comparatively few of these have, however, been conducted with the explicit purpose of relating environmental changes to those observed in the assemblage and community being monitored. Although

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purely descriptive monitoring such as this may be of some value as evidence of past invertebrate community patterns, studies initially aimed at identifying causal relationships are potentially far more useful. In addition, those studies that have examined the impact of specific environmental changes have not used communities as here defined, but looser assemblages of species (McGeoch 1994). A further shortcoming of past bioindicator studies in South Africa is that they have generally been short-term and no longer than a season or two in duration. The value of community monitoring lies predominantly in medium to long term detection of trends and changes. If a community is identified as a suitable monitoring tool in a short term study (often taking the form of projects for degree purposes), this should be followed up by continued monitoring if the goal of predicting the consequences of environmental change is ever to be realized.

The approach to monitoring and selecting indicator species or groups in South Africa has, thus, generally been to address small-scale and specifically localized forms of environmental change. The most pressing environmental problems are, in contrast, those occurring on a large scale. With the present rate and extent of habitat conversion in South Africa (Scholtz & Chown 1993), and the predicted rapid rate of climate change, the past, piecemeal approach to monitoring ecosystem change cannot be afforded. A new approach is required to timeously match this unprecedented rate of landscape and climate change with the knowledge and foresight required to adequately conserve biodiversity and to ensure the maintenance of ecosystem processes and the sustainable utilization of limited resources. This approach should involve co-ordinated, regional scale, long-term, comparative studies that address the impact of change on the distribution and abundance of species and their interactions, and how this in turn affects ecosystem processes. Studies such as these will, in a relatively short time, provide comparisons across specified gradients and facilitate the prediction of the impact of environmental change on terrestrial ecosystems. Communities suitable for this approach must therefore necessarily be regionally widespread, relatively easy to define and preferably encompass groups of species for which baseline taxonomic and biological knowledge is available.

The Lepidoptera community in *Ravenelia macowaniana* galls on *Acacia karroo*

Two fundamental points which emerge from the discussion above are that gall-inhabiting herbivore insect communities that are regionally widespread make excellent

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candidates for multiscale community studies, and that a regional environmental monitoring programme involving species sensitive to both habitat alteration and climate change is sorely needed in South Africa. The primary goals of this research are, therefore, twofold. First to examine the structure and functioning of the Lepidoptera community that inhabits fungus-induced galls on *Acacia karroo* and to contribute, thereby, to the understanding of the community ecology of herbivore insects resident in discrete plant structures. Second, to evaluate the potential of this association, *i.e.* between *A. karroo*, *Ravenelia macowaniana*-induced galls and the Lepidoptera community, to be used as a bioindicator in a regional monitoring programme.

The first chapter of this thesis provides a description of the biology, seasonality and distribution of the association between *A. karroo*, the rust fungus and the Lepidoptera community. The possible advantages of the association to the Lepidoptera species in the community are also discussed. The taxonomy and larval biologies of the Lepidoptera species in the community are discussed in Chapter 2 and diagnoses of, and a key to, the larvae are provided. Chapter 3 examines biotic interactions between members of the Lepidoptera community. The influence of local habitat quality (Chapter 4) and regional climate differences (Chapter 5) on the structure and functioning of the community are dealt with next. Chapter 6 presents a spatially inclusive analysis of individual species properties with regard to their commonness or rarity in the community and an evaluation of the criteria for identifying indicator and pivotal species in communities. In Chapter 7 an analysis of the mechanisms and processes, identified in previous chapters, operative in determining the local structure and functioning of the Lepidoptera community is presented. Finally, Chapter 8 is an assessment of the potential of the Lepidoptera community in *R. macowaniana* galls to be used as a bioindicator in an environmental monitoring programme.

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REFERENCES

Askew, R.R. 1980. The diversity of insect communities in leaf mines and plant galls. *Journal of Animal Ecology* **49**, 817-829.

Bernays, E.A. & Chapman, R.F. 1994. *Host-Plant Selection by Phytophagous Insects.* Chapman & Hall, New York.

Bultman, T.L. & Faeth, S.H. 1985. Patterns of intra- and interspecific association in leaf-mining insects on three oak species. *Ecological Entomology* **10**, 121-129.

Cammell, M.E. & Knight, J.D. 1992. Effects of climatic change on the population dynamics of crop pests. *Advances in Ecological Research* **22**, 117-162.

Carpenter, S.R., Frost, T.M., Kitchell, J.F. & Kratz, T.K. 1993. Species dynamics and global environmental change: a perspective from ecosystem experiments. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change.* Sinauer Associates, Sunderland, pp. 267-279.

Chown, S.L. 1994. Historical ecology of sub-Antarctic weevils (Coleoptera: Curculionidae): patterns and processes on isolated islands. *Journal of Natural History* **28**, 411-433.

Claridge, M.F. 1987. Insect assemblages - diversity, organization, and evolution. In Gee, J.H.R. & Giller, P.S. (Eds). *Organization of Communities Past and Present.* Blackwell Scientific, Oxford, pp. 141-162.

Clarke, K.R. & Warwick, R.M. 1994. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation.* Natural Environmental Research Council, United Kingdom.

Cody, M.L. 1989. Discussion: structure and assembly of communities. In Roughgarden, J., May, R.M. & Levin, S.A. (Eds). *Perspectives in Ecological Theory.* Princeton University Press, New Jersey, pp. 227-241.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* **122**, 661-696.

Connor, E.F., Adams-Manson, R.H., Carr, T.G. & Beck, M.W. 1994. The effects of host plant phenology on the demography and population dynamics of the leaf-mining moth, *Cameria hamadryadella* (Lepidoptera: Gracillariidae). *Ecological Entomology* **19**, 111-120.

Cooper-Driver, G. 1976. Chemotaxonomy and phytochemical ecology of bracken. *Botanical Journal of the Linnean Society* **73**, 35-46.

Cornell, H.V. & Lawton, J.H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**, 1-12.

Damman, H. 1993. Patterns of interaction among herbivore species. In Stamp, N.E. & Casey, T.M. (Eds). *Caterpillars Ecological and Evolutionary Constraints on Foraging.* Chapman & Hall, New York, pp. 132-169.

Dempster, J.P. 1983. The natural control of populations of butterflies and moths. *Biological Review* **58**, 461-481.

Dennis, R. L. H. & Shreeve, T. G. 1991. Climate change and the British butterfly fauna: opportunities and constraints. *Biological Conservation* **55**, 1-16.

Denno, R.F., McClure, M.S. & Ott, J.R. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology* **40**, 297-331.

Diamond, J. & Case, T. J. 1986. *Community Ecology.* Harper & Row, New York.

Digitised by the Department of Library Services in support of open access to information, University of Pretoria, 2021

Dobson, A., Jolly, A. & Rubenstein, D. 1989. The greenhouse effect and biological diversity. *Trends in Ecology and Evolution* **4**, 64-68.

Drake, J.A. 1990. Communities as assembled structures: do rules govern pattern? *Trends in Ecology and Evolution* **5**, 159-164.

Dunson, W.A. & Travis, J. 1991. The role of abiotic factors in community organization. *The American Naturalist* **138**, 1067-1091.

Elton, C. S. 1927. *Animal Ecology*. Sidgwick & Jackson, London.

Fajer, E. D., Bower, M. D. & Bazzaz, F. A. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Science* **243**, 1198-1200.

Gates, D.M. 1993. *Climate Change and its Biological Consequences*. Sinauer Associates, Massachusetts.

Hanski, I. 1983. Coexistence of competitors in patchy environment. *Ecology* **64**, 493-500.

Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* **9**, 131-135.

Hassell, M.P. 1985. Insect natural enemies as regulating factors. *Journal of Animal Ecology* **54**, 323-334.

Heard, S.B. 1994. Processing chain ecology: resource condition and interspecific interactions. *Journal of Animal Ecology* **63**, 451-464.

Hendrix, S.D. 1980. An evolutionary and ecological perspective of the insect fauna of ferns. *The American Naturalist* **115**, 171-196.

Hunter, M.D. & Price, P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**, 724-732.

Jermy, T. 1985. Is there interspecific competition between phytophagous insects? *Zeitschrift fuer Zoologische Systematik und Evolutionsforschung* **23**, 275-285.

Kingsolver, J.G., Huey, R.B. & Kareiva, P.M. 1993. An agenda for population and community research on global change. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland, pp. 480-486.

Kremen, C., Merenlander, A.M. & Murphy, D.D. 1994. Ecological monitoring: a vital need for integrated conservation and development programs in the tropics. *Conservation Biology* **8**, 388-397.

Lawton, J.H. 1976. The structure of the arthropod community on bracken. *Botanical Journal of the Linnean Society* **73**, 187-216.

Lawton, J.H. 1982. Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *Journal of Animal Ecology* **51**, 573-595.

Lawton, J.H. 1984. Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. In Strong, D.R., Simberloff, D., Abele, L.G. & Thistle, A.B. (Eds). *Ecological Communities: Conceptual Issues and the Evidence*. University Press, Princeton, pp. 67-99.

Lawton, J.H. & Hassell, M.P. 1981. Asymmetrical competition in insects. *Nature* **289**, 793-795.

Lawton, J.H. & Price, P.W. 1979. Species richness of parasites on hosts: agromyzid flies on British Umbelliferae. *Journal of Animal Ecology* **48**, 619-637.

Lawton, J. H. & Strong, D. R. 1981. Community patterns and competition in folivorous insects. *The American Naturalist* **118**, 317-338.

Lawton, J.H., Lewinsohn, T.M. & Compton, S.G. 1993. Patterns of diversity for the insect

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herbivores on bracken. In Ricklefs, R.E. & Schluter, D. (Eds). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 178-184.

Lessells, C.M. 1985. Parasitoid foraging: should parasitism be density dependent? *Journal of Animal Ecology* **54**, 27-41.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**, 1943-1967.

Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J. & Risser, P.G. 1991. The sustainable biosphere initiative: an ecological research agenda. *Ecology* **72**, 371-412.

Matson, P.A. & Hunter, M.D. 1992. Special feature: the relative contributions of top-down and bottom-up forces in population and community ecology. *Ecology* **73**, 1.

McGeoch, M.A. 1994. The use of invertebrate assemblages for environmental monitoring: *status quo* in South Africa and future directions. *Abstracts Volume: Zoological Society of Southern Africa Symposium*, Pietermaritzburg, July 1994, p. 93.

Menge, B. A. & Olson, A. M. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* **5**, 52-57.

Menge, B. A. & Sutherland, J. P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**, 730-757.

Minchella, D.J. & Scott, M.E. 1991. Parasitism: a cryptic determinant of animal community structure. *Trends in Ecology and Evolution* **6**, 250-254.

Pimm, S.L. 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. The University of Chicago Press, Chicago.

Pitelka, L.F. 1994. Ecosystems response to elevated CO_2. *Trends in Ecology and Evolution* **9**, 204-207.

Price, P.W. 1988. Inversely density-dependent parasitism: the role of plant refuges for hosts. *Journal of Animal Ecology* **57**, 89-96.

Rahel, F.J. 1990. The hierarchical nature of community persistence: a problem of scale. *The American Naturalist* **136**, 328-344.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**, 167-171.

Ricklefs, R.E. & Schluter, D. 1993. Species diversity: regional and historical influences. In Ricklefs, R.E. & Schluter, D. (Eds). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 350-364.

Samways, M.J. 1994. *Insect Conservation Biology*. Chapman & Hall, London.

Schlettwein, C.H.G. & Giliomee, J.H. 1987. Comparisons of insect biomass and community structure between fynbos sites of different ages after fire with particular reference to ants, leafhoppers and grasshoppers. *Annale Universiteit van Stellenbosch* Serie A3, **2**, 76 pp.

Schoener, T. W. 1983. Field experiments on interspecific competition. *The American Naturalist* **122**, 240-285.

Scholtz, C.H. & Chown, S.L. 1993. Insect conservation and extensive agriculture: the savanna of southern Africa. In Gaston, K.J., New, T.R. & Samways, M.J. (Eds). *Perspectives on Insect Conservation*. Intercept Ltd, Andover, pp. 75-96.

Shorrocks, B. & Rosewell, J. 1987. Spatial patchiness and community structure: coexistence

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and guild size of drosophilids on ephemeral resources. In Gee, J.H.R. & Giller, P.S. (Eds). *Organization of Communities Past and Present*. Blackwell Scientific, Oxford, pp. 29-52.

Simberloff, D. & Dayan, T. 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* **22**, 115-143.

Slansky, F. 1993. Nutritional ecology: the fundamental quest for nutrients. In Stamp, N.E. & Casey, T.M. (Eds). *Caterpillars Ecological and Evolutionary Constraints on Foraging*. Chapman & Hall, New York, pp. 29-91.

Southwood, T. R. E. 1987. The concept and nature of the community. In Gee, J.H.R. & Giller, P.S. (Eds). *Organization of Communities Past and Present*. Blackwell Scientific, Oxford, pp. 3-27.

Stamp, N.E. 1993. A temperate region view of the interaction of temperature, food quality, and predators on caterpillar foraging. In Stamp, N.E. & Casey, T.M. (Eds). *Caterpillars Ecological and Evolutionary Constraints on Foraging*. Chapman & Hall, New York, pp. 478-508.

Stork, N.E. 1988. Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society* **35**, 321-337.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific, Oxford.

Turner, T. R. G., Gatehouse, C. M. & Corey, C. A. 1987. Does solar energy control organic diversity? butterflies, moths and the British climate. *Oikos* **48**,195-205.

Waring, G.L. & Price, P.L. 1989. Parasitoid pressure and the radiation of a gall forming group (Cecidomyiidae: *Asphodylia* spp.) on creosote bush (*Larrea tridentata*). *Oecologia* **76**, 293-299.

Wilson, J.B. 1995. Null models for assembly rules: the Jack Horner effect is more insidious than the Narcissus effect. *Oikos* **72**, 139-144.

Wolda, H. 1987. Seasonality and the community. In Myers, A.A. & Giller, P.S. (Eds). *Analytical Biogeography: An Integrated Approach to the Study of Animal and Plant Distributions*. Chapman & Hall, London, pp. 69-95.

Wolda, H. 1988. Insect seasonality: why? *Annual Review of Ecology and Systematics* **19**, 1-18.

Wootton, J.T. 1994. The nature of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**, 443-466.

Wright, M.G. 1993. Insect conservation in the African Cape Fynbos, with special reference to endophagous insects. In Gaston, K.J., New, T.R. & Samways, M.J. (Eds). *Perspectives on Insect Conservation*. Intercept Ltd, Andover, pp. 97-110.

Uvarov, B.P. 1931. Insects and climate. *Transactions of the Entomological Society of London* **79**, 1-239.

Zwölfer, H. 1979. Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls. *Fortschritte der Zoologie* **25**, 331-353.

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CHAPTER 1

The association between the Lepidoptera community and *Ravenelia macowaniana* Pazschke galls on *Acacia karroo* Hayne in South Africa[1]

A community of phytophagous Lepidoptera inhabit the large fleshy galls induced by the rust fungus, *Ravenelia macowaniana* Pazschke (Uredinales, Pucciniaceae) (Doidge 1932) on *Acacia karroo* Hayne (Fig 1.1). *Acacia karroo* is distributed throughout Africa, with the exception of wet and cold regions and on white silicon, sour soils (Swartz, pers. comm.), and is the most widespread and eurytopic of the *Acacia* species in South Africa (Swartz 1982; Palgrave 1985). Although it is not known whether the distribution of this host-specific fungus overlaps entirely with that of its host, Doidge (1932) recorded *R. macowaniana* in Central Africa and in the Gauteng, Orange Free State, Transkei, Eastern Cape and parts of Kwazulu-Natal in South Africa. The distribution of the association between the fungus and the Lepidoptera is regionally widespread, as Lepidoptera larvae have been found in these galls in a number of geographically separate regions of South Africa (Table 1.1; Fig. 1.2).

Similar associations between rust-fungus galls and lepidopteran larvae have been reported from Australia and New Zealand. Lepidoptera occur in a rust-fungus induced gall on *Acacia decurrens* (J.Wendl.) in Australia (New 1982) and one lepidopteran species has been recorded from '*Acacia* rust galls' in New Zealand (Wise 1962). New (1982) described the Lepidoptera community in galls induced by *Uromycladium tepperianum* (Sacc.) Mc Alp. (Uredinales, Pucciniaceae) on *Acacia decurrens* in Melbourne, Australia.

In South Africa, associations between Lepidoptera and galls are not uncommon. A number of species has been recorded in association with stem, axial and fruit galls on a range of host plant species (Scholtz 1978; Gandar 1979; Scoble & Scholtz 1984). All of these galls are known, or in one instance at least thought, to be induced by the Lepidoptera species that inhabit them, *i.e.* members of the families Lyonetiidae, Momphidae, Gelechiidae and Thyrididae (Scholtz 1978; Scoble & Scholtz 1984). The Lepidoptera - *R. macowaniana* gall association is, therefore, unique in two respects. First, the gall is not induced by the Lepidoptera that inhabit it and second, in contrast to the above-mentioned associations, more

[1] published in part as McGeoch 1993

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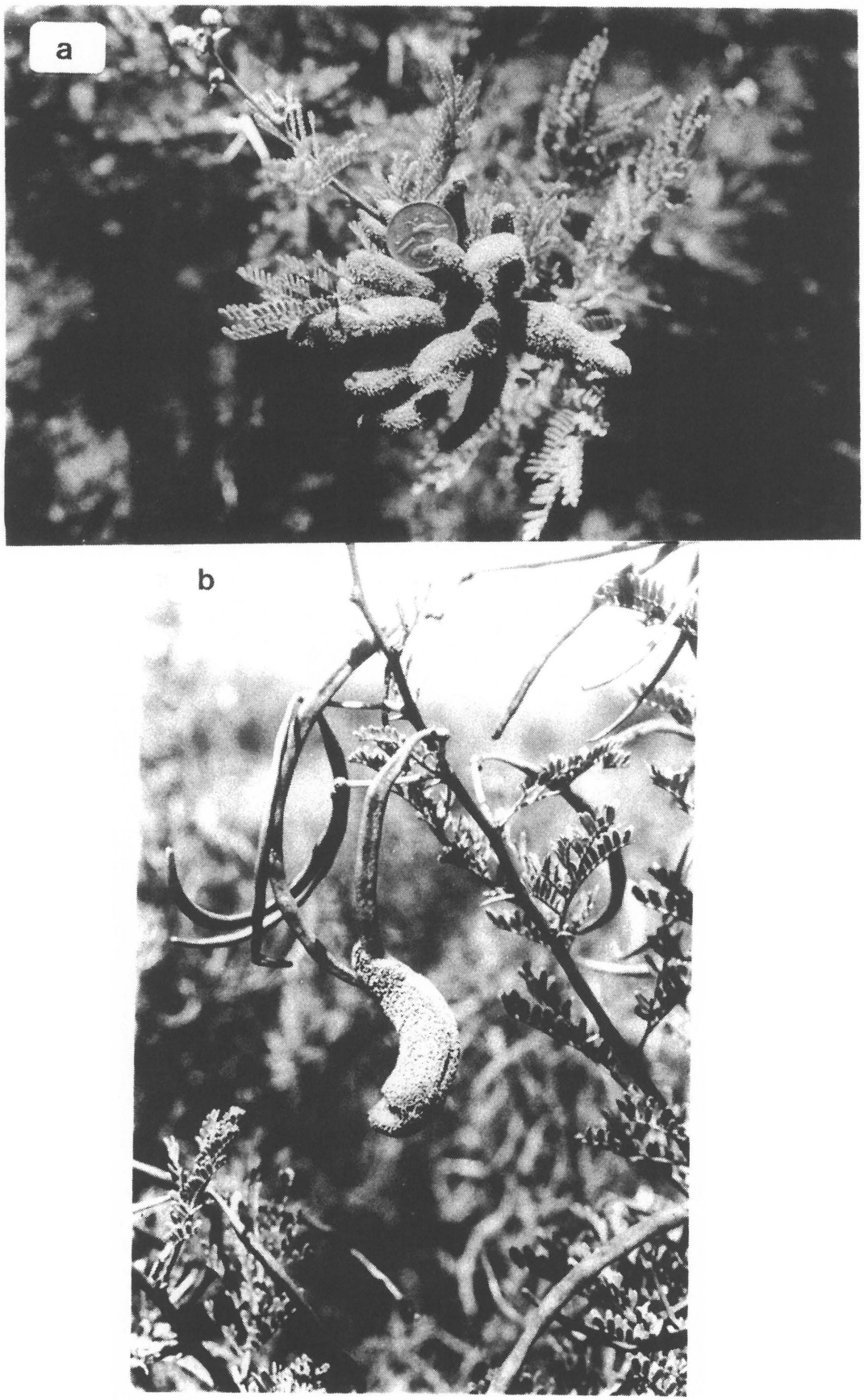

Fig. 1.1. *Ravenelia macowaniana* Pazschke galls induced on a flowering shoot (a) and a seed-pod (b) of *Acacia karroo* Hayne.

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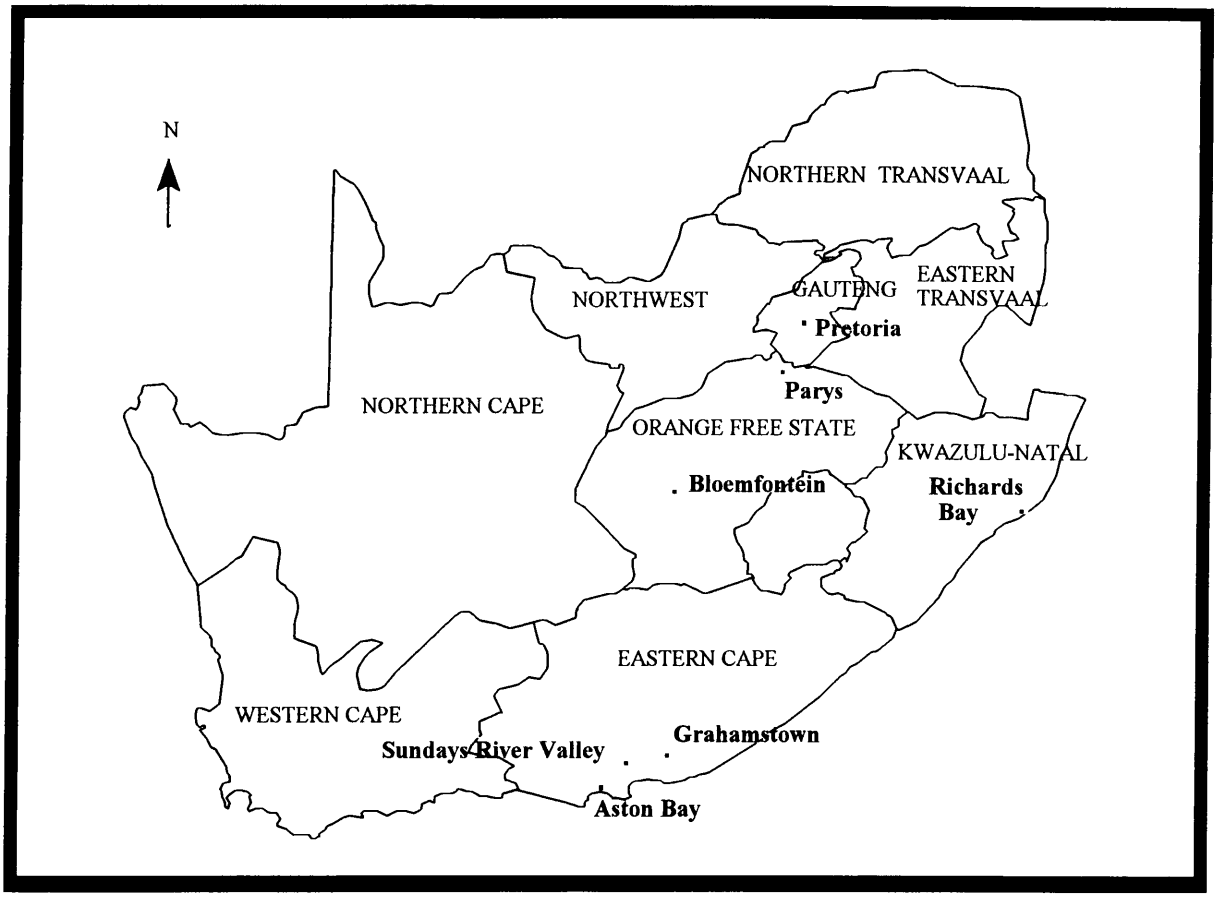

Fig. 1.2. Provinces of South Africa (capital letters) and localities from which galls were sampled (bold); the Pretoria area includes Boekenhoutskloof, Hartebeespoort, Pienaarspoort, Moreleta Nature Reserve and Proclamation Hill.

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than a single Lepidoptera species inhabits the *R. macowaniana* galls simultaneously. This form of gall-habitation by insects is thought to hold certain advantages for the inhabitants. However, hypotheses concerning the adaptive significance of a gall-inhabiting lifestyle deal almost exclusively with insect gall-inducers (*e.g.* Fernandes & Price 1992; Price *et al.* 1987). A number of these hypotheses may, however, also apply to the secondary habitation and utilization of galls, such as by the Lepidoptera in fungus-induced galls on *A. karroo*.

In this chapter an account of *R. macowaniana*-gall phenology, seasonality and distribution is presented, and the association between the galls and the Lepidoptera larvae is discussed. The possible advantages of the association to the Lepidoptera are also considered.

STUDY SITES and METHODS

Ravenelia macowaniana galls were sampled and monitored between January 1991 and March 1994. The localities from which galls were recorded and sampled during the study are listed in Table 1.1 and the dates on which they were sampled in Table 1.2. A minimum of 100 galls was collected in each sample, although low gall abundance at certain times of the year and in certain seasons resulted in smaller samples being collected. A minimum of two and a maximum of 10 galls were collected from single trees. After removal from the tree each gall was weighed and described (diameter, shape, colour and plant-tissue condition). Differences in mean gall masses between localities and sampling months were determined using Kruskal-Wallis one-way analyses by ranks and Dunn's distribution free multiple comparisons test (the data were not normally distributed before or after transformation) (Siegel 1956; Zar 1984). Gall abundance was monitored throughout the study period at each locality by walking around each tree prior to sampling and counting individual galls. On trees with over 100 galls estimates were made to the nearest 20 galls. The duration of individual gall development was determined by marking branches and recording the development time and changes in size, appearance and plant-tissue condition of galls on these branches.

Percentage gall, flower, shoot and leaf nitrogen content was determined using the Kjeldahl method for total nitrogen (Jackson 1958). The moisture content of galls, flowers, shoots and leaves was determined by weighing a sample of fresh galls, flowers, shoots and leaves, oven-drying these at 60°C to constant mass, and weighing them dry. The differences in nitrogen and moisture levels between these tissue types were then assessed using one-way analyses of variance on log-transformed data and Tukey's multiple range test (Sokal & Rohlf

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1981).

In the laboratory, between 10 and 200 galls from each gall sample were placed individually into 400 ml plastic bottles lined with newspaper and covered with gauze lids to allow ventilation of the container. The Lepidoptera larvae were allowed to complete their development in the galls in the rearing containers and emerging adults were collected for identification. Adult Hymenoptera emerging in the containers were also collected. The remaining galls in each sample were carefully prised open and all larvae removed, preserved and later identified (see Chapter 2, McGeoch & Krüger 1994). A record was kept of the number of parasitized larvae in each gall and of any other arthropods present. Once all the Lepidoptera larvae and pupae had been removed from the gall, a visual estimate was made, to the nearest 10%, of the percentage of gall tissue consumed by larvae in the gall. In old and dead galls the number of previously occupied galls were taken as those that showed evidence of larval feeding on the gall tissue, as well as by the presence of old burrows, frass, exuviae and old pupal cases. The number of galls occupied in each sample was taken as the percentage of galls sampled in which Lepidoptera larvae or pupae were present.

RESULTS

Gall phenology and abundance

Galls first become visible between November and January as fleshy green swellings on the apex of flower and seed-pod pedicels and new galls are formed between November and March.

Flower galls are most commonly spherical with radiating arms of varying lengths (Fig. 1.1a), but seed-pod galls retain the basic sickle-shape of the *A. karroo* seed-pod (Fig. 1.1b). Seed-pod galls develop later in the season (late January to March) during pod development on *A. karroo*. Seed-pod galls are comparatively rare and flower galls are most commonly encountered.

Five gall age-categories were distinguished:

1. Growing galls: still increasing in diameter, light-green in appearance and internal tissue green and moist, peduncle green;
2. Post-growth galls: no longer increasing in diameter, light to rust-brown in appearance, internal tissue green, peduncle green;
3. Lignifying galls: brown to rust-coloured in appearance, internal tissue drier and lignified

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in patches, peduncle brown-green;

4. Dead galls: dark brown in appearance, internal tissue completely lignified and woody, peduncle woody;

5. Old galls: galls black and brittle, these were dead galls which had remained attached to the tree for longer than the single development season of three to five months.

Growing galls were present in January and February, except at Aston Bay where growing galls were present from November until March (Table 1.2)[2]. After March, all galls remaining on the trees in all regions were dead (age-category 4). Many old galls (age-category 5) remain on the trees for a number of months and some even into the following growing season. Gall life-span (time duration from age-category 1 to 4) ranged from 28 to 54 days (mean = 42.86, S.E.= 4.93, n = 7). Maximum gall size (duration of age category 1) is reached between 10 and 31 days (mean = 19.00, S.E.= 4.24, n = 7). Potentially larger galls take longer to reach maximum size. Gall size at age-category 4 (*i.e.* stage at which no further growth will occur) ranges between 5 mm and 70 mm in diameter (mean = 24.51, S.E. = 1.21, n = 100).

In most samples, over 90% of the galls were, or had been, occupied by Lepidoptera larvae (Table 1.2). Of these, the percentage gall tissue removed in each gall ranged between 10% and 80% with medians of between 10% and 70% (Table 1.2).

Gall masses were highest in January and February (younger galls) and showed a tendency to decrease in mass after February as the galls aged (Table 1.3). However, gall masses within regions varied between years, and in some years galls weighed the most in January, but in other years most in February (*e.g.* Parys, Table 1.3). This is indicative not only of interseasonal variation in gall masses, but also of interseasonal variation in the onset of galling. Aston Bay, Parys and Bloemfontein were the localities with the highest mean gall masses, followed by Boekenhoutskloof, Hartebeespoort and Parys (Table 1.4). Richards Bay, Sundays River Valley and Grahamstown had the lowest gall masses (Table 1.4).

The local distribution of *R. macowaniana* is patchy. The abundance of galls on individual trees is highly variable (Table 1.5) and ranges from one gall to over 100 galls per tree. The number of trees galled in an area shows similar high variation, although this was not quantified. Observations also suggest that extremely high gall densities may eventually

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[2] data from Hartebeespoort, Pienaarspoort, Moreleta Nature Reserve and Proclamation Hill (listed 2 to 5 in Table 1.1) are not presented here, see Chapter 4

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kill the tree.

Ravenelia macowaniana galls contain a higher percentage nitrogen than *A. karroo* flowers, shoots and leaves present on the tree at the same time (Table 1.6, $F = 8.69$, d.f. $= 34$, $P<0.001$), but only significantly higher than *A. karroo* shoots. The water content of galls, however, was significantly higher than either *A. karroo* buds, leaves or shoots (Table 1.6, $F = 68.65$, d.f. $= 45$, $P<0.001$).

The Lepidoptera associated with *R. macowaniana* galls

Twenty-two Lepidoptera species (Table 1.7) were recorded in *R. macowaniana* galls and the identification and life-histories of these species are discussed in Chapter 2. Lepidoptera were only present in dead galls after March at Aston Bay. Old galls (age category 5) were not inhabited by Lepidoptera (larvae or pupae) in any other region and Lepidoptera were, therefore, present in galls in these regions only between January and March.

Non-lepidopterans

The Lepidoptera in the galls are parasitized by hymenopteran parasitoids. Adult parasitoids emerged from galls and ectoparasitic and endoparasitic larvae were found on lepidopteran larvae in the galls. The parasitoids included representatives of the Families Braconidae (incl. *Chelonus* sp.), Encyrtidae (*Cerchysiella* sp.), Perilampidae (*Perilampus* sp.), Bethylidae and Ichneumonidae. The level of parasitism was, however, generally low and ranged from 0.00 % to 3.60 % (Table 1.8).

One other arthropod, *Phalacrus* sp. (Coleoptera, Phalacridae), was regularly found on live galls (age categories 1 - 3). Phalacrid larvae are fungal-spore feeders (Endrödy-Younga 1985) and the larvae fed on spores on the gall surface. Phalacrid larvae were recorded sporadically on galls in all the regions sampled.

A variety of arthropods, including spiders, mites, ants, psocopterans and wood-boring Coleoptera, occupied the deserted lepidopteran tunnels in dead galls (gall age-categories 4 & 5).

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Table 1.1. Localities from which Lepidoptera larvae were sampled (S) and recorded (R) in *Ravenelia macowaniana* Pazschke galls on *Acacia karroo* Hayne in South Africa.

Locality	Co-ordinates	
Boekenhoutskloof (Gauteng)	25.33S 28.27E	S
Hartebeespoort (Gauteng)	25.45S 27.52E	S
Pienaarspoort (Gauteng)	25.44S 28.25E	S
Moreleta Nature Reserve (Gauteng)	25.46S 28.16E	S
Proclamation Hill (Gauteng)	25.45S 28.07E	S
Brits (Gauteng)	25.38S 27.46E	R
Nelspruit (Eastern Transvaal)	25.30S 30.54E	R
Parys (Orange Free State)	26.53S 27.30E	S
Bloemfontein (Orange Free State)	29.10S 26.15E	S
Richards Bay (Kwazulu-Natal)	28.38S 32.20E	S
Olifantshoek (Northern Cape)	27.51S 22.55E	R
Grahamstown (Eastern Cape)	33.17S 32.05E	S
Sundays River Valley (Eastern Cape)	33.30S 25.40E	S
Aston Bay (Eastern Cape)	34.10S 24.55E	S

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Table 1.2. Gall ages (categories 1, youngest to 4, dead galls) (median and range), percentage of gall tissue consumed (median and range) and percentage of galls occupied by Lepidoptera larvae in each region at every sampling period; n = number of galls sampled.

Locality Date:	Age	% of Gall Consumed	% of Galls Occupied	n
Boekenhoutskloof				
1992: January	2 (1-4)	10 (10-70)	72	103
February	2 (1-4)	30 (10-80)	92	86
March	4 (2-4)	30 (20-80)	89	100
Parys				
1993: January	3 (1-4)	40 (10-70)	96	105
February (early)	3 (1-4)	40 (10-80)	81	120
February (late)	2 (2-4)	30 (10-70)	98	110
March	4 (3-4)	50 (20-70)	98	100
1994: January	2 (1-4)	30 (10-80)	97	106
February	4 (4)	50 (10-80)	99	100
Bloemfontein				
1992: February	3 (1-4)	40 (10-70)	96	196
1993: January	3 (1-4)	30 (10-80)	83	399
March	4 (2-4)	30 (10-70)	100	100
1994: January	2 (1-4)	30 (10-80)	92	200
Richards Bay				
1994: February	4 (2-4)	70 (10-80)	97	104
Grahamstown				
1994: February	3 (1-4)	70 (10-80)	100	121
Sundays River Valley				
1994: February	3 (2-4)	60 (10-80)	99	196
Aston Bay				
1991: November	1 (1-3)	10 (10-30)	99	200
1992: February	1 (1-4)	30 (10-80)	85	100
1993: January	3 (1-4)	20 (10-80)	96	400
March	4 (1-4)	50 (10-80)	96	200
May	4 (4)	40 (10-80)	99	200
1994: January	2 (1-4)	30 (10-80)	97	301
February	3 (2-4)	50 (20-80)	100	106

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Table 1.3. Mean ± S.E. of gall mass (g) at each sampling date and locality; n = number of galls; different letters (bold) denote a significant difference of $P < 0.01$ between means within localities.

Locality / Date		n	Mean±S.E.	H=; P<
Boekenhoutskloof				8.13; 0.02
1992	January	103	6.13±0.71	**a**
	February	86	4.51±0.53	**b**
	March	100	4.49±0.48	**b**
Hartebeespoort				44.15; 0.001
1992	January	34	2.19±0.45	**a**
	February	39	8.77±1.32	**b**
	March	36	3.25±0.36	**c**
Pienaarspoort				0.67; 0.72
1992	January	40	4.14±0.58	**a**
	February	40	6.18±1.32	**a**
	March	18	4.62±1.19	**a**
Parys				21.29; 0.001
1993	January	65	4.75±0.49	**ab**
early	February	99	7.71±1.44	**ac**
late	February	100	6.09±0.55	**c**
	March	33	3.73±0.56	**d**
1994	January	103	5.89±0.89	**bd**
	February	21	7.64±1.17	**e**
Bloemfontein				52.59; 0.001
1992	February	196	6.89±0.51	**a**
1993	January	296	5.57±0.38	**b**
	March	100	2.79±0.22	**c**
1994	January	200	6.88±0.55	**a**
Aston Bay				195.67; 0.001
1991	November	64	2.96±0.34	**b**
1992	February	80	4.88±0.48	**a**
1993	January	174	13.22±0.97	**c**
	March	76	5.24±0.34	**a**
	May	72	4.41±0.34	**a**
1994	January	94	2.84±0.39	**d**
	February	98	4.69±0.45	**e**

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Table 1.4. Mean ± S.E. of gall mass (g) at each locality; H = 61.99, P<0.001; n = number of galls; different letters (bold) denote a significant difference of P < 0.01 in means between localities.

Locality	n	Gall mass	
Boekenhoutskloof	289	5.07 ± 0.34	**a**
Hartebeespoort	109	4.89 ± 0.57	**a**
Pienaarspoort	981	5.06 ± 0.63	**a**
Parys	421	6.11 ± 0.44	**b**
Bloemfontein	792	5.88 ± 0.24	**b**
Richards Bay	100	3.13 ± 0.32	**c**
Grahamstown	103	3.62 ± 0.32	**d**
Sundays River Valley	81	3.43 ± 0.31	**e**
Aston Bay	658	6.57 ± 0.33	**b**

Table 1.5. Abundance of galls (mean ± S.E.) on individual *Acacia karroo* trees at sampled localities; n = number of trees.

Locality	Abundance	n
Boekenhoutskloof	14.74 ± 1.74	70
Hartebeespoort	2.42 ± 0.26	55
Pienaarspoort	5.22 ± 2.19	104
Parys	10.43 ± 1.53	100
Bloemfontein	11.04 ± 0.14	99
Aston Bay	11.07 ± 0.24	69

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Table 1.6. Percentage nitrogen and water content of *Ravenelia macowaniana* galls and *Acacia karroo* flowers buds, leaves and young shoots; different letters (bold) denote significantly different means according to Tukey's 95% H.S.D. confidence intervals (C.I.), n = number of samples.

Tissue	%Nitrogen			% Water		
	mean±S.E.	C.I.	n	mean±S.E.	C.I.	n
galls	2.67 ± 0.11 **a**	2.49-2.85	20	71.46 ± 0.68 **a**	70.29-72.65	20
buds	2.24 ± 0.04 **ab**	1.87-2.59	5	62.90 ± 0.61 **b**	60.76-65.06	10
leaves	2.14 ± 0.15 **ab**	1.78-2.50	5	59.53 ± 0.84 **bc**	57.86-61.19	10
shoots	1.66 ± 0.08 **b**	1.30-2.03	5	58.44 ± 0.89 **c**	56.77-60.10	10

DISCUSSION

Ravenelia macowaniana galls develop on the flowering shoots and seed-pods of *A. karroo* and gall development occurs only during certain months of the year. The galls are relatively short-lived and lepidopteran larval development in the galls is restricted, in most species, to a short period each year. The seasonality of gall development is, therefore, an important component of the functioning of this community of Lepidoptera. The period during which new gall development takes place is usually two to three months in duration, but at Aston Bay gall development begins earlier (November) and ends later (March). Newly developed galls have also been recorded from Richards Bay in November and live gall tissue is available to the lepidopteran larvae for a longer period in coastal than in interior regions.

Variation in annual rainfall patterns and tree water status appears to affect the seasonality of gall development within regions, and between years. The duration of the gall development period can also change from year to year (*e.g.* Parys, January to March 1993 compared to January to February 1994, Table 1.2). Interseasonal variability in the flowering phenology of *A. karroo* is high and is dependent on annual rainfall patterns, tree water status and the age of the tree (Van Rooyen 1984; P.J. Robbertse pers. comm.). Because galls develop from the flowers and seed-pods of *A. karroo*, annual gall development may also, indirectly, be dependent on these factors. For example, during 1993 and 1994 no gall development occurred at any of the sampling regions within the Gauteng region (see Table

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1.1). Rainfall was well below average in the two years preceding the 1993 gall season and above average during the 1994 season. Although rainfall was high from November 1993 to March 1994, the *A. karroo* trees in the region flowered very poorly. Poor flowering in both drought and very wet years is evidently a common phenomenon in *A. karroo* (P.J. Robbertse pers. comm.) and may be one of the reasons why gall development did not occur. Evidence of vascular-plant race-resistance to fungal pathogens has been reported elsewhere (Burdon 1991), and this may contribute to the variation in the number of trees galled, as well as to which particular trees are galled within regions. The ephemeral nature of, and high spatial and temporal variation in, gall development suggests that the adult moths should have good host-location (gall finding) abilities, that larval development should be rapid (perhaps facilitated by high gall-tissue quality, see below) and that species should have alternative host plants.

Nitrogen and moisture levels were higher in gall tissue than in other plant tissue available to Lepidoptera larvae on *A. karroo* (*i.e.* leaves, shoots and flowers) and the nutritional value of the *R. macowaniana* gall tissue is therefore high. Galls have previously been shown to provide one of the highest quality food substrates (along with seeds and pollen) to herbivorous insects (Roskam 1992). High water content also provides the larvae with higher humidity levels than would be encountered by external feeders and this may reduce desiccation and promote larval survival (Fernandes & Price 1992; Slansky 1993). The performance (growth rate and assimilation efficiency) of Lepidoptera larvae is known to decrease with a decline in plant-tissue water and nitrogen content (Slansky & Scriber 1985). This may explain the high occupancy of *R. macowaniana* galls by Lepidoptera.

Over 90% of galls in the majority of samples were occupied by Lepidoptera larvae, although never more than 80% of each gall was consumed. Beyond the 80% level of gall tissue consumption the gall begins to disintegrate and lose its integrity. Feeding by the larvae also facilitates an increase in the rate of dehydration of gall tissue (see also New 1982). This renders the remaining gall tissue progressively less suitable for consumption by species that feed on live gall tissue. The percentage of gall tissue consumed once galls reach age-category 4 (dead galls) may thus partly depend on the rate of dehydration and aging of the gall tissue.

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Table 1.7. Moth species recorded in *Ravenelia macowaniana* galls in South Africa.

Family Species
Noctuidae
1. *Characoma submediana* Wiltshire[1]
2. *Eublemma brachygonia* Hampson
Tortricidae
3. *Cydia* (*Cydia*) *victrix* (Meyrick)
4. *Cydia* (*Cydia*) *aphrospila* (Meyrick)
5. *Cryptophlebia peltastica* (Meyrick)
6. *Lobesia stericta* (Meyrick)
Pyralidae
7. *Euzophera* sp. nr. *verrucicola* Hampson[1]
8.-13. indet. Phycitinae 1-6
Cosmopterigidae
14. *Ascalenia pulverata* (Meyrick)
15. *Anatrachyntis tripola* (Meyrick)[1]
Gelechiidae
16. *Anarsia gravata* Meyrick[1]
17. *Anarsia nimbosa* Meyrick
18. *Anarsia* (nr.) *amalleuta* Meyrick
19. *Anarsia* sp.
20. *Encolpotis xanthoria* Meyrick
Oecophoridae
21. *Schiffermuelleria pedicata* Meyrick
Tineidae
22. *Phthoropoea oenochares* (Meyrick)

[1] Referred to in McGeoch (1993) as 1, *Pardasena* sp.nr. *virgulana* (Mabille); 7, *Getulia* sp.nr. *semifuscella* Ragonot; 15, *Caloptilia* sp.; 16, *Anarsia nimbosa* Meyrick.

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Table 1.8. Percentage of Lepidoptera larvae parasitized by hymenopteran parasitoids and the range of percentage parasitism in each sample; n = total number of larvae recorded.

Locality	Total %	Range%	n
Boekenhoutskloof	0.36	0.00 - 0.96	558
Proclamation Hill	0.00	-	431
Hartebeespoort	0.76	0.00 - 3.61	395
Pienaarspoort	0.21	0.00 - 0.42	483
Moreleta	0.00	-	320
Parys	0.37	0.12 - 3.16	2714
Bloemfontein	0.70	0.00 - 0.84	2292
Richards Bay	0.00	-	223
Aston Bay	0.63	0.25 - 1.16	5545
Sundays River Valley	0.19	-	1548
Grahamstown	1.07	-	747

Lepidopteran larvae constituted the large majority of the arthropod fauna in living galls and it is, therefore, likely that the majority of adult parasitoids reared had lepidopteran hosts. Price (1988) showed that insect herbivores in galls often have a lower probability of being parasitized with increasing gall diameter and he estimated that 30% parasitism of the single herbivore galler he studied would prevent the host population from being maintained by local reproduction. Considering the multispecies community in fungus galls and the comparatively low degree of parasitism, it seems unlikely that parasitism plays a major role in regulating lepidopteran population densities in this community.

The high occupancy rate of *R. macowaniana* galls, and the data presented above, suggest that *R. macowaniana* galls do provide the Lepidoptera larvae with some advantage. In addition, *A. karroo* is known to respond to leaf-herbivory by increasing tannin levels that act as digestion inhibitors in herbivores (Owen-Smith & Cooper 1987; Strong *et al.* 1984; Teague 1989) and gall tissues have been shown to often have lower levels of secondary plant compounds, such as tannins (Cornell 1983; Price *et al.* 1987). If *R. macowaniana* gall tissue does contain lower tannin levels than other plant tissue on *A. karroo*, this is a further

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advantage to larval development associated with gall feeding. Parasitism and predation levels found here were very low and, if *R. macowaniana* galls offer some protection from parasitism, the level of protection may also be higher than in insect-induced galls. Insect-induced galls are usually only occupied by a single galler-species and these insects are often parasitized by host-specific parasitoids (*e.g.* Price 1992; Price & Clancy 1986; Wiebes-Rijks & Shorthouse 1992). In *R. macowaniana* galls, not only do parasitoids encounter numerous lepidopteran species per gall, but the gall seasonality and distribution is highly variable and the association between the Lepidoptera and the galls is only secondary. The probability of a parasitoid locating a suitable host is, therefore, lower than in obligatory insect-gall relationships and selection for gall-searching behaviour and host-specificity will be weak. The hypotheses concerning the adaptive significance of gall-habitation include, for example, the 'non-adaptive' hypothesis (Price *et al.* 1987). This predicts that there are no advantages associated with gall-habitation other than those that would also be associated with a boring or mining lifestyle (Price *et al.* 1987). Alternatively, the nutrition hypothesis predicts that the high nutritional quality of the gall-tissue provides enhanced nutrition for the gall-inhabitant, and the microenvironment hypothesis that the gall provides protection from harsh environmental conditions (Price *et al.* 1987). A further hypothesis is that galls may provide their inhabitants with protection from natural enemies (Price *et al.* 1987). Although there has been no formal testing of these hypotheses for secondary gall-inhabitants, there is circumstantial evidence that in the community in *R. macowaniana* galls some of the above hypotheses could be accepted, *i.e. R. macowaniana* galls appear to provide the Lepidoptera larvae that inhabit them with both nutritional and micro-environmental advantages, as well as with protection from natural-enemies.

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REFERENCES

Burdon, J.J. 1991. Fungal pathogens as selective forces in plant populations and communities. *Australian Journal of Ecology* **16**, 423-432.

Cornell, H.V. 1983. The secondary chemistry and complex morphology of galls formed by the Cynipidae (Hymenoptera): how and why? *American Midland Naturalist* **110**, 225-234.

Doidge, E.M. 1932. A preliminary study of the South African rust fungi. *Bothalia* **2**, 1-213.

Endrödy-Younga, S. 1985. Coleoptera (part). In Scholtz, C.H. & Holm, E. (Eds). *Insects of Southern Africa*. Butterworths, Durban, pp. 188-280.

Fernandes, G.W. & Price, P.W. 1992. The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats. *Oecologia* **90**, 14-20.

Gandar, M.V. 1979. The effect of the gall forming moth *Dactylethra siccifolii* Walshingham (Lepidoptera Gelechiidae:) on *Solanum panduraeforme* (Solanaceae). *Journal of the Entomological Society of Southern Africa* **42**, 283-285.

Jackson, M.L. 1958. *Soil Chemical Analysis*. Constable, London.

McGeoch, M.A. 1993. The microlepidoptera associated with a fungus gall on *Acacia karroo* Hayne in South Africa. *African Entomology* **1**, 49-56.

McGeoch, M.A. & Krüger, M. 1994. Identification and diagnoses of Lepidoptera larvae inhabiting galls induced by *Ravenelia macowaniana* Pazschke on *Acacia karroo* Hayne in South Africa. *African Entomology* **2**, 47-53.

New, T.R. 1982. Lepidoptera from *Uromycladium* galls on *Acacia*. *Australian Journal of Zoology* **30**, 357-364.

Owen-Smith, N. & Cooper, S.M. 1987. A palatability classification of the woody plants in a South African savanna with reference to browsing ruminants. *Ecology* **68**, 319-331.

Palgrave, K.C. 1985. *Trees of Southern Africa*. 2nd edition. Struik, Cape Town.

Price, P.W. 1988. Inversely density-dependent parasitism: the role of plant refuges for hosts. *Journal of Animal Ecology* **57**, 89-96.

Price, P.W. 1992. Evolution and the ecology of gall-inducing sawflies. In Shorthouse, J.D. & Rohfritsch, O. (Eds). *Biology of Insect-Induced Galls*. Oxford University Press, New York, pp. 208-224.

Price, P.W. & Clancy, K.M. 1986. Interactions among three trophic levels: gall size and parasitoid attack. *Ecology* **67**, 1593-1600.

Price, P.W., Fernandes, G.W. & Waring, G.L. 1987. Adaptive nature of insect galls. *Environmental Entomology* **16**, 15-24.

Roskam, J.C. 1992. Evolution of the gall-inducing guild. In Shorthouse, J.D. & Rohfritsch, O. (Eds). *Biology of Insect-Induced Galls*. Oxford University Press, New York, pp. 34-49.

Scholtz, C.H. 1978. Notes on plant galls formed by Lepidoptera in the Transvaal. *Journal of the Entomological Society of Southern Africa* **41**, 45-49.

Scoble, M.J. & Scholtz, C.H. 1984. A new, gall-feeding moth (Lyonetiidae: Bucculatricinae) from South Africa with comments on larval habits and phylogenetic relationships. *Systematic Entomology* **9**, 83-94.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioural Sciences*. McGraw-Hill, New York.

Slansky, F. 1993. Nutritional ecology: the fundamental quest for nutrients. In Stamp, N.E. & Casey, T.M. (Eds). *Caterpillars Ecological and Evolutionary Constraints on*

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Foraging. Chapman & Hall, New York, pp. 29-91.

Slansky, F. & Scriber, J.M. 1985. Food consumption and utilization. In Kerkut, J.A. & Gilbert, L.I. (Eds). *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Pergamon Press, Oxford, pp. 87-151.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. Second edition. W.H. Freeman & Company, San Fransisco.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Blackwell, Oxford.

Swartz, P.P. 1982. *n' Numeries - taksonomiese evaluering van die takson Acacia karroo Hayne in Suidelike Afrika*. MSc Thesis, unpublished, University of Pretoria, Pretoria.

Teague, W.R. 1989. Patterns of selection of *Acacia karroo* by goats and changes in tannin levels and *in vitro* digestibility following defoliation. *Journal of the Grassland Society of Southern Africa* **6**, 230-235.

Van Rooyen, N. 1984. *'n Fenologiese studie van die plantegroei van die Roodeplaatdam-Natuurreservaat*. PhD Thesis, unpublished, University of Pretoria, Pretoria.

Wieber-Rijks, A.A. & Shorthouse, J.D. 1992. Ecological relationships of insects inhabiting cynipid galls. In Shorthouse, J.D. & Rohfritsch, O. (Eds). *Biology of Insect-Induced Galls*. Oxford University Press, New York, pp. 238-257.

Wise, K.A.J. 1962. *Parectopa leucocyma* (Meyrick) (Lepidoptera: Gracillaridae) rediscovered as a leaf-miner of Kauri (*Agathis australis* Salisb.). *Transactions of the Royal Society of New Zealand Zoology* **1**, 373-375.

Zar, J.H. 1984. *Biostatistical Analysis*. Second edition. Prentice-Hall, New Jersey.

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CHAPTER 2

The Lepidoptera that inhabit *Ravenelia macowaniana*-induced galls[1]

A larval community of 22 Lepidoptera species regularly inhabit galls induced by the host-specific rust fungus *Ravenelia macowaniana* Pazschke (Uredinales: Pucciniaceae) on *Acacia karroo* Hayne. Five of these species, *Cydia* (*Cydia*) *victrix* (Meyrick), *Ascalenia pulverata* (Meyrick), *Anarsia gravata* Meyrick, *Characoma submediana* Wiltshire, and *Euzophera* sp. nr. *verrucicola* Hampson, are dominant members of the community constituting approximately 90% of larvae in the galls (Chapters 5 & 6). These five species were recorded over a number of seasons across a broad latitudinal range; they appear not only to be the most dominant, but also the most widespread moth species in the community in South Africa.

Differences in the composition and relative abundances of the larval assemblage, associated with *R. macowaniana*-induced galls, have been found between climatic regions (Chapter 5), as well as between sites with varying degrees of habitat quality (Chapter 4). In particular, the five dominant species were found to be more useful indicators of habitat quality than the rarer, less abundant species (Chapter 6). Therefore, the moth community, which is spatially and temporally defined and relatively easy to sample, is a potentially useful indicator of changes in climate and habitat quality (Chapter 8). However, because larval mortality during rearing in the laboratory is high, the larvae are extracted and identified rather than rearing them to adults. (Some larvae from each sample should be reared, however, to confirm larval identifications.)

This Chapter provides a means of identifying the larvae in the community to facilitate the widespread use of the community as an indicator (or monitoring) system. Diagnoses, illustrations, instar numbers, and head capsule sizes of the larvae of the five dominant species in the assemblage, as well as a key to 18 species (12 species and one species complex) are presented. Localities and biological notes extracted from the labels of the few specimens of these species housed in the Lepidoptera collection at the Transvaal Museum (Pretoria, South Africa) are briefly listed.

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[1] published in part as McGeoch & Krüger 1994

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MATERIALS and METHODS

Galls were collected from three sites in the vicinity of Pretoria between January and March of 1991 and 1992, *i.e.* Boekenhoutskloof, Hartebeespoort, and Pienaarspoort (Chapter 1, Table 1.1). Galls were also sampled from Bloemfontein, Parys, and Aston Bay (Chapter 1, Table 1.1) between 1991 and 1994. Larvae were removed from the galls and preserved in a glacial acetic acid (8 % v/v); 10 % formaldehyde (3 % v/v); 96 % ethyl alcohol (30 % v/v) and distilled water (59 % v/v) mixture. The larvae from additional galls were reared so that the adult moths could be used to confirm larval identifications.

The head capsule width of each individual was measured with an ocular micrometer on a dissection microscope and head capsule size class frequency distributions were compiled for each species. The boundaries of the instar head capsule size ranges were chosen as the midpoints of the classes with the lowest frequency between successive frequency peaks (Beaver & Sanderson 1989). Dyar's coefficient (k) of geometric increase in head capsule width between larval instars for each species was calculated from $y = ak^n$ (y, final width; a, initial width; n, number of instars) (Sehnal 1985).

Final instar larvae of the five dominant species were illustrated, diagnosed and used in the key.

Stehr's (1987) key to Lepidoptera larvae of America north of Mexico correctly separated the South African species to family and the key here was compiled using a combination of these, and other chosen, characters. Segment numbering and chaetotaxy used in the diagnoses and larval key are based on Stehr (1987).

RESULTS and DISCUSSION

Species in the community

The 22 Lepidoptera species recorded in *R. macowaniana*-induced galls and the localities from which they were sampled are listed in Table 2.1. The 17 species for which diagnoses are not given were collected too infrequently and in insufficient numbers to determine the number of larval instars. Larvae could, therefore, not be positively recognized as final instar larvae and diagnoses were not compiled. These species could, nonetheless, be included in the key using characters that are present irrespective of the larval instar

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examined. Four of these 17 species were recorded only from the Eastern Cape Province and one of these only occurred in galls during winter months (species no.'s 6, 15, 21 and 22; Table 2.1).

Diagnoses of fourth instar larvae

Characoma submediana Wiltshire (Noctuidae) (Fig. 2.1 no.'s 1 & 6)
Head, thorax and abdomen with pinkish brown markings, darker on dorsal surface. Length 9-14 mm. Crochets arranged in mesoseries. A3-6 crochets homoideous. T1 with L group bisetose. A3-6 prolegs of equal size.

Euzophera sp. nr. *verrucicola* Hampson (Pyralidae) (Fig. 2.1 no.'s 2, 7 & 11)
Head capsule usually light yellowish brown. Thorax and abdomen dark grey-black. Length 12-16 mm. Crochets arranged in a multiserial circle. T1 prespiracular group bisetose. T2 and T3 with three L setae.

Cydia (*Cydia*) *victrix* (Meyrick) (Tortricidae) (Fig. 2.1 no.'s 3, 12, 15 & 18)
Larva pale, usually with conspicuous grey setal bases. Length 8-10 mm. Crochets arranged in a uniserial circle/penellipse. T1 prespiracular group trisetose. SD1 on A8 anterior to spiracle.

Ascalenia pulverata (Meyrick) (Cosmopterigidae) (Fig. 2.1 no.'s 4 & 14)
Larva pale with no markings. Length 6-8 mm. Crochets arranged in a circle/penellipse. T1 prespiracular group trisetose. SD1 on A8 dorsal to spiracle. A9 with SD1 seta-like rather than hair-like. Head seta L1 closer to A3 than A3 is to A2.

Anarsia gravata Meyrick (Gelechiidae) (Fig. 2.1 no.'s 5, 8 & 9)
Head capsule dark brown to black. Abdomen usually pink. Length 8-10 mm. Crochets arranged in lateropenellipse. Crochets on A10 forming two groups. Anal comb present. T1 prespiracular group unisetose.

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Table 2.1. Moth species recorded in *Ravenelia macowaniana* galls from K, Boekenhoutskloof, H, Hartebeespoort, P, Pienaarspoort, Y, Parys, B, Bloemfontein, R, Richards Bay, G, Grahamstown, V, Sundays River Valley and A, Aston Bay; S, during summer months (January to March) and W, during winter months (May to July).

Species / **Family**	Region								
	K	H	P	Y	B	R	G	V	A
Noctuidae									
1. *Characoma submediana* Wiltshire[1]	S	S	S	S	S	S	S	S	S
2. *Eublemma brachygonia* Hampson	S	S	S	-	-	-	-	-	-
Tortricidae									
3. *Cydia* (*Cydia*) *victrix* (Meyrick)	S	S	S	S	S	S	S	S	S
4. *Cydia* (*Cydia*) *aphrospila* (Meyrick)	S	-	-	-	-	-	-	-	-
5. *Cryptophlebia peltastica* (Meyrick)	-	S	-	S	S	S	S	S	S
6. *Lobesia stericta* (Meyrick)	-	-	-	-	-	-	S	S	-
Pyralidae									
7. *Euzophera* sp. nr. *verrucicola* Hampson[1]	S	S	S	S	-	S	-	S	S
8.-13. indet. Phycitinae 1-6	S	-	S	S	S	S	S	S	SW
Cosmopterigidae									
14. *Ascalenia pulverata* (Meyrick)	S	S	S	S	S	S	S	S	S
15. *Anatrachyntis tripola* (Meyrick)[1]	-	-	-	-	-	-	-	S	SW
Gelechiidae									
16. *Anarsia gravata* Meyrick[1]	S	S	S	S	S	S	S	S	S
17. *Anarsia nimbosa* Meyrick	S	-	-	-	-	-	-	-	-
18. *Anarsia* (nr.) *amalleuta* Meyrick	-	-	-	-	S	-	-	-	-
19. *Anarsia* sp.	S	-	-	-	-	-	-	-	-
20. *Encolpotis xanthoria* Meyrick	-	-	-	-	-	S	-	S	S
Oecophoridae									
21. *Schiffermuelleria pedicata* Meyrick	-	-	-	-	-	-	-	-	S
Tineidae									
22. *Phthoropoea oenochares* (Meyrick)	-	-	-	-	-	-	-	-	W

[1] Referred to in McGeoch (1993) as 1, *Pardasena* sp.nr. *virgulana* (Mabille); 5, *Getulia* sp.nr. *semifuscella* Ragonot; 13, *Caloptilia* sp.; 14, *Anarsia nimbosa* Meyrick.

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Fig. 2.1 (1-20). Lateral (a) and dorsal (b) views of the final instar larvae of: **1**, *Characoma submediana* Wiltshire; **2**, *Euzophera* sp. nr. *verrucicola* Hampson; **3**, *Cydia* (*Cydia*) *victrix* (Meyrick); **4**, *Ascalenia pulverata* (Meyrick); **5**, *Anarsia gravata* Meyrick (scale bar = 1 mm). Larval characters highlighted in the key to larvae inhabiting *Ravenelia macowaniana*-induced galls; ventral aspect of a proleg of: **6**, *C. submediana* and **7**, *E.* sp. nr. *verrucicola*; **8**, latero-ventral aspect of proleg of *A. gravata*; **9**, crochets on A10 of *A. gravata*; **10**, lateral view of A4 of *E. xanthoria*; lateral view of head and T1 of **11**, *E.* sp. nr. *verrucicola* and **12**, *C.* (*C.*) *victrix*; **13**, lateral view of A4 of *S. pedicata*; lateral view of A8 of **14**, *A. pulverata* and **15**, *C.* (*C.*) *victrix*; **16**, lateral view of head of *P. oenochares*; dorsal view of A9 of **17**, *A. tripola* and **18**, *C.* (*C.*) *victrix*; **19**, lateral view of T2 of larvae in the Phycitinae complex; **20**, lateral view of A8 of *C. peltastica* (scale bar = 0.25 mm).

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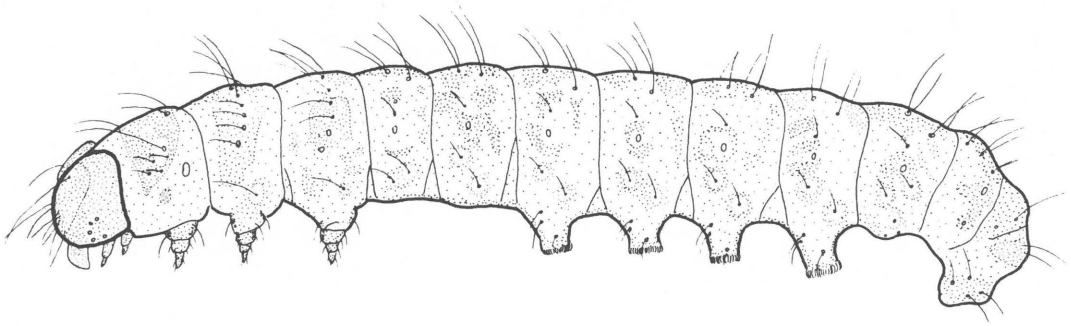
1a



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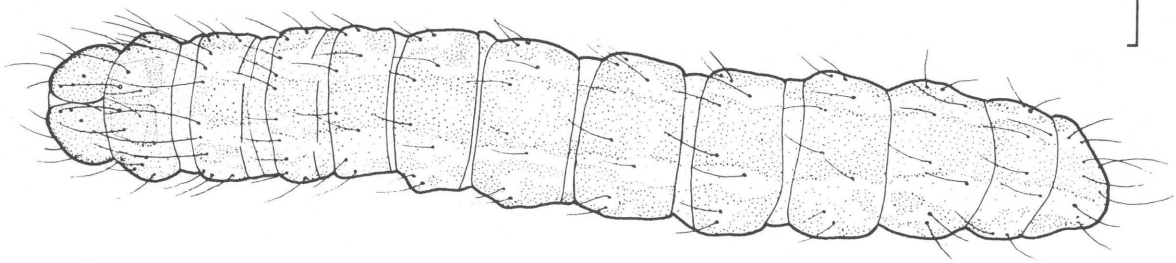

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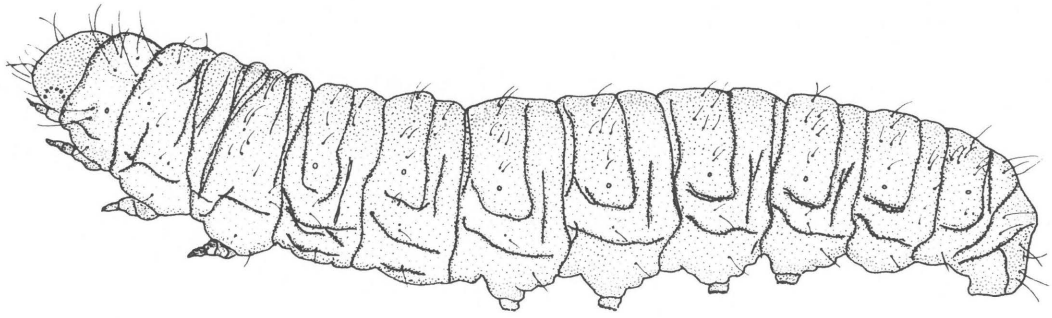

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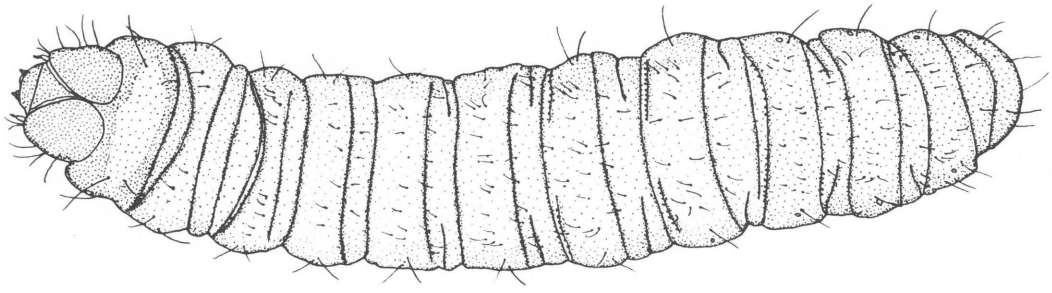

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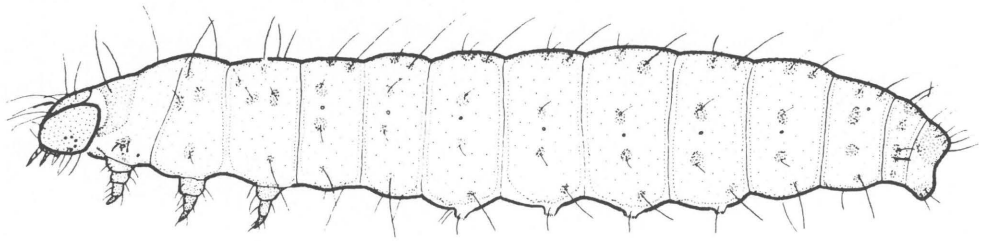

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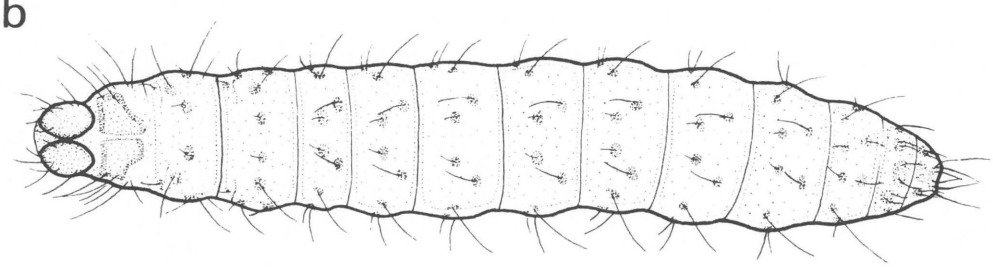

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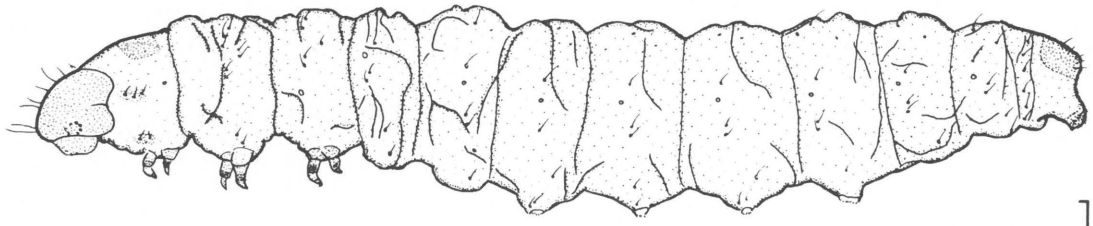

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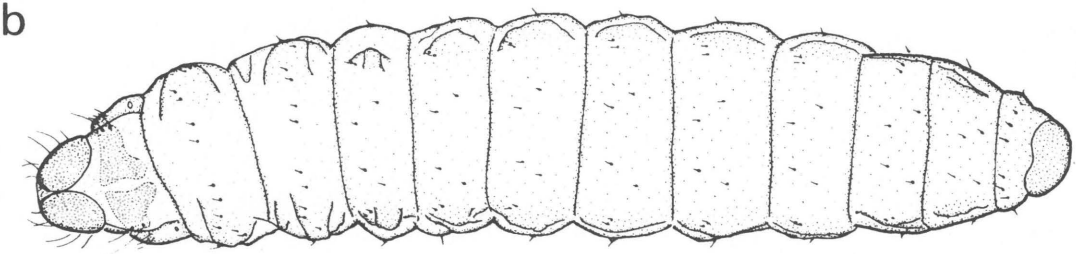

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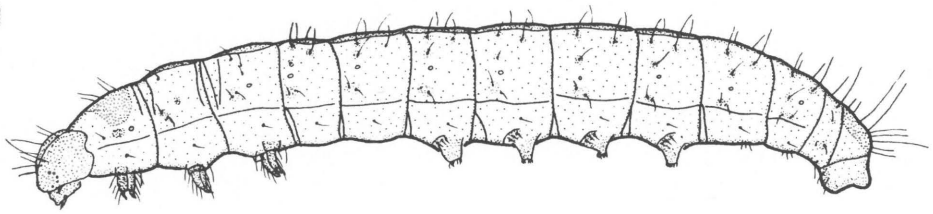

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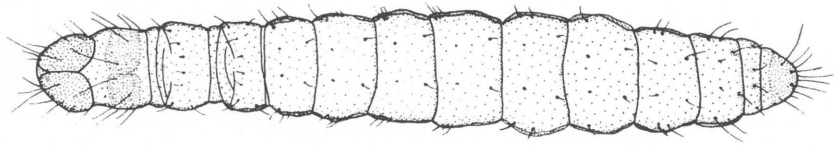

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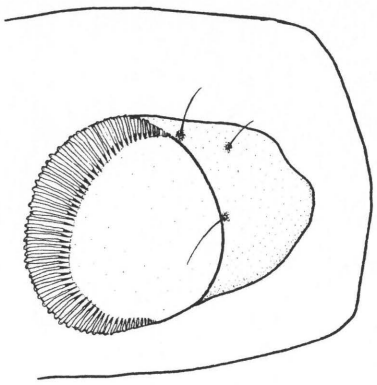

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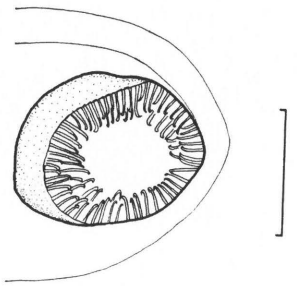

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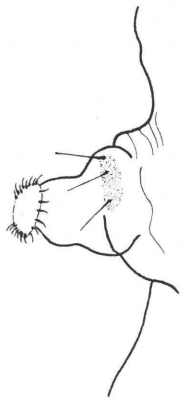

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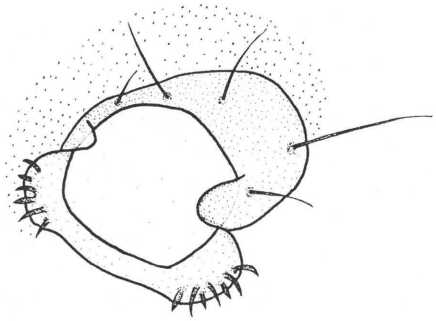

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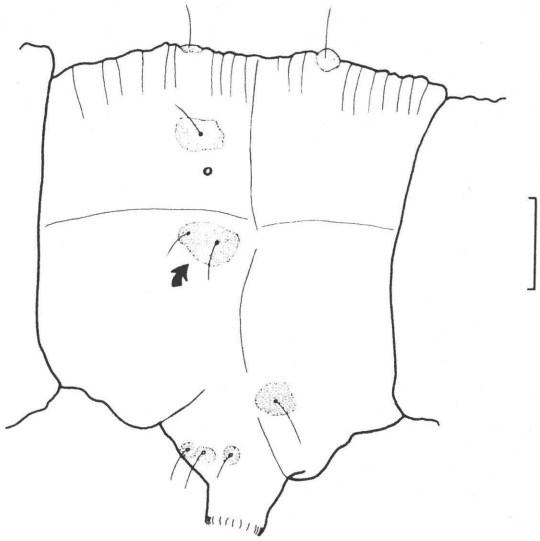

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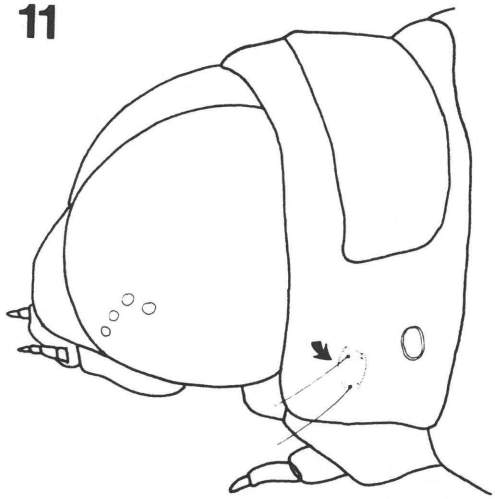

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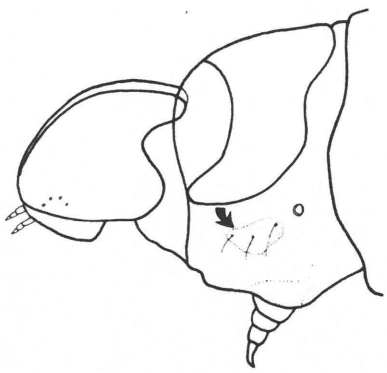

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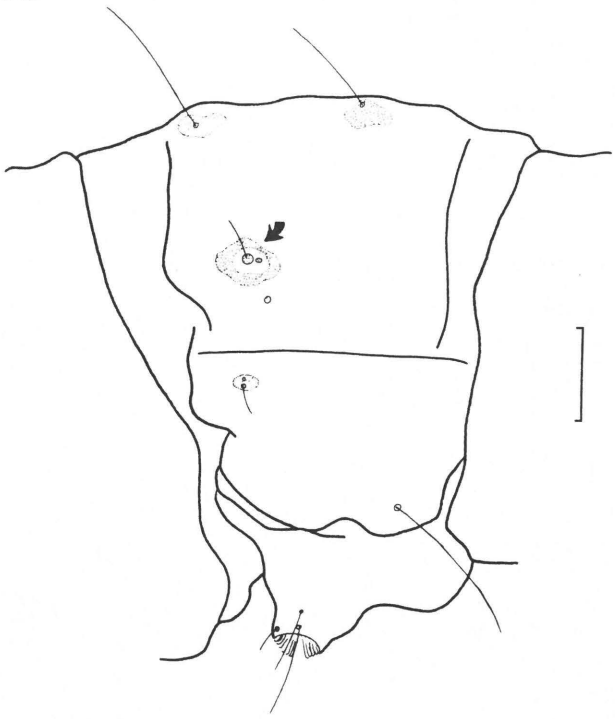

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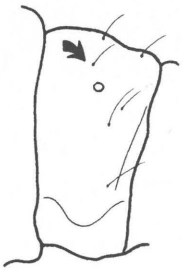

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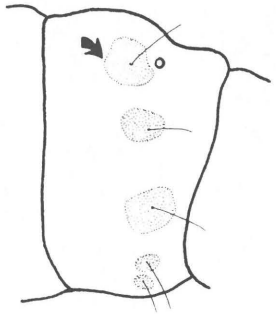

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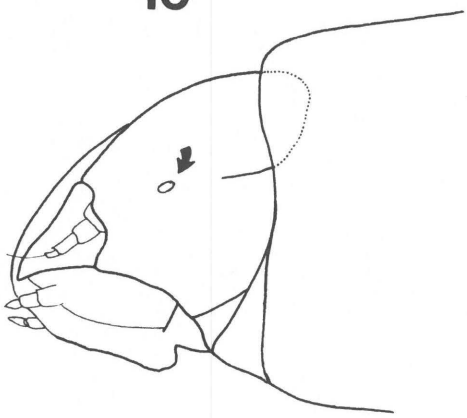

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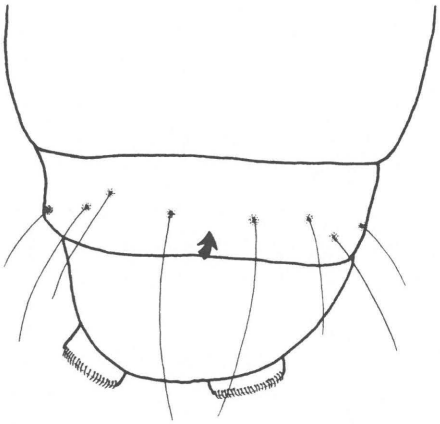

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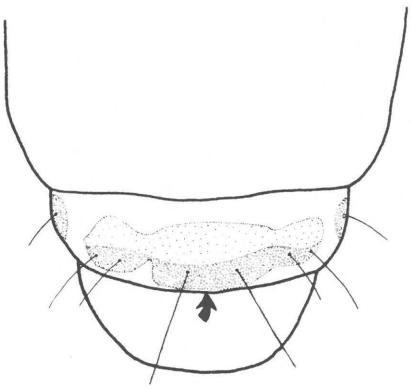

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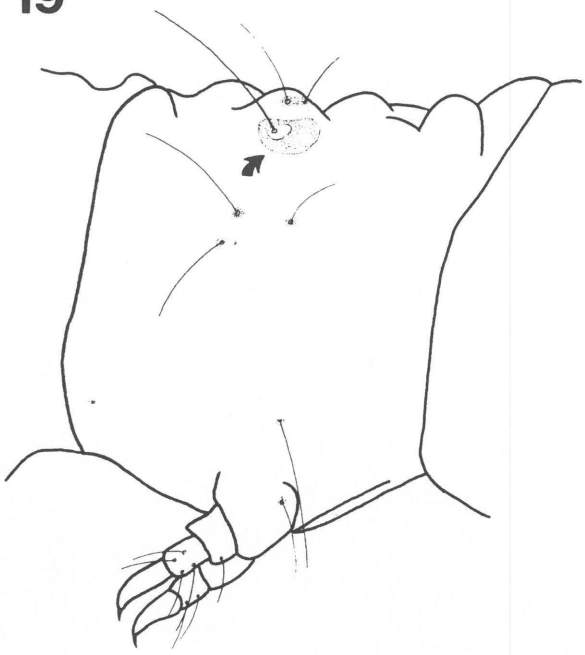

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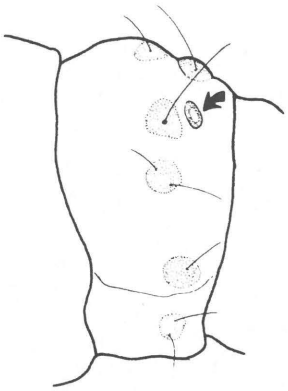

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Instar numbers and head capsule sizes

Characoma submediana Wiltshire, *Euzophera* sp. nr. *verrucicola* Hampson, *Cydia* (*Cydia*) *victrix* (Meyrick), *Ascalenia pulverata* (Meyrick) and *Anarsia gravata* Meyrick all have four instars. Although Lepidoptera may have between three and eleven instars the same number of instars in these species may be due, partly, to their exposure to similar conditions within the gall environment during larval development (Sehnal 1985). Mean head capsule widths and ranges for each of the species are presented in Table 2.2. The geometric increase in head capsule width found for each species was approximately 1.40 (Table 2.3), which is consistent with that recorded for other Lepidoptera (Sehnal 1985).

The head capsule widths can not only be used to separate larval instars, but can assist in the correct identification of these species by excluding individuals which do not fall within the correct head capsule size ranges.

Key to larvae

With a combination of the key presented below, illustrations, and head capsule width measurements, the larvae of the five dominant moth species, as well as the 13 other species (7 species and 1 species complex) which regularly occur in the galls (albeit in low numbers) during the gall growth season can be identified. The key uses a number of general family and subfamily characters (as well as additional characters where necessary) which are sufficient for identifying the species which inhabit *R. macowaniana* galls. Four species (no.'s 3, 15, 16 and 17; Table 2.1) were not included in the key. The first of these, *Cydia* (*Cydia*) *aphrospila* (species no. 4), was recorded only during the first sampling season (1991) in very low numbers at one of the Gauteng sites (McGeoch 1993) and has not been found in samples since. In addition, only adults were collected, and the species could, therefore, not be included in the larval key. The taxonomy of the three *Anarsia* species (no.'s 15, 16 and 17) is unclear, and because only isolated individuals were found, these have been omitted from the key until their identities and distributions are better known. Because of the extremely low and patchy incidence of these four species their omission will not detract from the overall utility of the larval key.

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Table 2.2. Mean head capsule widths (mm) and ranges for each larval instar, and increments between instars, of the five dominant Lepidoptera species in *Ravenelia macowaniana* galls; n = number of larvae.

Species Instar	n	Mean ± S.D. (mm)	Range (mm)	Increment
Characoma submediana				
I	51	3.49±0.79	2.24-5.36	1.79
II	43	6.27±0.56	5.43-7.45	1.47
III	61	9.24±0.77	7.75-11.07	1.47
IV	36	13.55±1.04	11.74-15.91	-
Euzophera sp. nr. *verrucicola* I	22	3.18±0.69	2.00-3.81	1.73
II	78	5.53±0.82	4.00-7.38	1.61
III	60	8.91±0.65	7.50-10.39	1.42
IV	90	12.68±1.01	10.51-14.70	-
Cydia (*Cydia*) *victrix*				
I	136	2.95±0.72	1.28-4.18	1.82
II	311	5.39±0.53	4.31-6.51	1.41
III	480	7.60±0.54	6.64-10.09	1.68
IV	8	12.76±0.84	11.07-13.87	-
Ascalenia pulverata				
I	18	2.03±0.39	1.44-2.74	1.60
II	88	3.27±0.25	2.80-3.84	1.46
III	191	4.75±0.42	3.92-5.78	1.37
IV	19	6.52±0.76	5.88-8.53	-
Anarsia gravata				
I	18	1.61±0.28	1.28-2.08	1.90
II	45	3.07±0.35	2.32-3.57	1.64
III	103	5.04±0.61	3.72-6.35	1.52
IV	96	7.67±0.54	6.51-8.99	-

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Key to the moth larvae inhabiting *Ravenelia macowaniana* galls on *Acacia karroo*.

1a. Crochets on ventral prolegs arranged in mesoseries (Fig. 2.1 no. 6).....2

b. Crochets on ventral prolegs arranged in a circle or penellipse (Fig. 2.1 no.'s 7,8)...3

2a. Prolegs present on A3-6 and A10 ..... *Characoma submediana*

b. Prolegs present on A5-6 and A10 ..... *Eublemma brachygonia*

3a. Crochets on A10 interrupted, forming two groups on each proleg (Fig. 2.1 no. 9)..4

b. Crochets on A10 entire 5

4a. L1 and L2 on the same darkly sclerotized (brown) pinaculum, similar to SD1 pinaculum, on A1-8 (Fig. 2.1 no. 10)..... *Encolpotis xanthoria*

b. L1 and L2 on A1-8 not on darkly sclerotized pinaculum ..... *Anarsia gravata*

5a. T1 prespiracular group bisetose (Fig. 2.1 no. 11)..... 6

b. T1 prespiracular group trisetose (Fig. 2.1 no. 12)..... 7

6a. SD1 setal base on T2 sclerotized and distinctly larger than other setal bases (Fig. 2.1 no. 13)..... Phycitinae complex

b. SD1 setal base on T2 not distinctly larger than other setal bases.....
.....*Euzophera* sp.nr. *verrucicola*

7a. SD1 on A8 dorsal to spiracle (Fig. 2.1 no. 14)..... 8

b. SD1 on A8 anterior to spiracle (Fig. 2.1 no. 15)..... 9

8a. Only one stemmatum on each side of head (Fig. 2.1 no. 16) .....
..... *Phthoropoea oenochares*

b. More than four stemmata on each side of head 10

9a. Anal comb present ..... *Lobesia stericta*

b. Anal comb absent 11

10a. SD1 on A1-8 on pinacula rings (Fig. 2.1 no. 19)..... *Schiffermuelleria pedicata*

b. SD1 on A1-8 not on pinacula rings 12

11a. Spiracle on A8 spherical ..... *Cydia* (*Cydia*) *victrix*

b. Spiracle on A8 dorsoventrally elongate (Fig. 2.1 no. 20)..... *Cryptophlebia peltastica*

12a. Crochets on prolegs A3-6 biordinal ..... *Anatrachyntis tripola*

b. Crochets on prolegs A3-6 uniordinal ..... *Ascalenia pulverata*

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Table 2.3. Dyar's coefficients (k) (Sehnal 1985) of geometric increase in head capsule width between larval instars for each species.

Species	k
Characoma submediana	1.40
Euzophera sp. nr. *verrucicola*	1.41
Cydia (*Cydia*) *victrix*	1.44
Ascalenia pulverata	1.34
Anarsia gravata	1.48

Information on specimens from the Transvaal Museum Lepidoptera collection

The collection dates of the specimens, localities in countries other than South Africa and in South Africa, and recorded biological notes of species with representative specimens in the Transvaal Museum collection are presented below:

Characoma submediana Wiltshire: 1907 - 1937, Zimbabwe, Gauteng, Eastern Cape, Kwazulu-Natal, reared from berries of *Lantana camara*.

Cydia (*Cydia*) *victrix* (Meyrick): 1907 - 1920, Gauteng, Kwazulu-Natal.

Cydia (*Cydia*) *aphrospila* (Meyrick): 1917 - 1924, Gauteng, Kwazulu-Natal.

Cryptophlebia peltastica (Meyrick): 1918 - present, Zimbabwe, Gauteng, Eastern & Northern Transvaal, Kwazulu-Natal, Eastern Cape. This species is a fruit crop pest (Anneke & Moran 1982).

Lobesia stericta (Meyrick): 1910 - 1981, Gauteng, Eastern & Northern Transvaal, Kwazulu-Natal, South-Western Cape, reared from litchi fruit.

Ascalenia pulverata (Meyrick): 1909-1925, Gauteng, Kwazulu-Natal.

Anatrachyntis tripola (Meyrick): 1915 - 1924, Zimbabwe, Gauteng, Eastern Transvaal, Kwazulu-Natal, reared from the stem of a cotton plant.

Anarsia gravata Meyrick: 1910 - 1918, Gauteng, Western Transvaal, Kwazulu-Natal.

Anarsia nimbosa Meyrick: 1912 - 1954: Zimbabwe, Gauteng, reared from *Acacia* galls.

Anarsia (nr.) *amalleuta* Meyrick: 1911 - present, Zimbabwe, Kwazulu-Natal.

Encolpotis xanthoria Meyrick: 1916 - 1981, Gauteng, Eastern and Western Transvaal, Kwazulu-Natal, Eastern Cape.

Schiffermuelleria pedicata Meyrick: 1916 - 1925, Eastern Transvaal.

Phthoropoea oenochares (Meyrick): 1921, Kwazulu-Natal.

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REFERENCES

Annecke, D.P. & Moran, V.C. 1982. *Insects and Mites of Cultivated Plants in South Africa*. Butterworths, Durban.

Beaver, R.J. & Sanderson, J.P. 1989. Classifying instars of the Navel Orangeworm (Lepidoptera: Pyralidae) based on observed head capsule widths. *Journal of Economic Entomology* **82**, 716-720.

McGeoch, M.A. 1993. The microlepidoptera associated with a fungus gall on *Acacia karroo* Hayne in South Africa. *African Entomology* **1**, 49-56.

McGeoch, M.A. & Krüger, M. 1994. Identification and diagnoses of Lepidoptera larvae inhabiting galls induced by *Ravenelia macowaniana* Pazschke on *Acacia karroo* Hayne in South Africa. *African Entomology* **2**, 37-43.

Sehnal, F. 1985. Growth and life cycles. In Kerkut, G.A. & Gilbert, L.I. (Eds). *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Volume 2. Pergamon Press, Oxford, pp. 2-80.

Stehr, F.W. 1987. Order Lepidoptera. In Stehr, F.W. (Ed.). *Immature Insects*. Kendall Hunt, Iowa, pp. 288-596.

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CHAPTER 3

Evidence of interactions between members of the Lepidoptera community

Vertical linkages in phytophagous insect communities are generally considered to be stronger and more prevalent than horizontal links within the herbivore trophic level (Andrewartha & Birch 1954; Hairston *et al.* 1960; Lawton & Strong 1981; Strong 1983; Lawton 1984). It has, however, been suggested that subtle horizontal linkages, in particular interspecific competitive interactions, are common in phytophagous insect communities, although they may be difficult to detect (Damman 1993; Denno *et al.* 1995; Southwood 1987; Wootton 1994). In addition, variation in the presence and strength of interactions dictate that interactions between species are likely to be inconsistent and transient in nature (Connell 1983; Futuyma 1986; Schoener 1983; Thompson 1988). This variation may be a result of genotypic variation, environment-mediated individual variation and variation in population abundances, which form the backbone of community pattern and function.

Interspecific competition may occur in phytophagous insect communities under two sets of conditions. It may occur when the impact of mortality factors, such as natural enemies, are suddenly reduced (Strong *et al.* 1984). It may also occur in high quality, ephemeral microhabitats (Strong *et al.* 1984). If a microhabitat provides plant tissue of high nutritional value, and at the same time a degree of protection from natural enemies, the benefits to polyphages of occupying that microhabitat may outweigh the costs associated with subsequently encountering competition (Whitham 1978; Zwölfer 1979). If so, the potential for resource limitation and competition in ephemeral, high quality microhabitats will be greater than in persistent, medium to low quality sites. Furthermore, if these microhabitats are patchily distributed, more species can be accommodated in the habitat (Hanski 1983; Shorrocks *et al.* 1979; Tilman 1994). As the level of interspecific aggregation approaches and exceeds the level of intraspecific aggregation, the probability of interspecific competition will increase (Ives 1991).

Manipulation experiments to test for competitive interactions in multispecies communities are cumbersome and often impracticable (Connell 1983). Therefore, indirect methods to detect the presence of competition are often the only alternative. Density-dependent body mass compensation is a structural characteristic of resource limited

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communities, and provides the strongest evidence of resource limitation and exploitation competition at the habitat unit level (Arthur 1987, p. 117-118; Shorrocks *et al.* 1979; Zwölfer 1979). When interspecific exploitation competition occurs for limited resources the consumption of resources by individuals of each species reduces the quantity of resource available to individuals of other species (Arthur 1987). At high densities this may result either in the death of individuals, dispersal to other habitats or a reduction in body mass of individuals within the habitat.

Further indirect evidence for the presence of interspecific competition is the presence of species associations and abundance covariations within a community (Arthur 1987; Schoener 1988). Although such patterns cannot be attributed exclusively to competition, the causal mechanism is most likely to be interspecific competition if it is found between ecologically similar species within a trophic level (Schluter 1984; Schoener 1988).

Ravenelia macowaniana Pazschke -induced galls on *Acacia karroo* Hayne provide an ephemeral, high quality resource for the larvae of 22 species of Lepidoptera. These species are morphologically and ecologically similar (McGeoch 1993; McGeoch & Kruger 1994) and spatial niche partitioning does not occur within galls. The galls are ephemeral (with a mean life span of 43 days) and live galls, that reach a maximum size of between 5 mm and 70 mm in diameter, are present for only two to four months each year (Chapter 1). In addition, the local and regional distribution of *R. macowaniana* galls is patchy and the density of galls on individual trees, as well as the number of trees galled within a locality, is extremely variable (McGeoch 1993). Live gall tissue has a higher nitrogen and moisture content than both reproductive and vegetative tissue on *A. karroo* trees at the same time (Chapter 1), providing the larvae with plant tissue of a high nutritional quality that is important for growth and development in herbivorous Lepidoptera (Mattson 1980; Stamp & Bowers 1990; Strong *et al.* 1984). The galls may also provide protection from parasitoids as fewer than one percent of Lepidoptera larvae in the galls are parasitized by hymenopteran parasitoids (Chapter 1).

The larvae of some Lepidoptera species inhabit dead galls that remain on trees through the winter months (McGeoch & Krüger 1994). These species are thought to feed on the dried gall tissue or to scavenge on detritus in old burrows. Because the species composition and resource quality of live and dead galls differ, the species using these may in a sense (see General Introduction) be regarded as distinct communities, although a certain amount of overlap in species composition occurs late in the gall development season

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(McGeoch 1993; McGeoch & Krüger 1994; Chapter 1).

This community thus meets the necessary and sufficient criteria to be resource limited and for interspecific competition to be a determinant of community structure and function (Arthur 1987). The aim of this study was, therefore, to determine if the herbivore trophic level within the gall-inhabiting community shows evidence of being structured by exploitation competition.

STUDY SITES and METHODS

Galls were sampled in South Africa from Aston Bay (34.10S 24.55E) in January and March 1993 and in January and February 1994 and from Sundays River Valley (33.30S 25.40E) in February 1994. Estimates were made of local gall density (mean number of galls per tree) during each sample period and maximum sample sizes were determined by local gall abundance. Between 100 and 400 galls were collected during each sampling period. A minimum of 2 and a maximum of 25 galls were sampled from each tree. The age and mass of sampled galls were determined (Chapter 1). The galls were cut open and the larvae from each gall extracted and stored separately in an ethyl-alcohol based fixative. These larvae were later identified (using the larval key, Chapter 2) and the number of individuals and species in each gall determined. The number of parasitized Lepidoptera larvae in each gall was also recorded. The percentage of each gall consumed was estimated to the nearest 10 % after all larvae had been removed from the gall.

Adult moths were reared from 200 dead galls from Aston Bay during March 1993 and from 200 live galls from Sundays River Valley during February 1994. Gall abundance was very low at Aston Bay in 1994 and this necessitated gall sampling from Sundays River Valley. The galls were weighed directly after sampling and placed individually into rearing containers. The containers were checked daily and emergent moths immediately removed, identified and the date of emergence recorded. The moths were dried to constant mass at 60°C for eight hours and weighed.

Species aggregation

Ives' (1991) measures of aggregation were used to determine the extent of positive intraspecific aggregation (J) and interspecific aggregation (C) of moth species in the galls. The relative increase in crowding caused by aggregation is calculated independently of mean

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densities in these measures of aggregation (Ives 1988). In addition, *J* and *C* are based on the same parameters and can therefore be compared (Giller & Doube 1994). *J* and *C* give the percentage increase in expected numbers of conspecifics (*J*) and heterospecifics (*C*) in the same habitat unit above that expected if the species were randomly distributed (Ives 1991). Interspecific aggregation measures (*C*) were calculated for each species (total of p species) against the sum of all other species in the gall, *e.g.* *C*ij, where i = species 1 and j = sum of species 2 to p. *C*ij then represents the increase in expected number of individuals of other species in galls occurring with species i above that expected if all species were independently distributed. *C*ij therefore gives a measure of multispecies, rather than pairwise, aggregation. Modification of Ives' (1991) *C* in this way is more meaningful in the community studied here and, according to Ives (personal communication), acceptable at this level of interpretation. The significance of positive intra- and interspecific aggregation measures was tested using chi-square dispersion tests (Pielou 1977) and Spearman rank correlations (Sokal and Rohlf 1981), respectively.

Mass Compensation

To determine the relationship between the number of larvae and adults per gall and gall mass (g) (*i.e.* per unit resource), between the total mass of moths per gall (g dry mass) and gall mass (g wet mass), and between the total moth mass (g dry mass) and number of moths emerging from each gall, least-squares linear regressions of log-transformed data were used (Sokal & Rohlf 1981).

The total mass of adult moths in a gall is expected to increase with the number of moths in the gall. However, the absolute mass of each moth, under resource limited conditions, may be lower at higher moth densities. The total adult mass may therefore be expected to increase proportionally less as moth density increases. To determine if there was a threshold density at which this occurred, the data on the number of individuals in galls were split into two sets on either side of a putative threshold and straight lines fitted to each set (Duggleby & Ward 1991). The data were repeatedly re-analysed as the putative threshold density was methodically increased. The threshold that yielded the 'best fit' was then identified as the threshold density above which total moth mass increased relatively less with increasing moth density (Duggleby & Ward 1991). The coefficients of variations of the residuals of the two best fit lines on either side of the threshold density were then calculated

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to compare the variations in total moth mass above and below the threshold density. Kruskal-Wallis one-way analyses by ranks were used to determine the significance of differences in moth density (number of individuals per unit gall mass) and biomass (moth dry mass per unit gall mass) in galls containing fewer moths than, and greater than or equal to, the threshold moth density.

Asymmetric interactions

Intraspecific variation in body mass may indicate that certain individuals encounter greater resource shortages than others. A comparison of body mass variation between species may also indicate that certain species experience greater resource shortages than others. However, a minimum number of individuals of each moth species is required for the sample variation in body mass to approximate the population variation and thus to give a true reflection of the extent of body mass variation in each species. To determine which species were sufficiently abundant to accurately reflect the species' variation in body mass, the minimum number of individual moths required to give an acceptable standard error of 5% of the mean species mass was calculated according to Southwood (1978, p. 21). Following Lewontin (1966), F-tests of the variance of $\log_e$ data were used to compare the variation in body masses of the species.

Spearman rank correlation coefficients (r_s) were used to investigate the relationship between individual adult mass for each species and the time (days) after sampling that they emerged.

Species association and abundance covariation

Schluter's (1984) variance ratio tests were used on larval data to identify possible associations between species and covariation between species abundances in the community. The technique compares the observed variance in the number of species or individuals with the variance expected under the null hypothesis that the presence or abundance of each species is independent of the others (Schluter 1984). This method for multispecies comparisons has the advantage that, if the biologies of the species are known, it can be used to distinguish between all possible interspecific interaction types which could produce similar patterns (Schluter 1984).

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RESULTS

Over 90% of the galls in all samples had been utilized to some extent by Lepidoptera larvae (evidenced by the presence of larvae themselves, pupae, pupal cases or frass) and more gall tissue was consumed in galls sampled later in the season than in those sampled earlier in the season (Table 3.1). Galls sampled in January were mainly growing galls, whereas by March the majority of the galls were dead (Table 3.1). Twelve species were recorded during the sampling period, although the species composition and relative abundances in live galls (sampled in January and February) and dead galls (sampled in March) were different (Tables 3.2 & 3.3). In live galls there were more species, as well as a lower dominance by individual species, than in dead galls. A single species was dominant in dead galls and the remaining species were present in very low abundances (Tables 3.2 & 3.3). Less than 0.60 % (32 parasitized larvae of a total of 5647 larvae) of the Lepidoptera larvae were parasitized in all samples. The mean gall masses, number of Lepidoptera species and individual larvae, as well as larval densities (number of larvae per gram of gall mass), for each sampling period are given in Table 3.4.

Table 3.1. Percentage of galls inhabited by Lepidoptera larvae, median and range (in parentheses) of gall ages (1, growing galls; 2, post-growth galls; 3, lignifying galls; 4, dead galls; 5, old galls) and median and range (in parentheses) of the percentage gall tissue consumed; n=number of galls.

Site Date	% Inhabited	Gall Age	% Gall Tissue Consumed	n
Aston Bay				
January 1993	93%	3 (1-4)	20 (0-80)	200
March 1993	98%	4 (1-4)	50 (0-80)	100
Aston Bay				
January 1994	96%	2 (1-4)	30 (0-80)	100
February 1994	100%	3 (2-4)	50 (20-80)	106
Sundays River Valley				
February 1994	99%	3 (2-4)	60 (10-80)	209

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Table 3.2. Absolute abundances of Lepidoptera larvae recorded in *Ravenelia macowaniana* galls from Aston Bay during January 1993 (1), March 1993 (2), January 1994 (3), February 1994 (4) and from Sundays River Valley during February 1994 (5); n = number of galls.

Family Species	n=	1 200	2 100	3 100	4 106	5 209
Noctuidae						
Characoma submediana Wiltshire		31	1	89	38	63
Tortricidae						
Lobesia stericta (Meyrick)		0	0	0	0	114
Cydia (Cydia) victrix (Meyrick)		1487	27	368	341	419
Cryptophlebia peltastica (Meyrick)		17	5	15	22	262
Pyralidae						
Euzophera sp. nr. *verrucicola* Hampson		122	40	25	74	2
indet. Phycitinae		75	10	4	12	37
Cosmopterigidae						
Ascalenia pulverata (Meyrick)		189	1	316	163	538
Anatrachyntis tripola (Meyrick)		2	253	0	40	26
Gelechiidae						
Anarsia gravata Meyrick		112	6	49	76	80
Encolpotis xanthoria Meyrick		33	0	11	25	7
Oecophoridae						
Schiffermuelleria pedicata Meyrick		0	1	0	0	0
Tineidae						
Phthoropoea oenochares (Meyrick)		0	0	0	19	0

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Table 3.3. Dry masses (mean ± S.D.), and absolute abundances of adult Lepidoptera reared from galls from Aston Bay in March 1994 (dead galls) and from Sundays River Valley in February 1994 (live galls).

Species	Dead Galls	Live Galls	Mass (mg)
Ascalenia pulverata	0	567	0.464±1.72
Cydia (Cydia) victrix	2	284	1.378±5.98
Cryptophlebia peltastica	0	139	11.629±63.67
Characoma submediana	0	57	3.984±20.17
Lobesia stericta	0	36	1.555±5.13
Anarsia gravata	2	31	1.216±5.11
Phycitinae complex	9	21	2.046±8.01
Phthoropoea oenochares	7	19	1.564±7.49
Encolpotis xanthoria	3	13	2.068±5.22
Euzophera sp. nr. *verrucicola*	12	12	3.301±24.06
Anatrachyntis tripola	412	5	0.408±2.56

Table 3.4. Mean ± S.E. of the number of species and individual larvae per gall, gall wet masses (g) and larval densities (number of larvae per gram of gall tissue) in galls at Aston Bay and Sundays River Valley (S.R.V.), number of galls in parentheses.

	Species	Larvae	Gall Mass	Density
Aston Bay				
January 1993	2.28 ± 0.17 (174)	11.89 ± 1.16 (174)	13.23 ± 0.96 (174)	1.13 ± 0.11 (174)
March 1993	1.52 ± 0.01 (76)	4.71 ± 0.62 (76)	5.24 ± 0.78 (76)	2.00 ± 0.47 (76)
January 1994	3.52 ± 0.14 (94)	9.34 ± 1.39 (94)	2.84 ± 0.38 (94)	4.30 ± 0.43 (94)
February 1994	1.46 ± 0.27 (98)	6.77 ± 0.62 (98)	4.69 ± 0.45 (98)	2.03 ± 0.18 (98)
S. R. V. February 1994	2.32 ± 0.14 (92)	5.56 ± 0.62 (92)	3.12 ± 0.27 (80)	1.65 ± 0.19 (80)

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Species aggregation

All the positive measures of intraspecific aggregation (*i.e.* positive *J* values indicating positive aggregation) were significant, and positive intraspecific aggregation occurred for between two to five species for each date and site (Table 3.5). However, significant interspecific aggregation also occurred, except in dead galls (Aston Bay, March 1993) (Table 3.6). Because the most frequent, significantly aggregated species in live galls were present in galls with a frequency of between 44 and 90% (Table 3.6), significant interspecific aggregation was therefore present in between 44 and 90% of the galls.

Table 3.5. Intraspecific aggregation of Lepidoptera species in galls, frequency of occurrence of species in galls, n = number of galls; *J* = Ives (1992) measure of intraspecific aggregation and probability of *J* different from zero based on chi-square index of dispersion with (d.f. = n-1), * frequency of species too small for calculation.

Species **Aston Bay**	Frequency in galls (n)	*J*%	chi^2	P<
January 1993				
C. (C.) victrix	90.81% (174)	169.76	3116.43	0.001
A. pulverata	28.74% (174)	85.72	1233.88	0.001
A. gravata	24.14% (174)	72.85	851.75	0.001
G. sp.nr. semifuscella	20.69% (174)	83.33	1133.08	0.001
January 1994				
C. (C.) victrix	86.17% (94)	116.76	655.27	0.001
C. submediana	44.68% (94)	141.79	486.62	0.001
A. pulverata	60.64% (94)	235.30	1525.33	0.001
A. gravata	28.72% (94)	25.94	259.86	0.001
G. sp.nr. semifuscella	8.51% (94)	28.00	445.00	0.001
February 1994				
C. (C.) victrix	83.67% (98)	53.45	660.48	0.001
A. pulverata	45.92% (98)	23.60	1590.84	0.001
A. gravata	35.71% (98)	38.57	290.07	0.001
G. sp.nr. semifuscella	30.61% (98)	12.79	174.72	0.001
March 1993				
A. gravata	2.56% (98)	11.11	*	*
G. sp.nr. semifuscella	15.39% (98)	190.54	1043.78	0.001
A. tripola	88.46% (98)	49.41	253.68	0.001
Sundays River Valley				
February 1994				
C. (C.) victrix	59.78% (92)	90.00	447.14	0.0001
C. peltastica	47.83% (92)	13.33	267.31	0.0001

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Table 3.6. Interspecific aggregation of Lepidoptera species in galls and frequency of occurrence of species in galls; n = number of galls; *C* = Ives (1991) measure of interspecific aggregation, and the probability of *C* being different from zero based on Spearman rank correlation coefficients (r_s).

Species	Frequency in galls (n)	*C*%	r_s	P<
Aston Bay				
January 1993				
C. (C.) victrix	90.8% (174)	87.32	0.42	0.0001
January 1994				
C. (C.) victrix	86.17% (94)	90.61	0.32	0.01
A. pulverata	60.63% (94)	52.56	0.37	0.001
C. submediana	44.68% (94)	40.49	0.46	0.0001
February 1994				
C. (C.) victrix	83.67% (98)	15.28	0.38	0.001
March 1993				
A. tripola	88.46% (78)	-18.32	-0.16	N.S.
Sundays River Valley				
February 1994				
C. (C.) victrix	59.78% (92)	9.37	0.55	0.0001

Mass Compensation

The regressions of the number of larvae on gall mass were positively significant except at Aston Bay, March 1993 (Table 3.7). That is larval density did not increase significantly with gall mass in the sample of predominantly dead galls. The regressions of gall mass and the number of adults emerging per gall, as well as gall mass and total mass of adults per gall, were significantly positive in both live and dead galls (Table 3.7). Galls in which larval mortality occurred while rearing the adults were excluded from the analysis. The relationship between total adult mass and gall mass in dead galls was also weaker and comparatively less significant than in live galls, although the relationship between the number of adults and gall mass in dead galls was strongly significant (Table 3.7). The positive relationship between Lepidoptera density and resource availability was thus stronger and more consistent in live than in dead galls.

A significant, positive relationship was found between the total number of moths that emerged per gall and the total mass of those moths in both dead and live galls (Table 3.8). However, in live galls a threshold density of 13 moths per gall, equivalent to a total moth

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dry mass of 6.23 mg, was identified at, and above which, this relationship did not hold (Table 3.8). The coefficient of variation of the residuals (from the regression of total moth mass on total number of moths) of live galls containing 13 or more moths was less (68.56%) than the residuals of galls with less than 13 moths (78.57.%) (Table 3.8). Moth density and biomass were also significantly different in galls with less than 13 individuals compared to galls with greater than or equal to 13 individuals (Table 3.9). No threshold to moth density was found in dead galls and the regressions were positively significant above and below all encountered densities (Table 3.8).

Table 3.7. Least-squares linear regressions (logY=a+b logX) of the number of larvae per gall on gall mass (g), Aston Bay in: **1**, January and **2**, March 1993, **3**, January and **4**, February 1994, and in Sundays River Valley: **5**, February 1994, and adult moths emerging per gall on gall mass and of the total mass of adult moths per gall (g) on gall mass (g), **6**, dead galls, **7**, live galls.

Linear Regression of:	Intercept±S.E.	Slope±S.E.	d.f.	r	P<
Number of larvae per gall on gall mass					
1.	0.14±0.21	0.75±0.09	173	0.54	0.0001
2.	0.95±0.17	0.16±0.11	75	0.17	NS
3.	1.29±0.12	0.56±0.11	93	0.48	0.0001
4.	0.89±0.14	0.54±0.10	97	0.50	0.0001
5.	0.56±0.13	0.61±0.11	80	0.54	0.0001
Number of adults per gall on gall mass					
6.	0.00±0.14	0.55±0.09	133	0.48	0.0001
7.	-0.07±0.13	0.91±0.07	200	0.69	0.0001
Total moth mass on gall mass					
6.	-6.91±0.19	0.22±0.12	133	0.17	0.05
7.	-7.14±0.33	1.18±0.17	104	0.57	0.0001

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Table 3.8. Least-squares linear regression (logY=a+b logX) of total adult mass (g) on the total number of individuals emerging from the gall for the total sample and the coefficients of variation (C.V.) of the residuals of each regression. A threshold density of 13 adult moths per gall was found for live galls.

Sample	Intercept±S.E.	Slope±S.E.	r	d.f.	P<	%C.V.
Dead galls						
Total	-7.29±0.08	0.89±0.07	0.76	133	0.001	64.92
Live galls						
Total	-6.51±0.17	0.98±0.09	0.64	173	0.001	81.67
< 13 moths	-6.51±0.21	0.96±0.14	0.51	136	0.001	78.57
≥ 13 moths	-3.90±1.22	0.09±0.42	0.04	36	NS	68.56

Table 3.9. Means ± S.E's of moth density (number of adults per gram of gall) and moth biomass (total moth mass (mg) per milligram of gall) for galls containing fewer than 13 moths and galls with greater than or equal to 13 moths, and Kruskal-Wallis one-way analyses by ranks on moth density and moth biomass, test statistic *H*, n = number of galls.

	mean ± S.E.	n	*H*	P<
Density		174	39.66	0.0001
< 13	0.74 ± 0.04	137		
≥ 13	1.38 ± 0.10	37		
Biomass (mg)		174	11.84	0.001
< 13	1.87 ± 0.23	137		
≥ 13	2.58 ± 0.49	37		

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Asymmetric interactions

Only *A. pulverata*, *C. (C.) victrix* and *C. peltastica* reared from live galls and *A. tripoli* reared from dead galls (Table 3.3) were sufficiently abundant to give an adequate reflection of species variation in body mass. The three species in the 1994 sample differed markedly in mean body mass. *Ascalenia pulverata* was the smallest (with the exception of *A. tripola* which occurred in extremely low numbers) and *C. peltastica* the largest of the species reared (Table 3.3). An analysis of the extent of variation in mean body mass of the three most abundant species in live galls showed that the dry mass of the larger species varied significantly more than that of the smaller species (Table 3.10).

There was a significant, negative correlation between the adult masses of individuals of the most abundant species and the length of time after gall sampling that they emerged (Table 3.11).

Species association and abundance covariation

The Lepidoptera species in galls at Aston Bay were significantly positively associated with each other in all samples except March 1993 where the association was positive but not significant (Table 3.12). At the same site the abundances of the species in the community covaried significantly and positively except in the February 1994 sample, where abundances covaried positively, but not significantly so (Table 3.12). The species in the Sundays River Valley sample were not significantly associated with each other (Table 3.12), however their abundances covaried significantly and positively (Table 3.12).

Table 3.10. F-test on the variance of $\log_e$ dry adult body mass (g) (Lewontin 1966) of the three most abundant species pairs; the largest species is the first in each pair.

Species	F	d.f.	P
C. peltastica, *C. (C.) victrix*	1.323	138, 283	<0.001
C. peltastica, *A. pulverata*	1.558	138, 566	<0.001
C. (C.) victrix, *A. pulverata*	1.178	283, 566	<0.001

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Table 3.11. Spearman rank correlation coefficients (r_s) of adult dry mass (g) versus order of emergence (time in days); n = number of individuals.

Species	r_s	n	P<
Dead galls			
Anatrachyntis tripola	-0.35	412	0.001
Live galls			
Ascalenia pulverata	-0.18	567	0.001
Cydia (Cydia) victrix	-0.42	284	0.001
Cryptophlebia peltastica	-0.27	139	0.002

Table 3.12. Variance ratios (VR) of species associations and covariations, n= number of galls, W = test statistic of variance ratio with a chi-square distribution (Schluter 1984).

	VR	n	W	P<
Association				
Aston Bay 1993				
January	1.58	175	275.71	0.01
March	1.26	85	106.79	0.1
Aston Bay 1994				
January	1.66	94	155.69	0.001
February	1.52	99	150.34	0.001
Sundays River Valley 1994				
February	1.16	92	106.83	0.1
Covariation				
Aston Bay 1993				
January	1.41	175	246.70	0.01
March	2.59	85	220.30	0.001
Aston Bay 1994				
January	2.00	94	188.01	0.001
February	1.05	99	104.36	0.1
Sundays River Valley 1994				
February	1.96	92	180.36	0.001

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DISCUSSION

R. macowaniana galls are an extensively utilized resource with over 90% of galls occupied and generally with more than a single individual and species occurring in each gall. The quantity of each gall consumed was also high, particularly later in the season. Once approximately 80% of the plant tissue within a gall has been consumed the gall begins to lose its integrity as a habitat and galls are not utilized beyond this limit. In addition, larval feeding in live galls accelerates the rate of tissue dehydration and hence ageing that results in a drop in gall tissue quality (McGeoch 1993; New 1982). A fully utilized gall may therefore show less than 80% removal of gall tissue. The majority of galls were therefore not only occupied, but also extensively utilized.

Although 12 Lepidoptera species utilized the galls, there were usually no more than three or four species in a single gall. The high quality of the resource and the patchiness of gall distribution therefore appear to facilitate the accommodation of a larger number of species locally than are accommodated in a single habitat unit, *i.e.* gall (see Chapter 1, p. 21).

Significant, positive intraspecific and interspecific aggregation occurred in live galls. Furthermore, species were interspecifically aggregated in between 44% to 90% of the galls. Interspecific competition in live galls may therefore be expected under resource limited conditions (Ives 1991). Significant intraspecific and insignificant interspecific aggregation occurred in dead galls and if competition was to occur it would therefore be predominantly intraspecific. *Anatrachyntis tripola*, the dominant species in dead galls, is also the smallest lepidopteran in the community and galls would have a much higher carrying capacity if occupied predominantly by this species than if occupied by a number of larger species.

In live galls the decrease in adult mass variation above the threshold density of 13 individuals, or 6.23 mg moth dry mass, is indicative of a density-dependent mass compensation response to resource limitation and shows that these larvae are resource limited. Such a decrease in the variation of sizes of organisms is common between competing individuals as a result of resource depletion (Weiner & Thomas 1986). The Lepidoptera in dead galls were not resource limited as no threshold to moth density occurred and the total mass of adults increased irrespective of the number of individuals present in the gall. The nature of the resource provided by dead galls is very different and dead galls are woody and

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dry (McGeoch 1993). In addition, the community in dead galls was dominated by a single species, *A. tripola* (constituting 92% of individuals, Table 3.2).

Two characteristics of competitive interactions are their asymmetry and intensity (Keddy 1994). One form of asymmetry demonstrated here was the differential effect of interspecific interactions in live galls on moth species of different sizes (see also Thompson 1988). Larger species showed greater dry mass variation than did smaller ones. Large organisms require a greater portion of available resources, and when resources are limiting larger species experience resource shortages more frequently than smaller species (Futuyma 1986, Pagel *et al.* 1991). A further asymmetric interactive effect in both dead and live gall-inhabiting moth communities was a 'processing chain component' (Heard 1994), where earlier colonizers reduce the quantity and quality of gall tissue available to later colonizers (Lawton & Hassell 1981). This was demonstrated by the negative rank correlation of mass on emergence date. Gall tissue quality deteriorates as the gall ages and is increasingly consumed by larvae and earlier colonizers of the gall will be at a competitive advantage. This form of priority effect is common in ephemeral resource patches (Beaver 1977).

Although the intensity of competitive interactions (frequency and strength of interactions) is notoriously difficult to determine in multispecies communities (Connell 1983), the threshold limit to moth density was encountered in 21 % of the live galls. Although density-dependent mass compensation is most severe at and above the threshold, the frequency of competition may be higher than 21%. It most likely already has an effect at lower densities, becoming more severe (and easier to detect) as the threshold is approached. The intensity of asymmetric competitive interactions could not be determined from the correlation coefficients between moth mass and time of emergence (these were low), because two variables are insufficient to explain this relationship (see Keddy 1994) and a number of factors, in addition to resource based ones, are known to influence body mass (Futuyma 1986).

Although density dependent mass compensation was demonstrated in live galls and the species were resource limited, species abundances did not covary negatively, nor were the species negatively associated. Species associations and abundance covariations need not be negative for competition to be the underlying mechanism structuring the community (Schluter 1984). Significant positive associations and abundance covariations between non-mutualistic, resource-limited species within the same trophic level, also implicate competition

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(Schluter 1984). Negative associations between species may be masked if the species respond strongly to a common habitat (Schoener & Adler 1991). The abundances of competing species may also covary positively in response to fluctuations in their identical, limited resource without the manifestation of significant species associations (as occurred in the Aston Bay, March 1993 and Sundays River Valley, February 1994 samples, Table 3.11) (Schluter 1984). However, within ephemeral resource patches which support one stage in the life history of a single generation, negative abundance covariation will not be evident at the habitat unit level, but rather at the local population level of future generations, unless competitive effects cause direct mortality or dispersal (which did not occur in the community examined here). Positive species associations thus demonstrate a common habitat affinity and positive abundance covariations a common response to resource conditions. Because the patterns of abundance covariation and species association found here were present within a single, resource limited trophic level, the underlying mechanism responsible for these patterns is interspecific competition (Schluter 1984).

Exploitative competition between Lepidoptera larvae within the *R. macowaniana* gall-inhabiting community produces density-dependent mass compensation effects. This will affect the reproductive success (and possibly also the dispersal ability) of the adult moths (Wickman & Karlsson 1989), population abundances of future generations and the structure of the gall-inhabiting community the following season. Woiwod & Hanski (1992) showed that annual density dependence in moth population abundances is pervasive and, although they did not examine the causative mechanisms, they showed that the average degree of density dependence increases with moth body size. In addition, Dempster (1983) showed that natural enemies did not appear to be density-dependent regulatory factors in Lepidoptera populations (however see Hassell 1985) and resource based density dependence is more likely to be operative, as was shown here.

Food quality is an important factor in the population ecology of many insects, particularly Lepidoptera, and many insect populations are resource limited as a result of specialized nutrient requirements (Chown 1992; Crawley & Pattrasudhi 1988; Dempster 1991; Pollard & Rothery 1994; Whitham 1978; Zwölfer 1979). In oligophagous and polyphagous insects these nutrient requirements may be met by facultative and opportunistic herbivory rather than obligatory insect host-plant relationships. At least three of the Lepidoptera species here, (*L. stericta*, *C. (C.) victrix* and *C. peltastica*), are known to have

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alternative hosts (de Villiers 1992) and their use of *R. macowaniana* galls is opportunistic. The frequency of interspecific competitive effects between oligophagous to polyphagous insect herbivores feeding opportunistically in high quality, ephemeral microhabitats, patchily distributed in both time and space, as suggested by Southwood (1987), may therefore be higher than presently estimated because of its low predictability and difficulty to detect.

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REFERENCES

Andrewartha, H.G. & Birch, L.C. 1954. *The Distribution and Abundance of Animals.* University of Chicago Press, Chicago.

Arthur, W. 1987. *The Niche in Competition and Evolution.* John Wiley & Sons, New York.

Beaver, R.A. 1977. Non-equilibrium 'island' communities: Diptera breeding in dead snails. *Journal of Animal Ecology* **46**, 783-798.

Chown, S.L. 1992. A preliminary analysis of weevil assemblages in the Sub-Antarctic: local and regional patterns. *Journal of Biogeography* **19**, 87-98.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* **122**, 661-696.

Crawley, M.J. & Pattrasudhi, R. 1988. Interspecific competition between insect herbivores: asymmetric competition between cinnabar moth and ragwort seed-head fly. *Ecological Entomology* **13**, 243-249.

Damman, H. 1993. Patterns of interaction among herbivore species. In Stamp, N.E. & Casey, T.M. (Eds). *Caterpillars Ecological and Evolutionary Constraints on Foraging*. Chapman & Hall, New York, pp. 132-169.

Dempster, J.P. 1983. The natural control of populations of butterflies and moths. *Biological Review* **58**, 461-481.

Dempster, J.P. 1991. The role of intra-specific competition in determining insect abundance. *Antenna* **15**, 105-109.

Denno, R.F., McClure, M.S. & Ott, J.R. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology* **40**, 297-331.

De Villiers, E.A. 1992. Control of the Litchi moth, *Agroploce peltastica* Meyr. *South African Litchi Growers' Association Yearbook* **4**, 8.

Duggleby, R.G. & Ward, L.C. 1991. Analysis of physiological data characterized by two regimes separated by an abrupt transition. *Physiological Zoology* **64**, 885-889.

Futuyma, D.J. 1986. *Evolutionary Biology*. Second edition. Sinauer, Sunderland.

Giller, P.S. & Doube, B.M. 1994. Spatial and temporal co-occurrence of competitors in Southern African dung beetle communities. *Journal of Animal Ecology* **63**, 629-643.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. 1960. Community structure, population control, and competition. *American Naturalist* **94**, 421-425.

Hanski, I. 1983. Coexistence of competitors in patchy environment. *Ecology* **64**, 493-500.

Hassell, M.P. 1985. Insect natural enemies as regulating factors. *Journal of Animal Ecology* **54**, 323-334.

Heard, S.B. 1994. Processing chain ecology: resource condition and interspecific interactions. *Journal of Animal Ecology* **63**, 451-464.

Ives, A.R. 1988. Aggregation and coexistence of competitors. *Annales Zoologici Fennici* **25**, 75-88.

Ives, A.R. 1991. Aggregation and coexistence in a carrion fly community. *Ecological Monographs* **61**, 75-94.

Keddy, P.A. 1994. Applications of the Hertsprung-Russell star chart to ecology: reflections on the 21st birthday of *Geographical Ecology*. *Trends in Ecology and Evolution* **9**, 231-234.

Lawton, J.H. 1984. Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. In Strong, D.R., Simberloff, D., Abele, L.G. &

Digitised by the Department of Library Services in support of open access to information, University of Pretoria, 2021

Thistle, A.B. (Eds). *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, pp. 67-99.

Lawton, J.H. & Hassell, M.P. 1981. Asymmetrical competition in insects. *Nature* **289**, 793-795.

Lawton, J.H. & Strong, D.R. 1981. Community patterns in folivorous insects. *The American Naturalist* **118**, 317-338.

Lewontin, R.C. 1966. On the measurement of relative variability. *Systematic Zoology* **15**, 141-142.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* **11**, 119-161.

McGeoch, M.A. 1993. The microlepidoptera associated with a fungus gall on *Acacia karroo* Hayne in South Africa. *African Entomology* **1**, 49-56.

McGeoch, M.A. & Krüger, M. 1994. Identification and diagnoses of Lepidoptera larvae inhabiting galls induced by *Ravenelia macowaniana* Pazschke on *Acacia karroo* Hayne in South Africa. *African Entomology* **2**, 47-53.

New, T.R. 1982. Lepidoptera from *Uromycladium* galls on *Acacia*. *Australian Journal of Zoology* **30**, 357-364.

Pagel, M.D., Harvey, P.H. & Godfray, H.C.J. 1991. Species-abundance, biomass, and resource-use distributions. *The American Naturalist* **138**, 836-850.

Pielou, E.C. 1977. *Mathematical ecology*. Second edition. John Wiley & Sons, New York.

Pollard, E. & Rothery, P. 1994. A simple stochastic model of resource-limited insect populations. *Oikos* **69**, 287-294.

Schluter, D. 1984. A variance test for detecting species associations with some example applications. *Ecology* **65**, 998-1005.

Schoener, T.W. 1983. Field experiments on interspecific competition. *The American Naturalist* **122**, 240-285.

Schoener, T.W. 1988. Ecological interactions. In Myers, A.A. & Giller, P.S. (Eds). *Analytical Biogeography an Integrated Approach to the Study of Animal and Plant Distributions*. Chapman & Hall, London, pp. 255-297.

Schoener, T.W. & Adler, G.H. 1991. Greater resolution of distributional complementarities by controlling for habitat affinities: a study with Bahamian lizards and birds. *The American Naturalist* **137**, 669-692.

Shorrocks, B., Atkinson, W. & Charlesworth, P. 1979. Competition on a divided and ephemeral resource. *Journal of Animal Ecology* **48**, 899-908.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. Second edition. Freeman & Company, San Fransisco.

Southwood, T.R.E. 1978. *Ecological Methods with Particular Reference to the Study of Insect Populations*. Chapman & Hall, London.

Southwood, T.R.E. 1987. The concept and nature of the community. In Gee, J.H.R. & Giller, P.S. (Eds). *Organization of Communities Past and Present*. Blackwell Scientific, Oxford, pp. 3-27.

Stamp, N.E. & Bowers, M.D. 1990. Phenology of nutritional differences between new and mature leaves and its effect on caterpillar growth. *Ecological Entomology* **15**, 447-454.

Strong, D.R. 1983. Natural variability and the manifold mechanisms of ecological communities. *The American Naturalist* **122**, 636-660.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984. *Insects on Plants: Community*

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Patterns and Mechanisms. Blackwell, Oxford.

Thompson, J.N. 1988. Variation in interspecific interactions. *Annual Review of Ecology and Systematics* **19**, 65-87.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**, 2-16.

Weiner, J. & Thomas, S. 1986. Size variability and competition in plant monocultures. *Oikos* **47**, 211-222.

Whitham, T.G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. *Ecology* **59**, 1164-1176.

Wickman, P.O. & Karlsson, B. 1989. Abdomen size, body size and the reproductive effort of insects. *Oikos* **56**, 209-214.

Woiwod, I.P. & Hanski, I. 1992. Patterns of density dependence in moths and aphids. *Journal of Animal Ecology* **61**, 619-629.

Wootton, J.T. 1994. The nature of indirect effects in ecological communities. *Annual Review of Ecology & Systematics* **25**, 443-466.

Zwölfer, H. 1979. Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls. *Fortschritte der Zoologie* **25**, 331-353.

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CHAPTER 4

Local habitat quality determinants of the structure of the Lepidoptera community

Increasing areas of pristine habitat are being destroyed and fragmented worldwide as a result of the human population explosion and subsequent increase in urbanization, industrialization and agricultural practises. As a consequence, the population sizes of plant and animal species are becoming smaller, their distribution ranges divided and constricted, and certain species locally and geographically extinct (Wilcox & Murphy 1985). The survival of populations in such remnant patches of habitat is dependent on the nature and condition of the patch, as well as on the size, population density and dispersal ability of the species (den Boer 1990). Agricultural and urban habitat patches supporting indigenous vegetation have previously been shown to be suitable habitats for insects (*e.g.* Samways 1989). Although subject to the quantity of optimal habitat and food resources in the patch, the minimum patch size required for the survival of insect populations is often small. Thomas (1984) has shown, for example, that a number of butterfly species may be viable with a minimum breeding area of as little as 0.5 to 1 ha.

When capable of surviving habitat fragmentation and alteration, insects make potentially useful indicators of local habitat quality. Numerous studies have been undertaken on the specific responses of aquatic insect species and communities to changes in water quality, and invertebrates have been widely used in the monitoring of aquatic systems (*e.g.* Berkman *et al.* 1986; Chessman 1995; Clark 1991; Williams *et al.* 1986). Less use has been made of terrestrial insects as indicators, although they are increasingly being used in environmental monitoring (Holloway 1980; Kremen 1992; Kremen *et al.* 1993; Noss 1990), especially the Coleoptera and Lepidoptera (*e.g.* Erhardt & Thomas 1991; New *et al.* 1995; Pollard 1991; Pearson & Cassola 1992). Lepidoptera are particularly useful because they are ubiquitous and diverse, often with specific vegetation and climate requirements, and Lepidoptera taxonomy is relatively advanced and accessible to amateurs (Samways 1994).

In complex habitats it is also often necessary to select a single component, or 'key indicator', whose responses to changes in habitat quality are indicative of the environment as a whole. Most often a key indicator is a single species whose indicator value is known, *i.e.* comprehensive information on the biology of the species and its responses to local environmental stresses is available (Hellawell 1991). Rare species (*i.e.* rare because they are

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highly specialized or localized) have proven to be particularly useful as key indicators, because they often have specific habitat requirements and are therefore good indicators of habitat change (Samways 1994; Usher 1986). Groups of species characteristically occurring together, *i.e.* communities, also have properties which can be used to obtain quantitative measures of environmental or ecosystem change (Hellawell 1991; Lenhard & Witter 1977). Changes in the structure (*e.g.* species abundance and diversity) and function (*e.g.* productivity) of communities result from local environmental stresses, either man-induced or natural (Sheehan 1984a), and community properties therefore provide 'key measures' (Hellawell 1991) for monitoring.

Insect larval communities in galls can be useful systems of comparison at both the species and community levels. They are relatively contained, more sessile than free-living insects and therefore easier to sample. The community of Lepidoptera larvae that inhabit *Ravenelia macowaniana* Pazschke galls on *Acacia karroo* Hayne has the additional advantage of *A. karroo* being abundant in both disturbed and undisturbed areas (Swartz 1982). *Acacia karroo* is a good colonizer of highly disturbed soils and as a result is conspicuous along roadsides, in overgrazed fields and on abandoned sites in developed areas. The aim of this part of the study was, therefore, to identify particular characteristics of local habitat quality that may be important determinants of Lepidoptera diversity in the *R. macowaniana* gall community. Second, to determine whether certain Lepidoptera species in the local community examined responded more consistently and clearly than others to differences in local habitat quality. Third, to determine which properties of the moth community, based on this local analysis, best reflected differences in habitat quality. In addition to their utility as indicators and monitors of habitat quality however, insect communities also provide valuable information on the impact of environmental changes on the functioning of terrestrial ecosystems and on the roles of individual species in communities. This local scale study will, therefore, be followed by a regional comparison (Chapter 5) and then incorporated into a larger scale analysis of community patterns and an evaluation of criteria for the selection of indicator species and the identification of pivotal species in communities based on an analysis of species properties (Chapter 6).

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STUDY SITES and METHODS

Galls were collected from 4 sites along the 25° S latitude line, passing through Pretoria (South Africa), to minimize temperature differences between the sites. The sites were, from west to east,: Hartebeespoort (HTB) (25°45'S : 27°52'E); Proclamation Hill (CPH) (25°45'S : 28°07'E); Moreleta Nature Reserve (MOR) (25°45'S : 28°16'E); and Pienaarspoort (PNP) (25°45'S : 28°25'E). Seven characteristics considered to be important determinants of habitat quality were chosen to describe each site, although it is acknowledged that numerous other factors may be involved (Table 4.1). Where absolute values were not available, the characteristics were scored (between 1 and 5) in a manner similar to scoring techniques used in conservation evaluation (Pressey & Nicholls 1991). HTB and PNP, on either end of the spectrum, are located in rural cattle-farming regions. MOR is located in an urban reserve, where the vegetation was inadvertently burnt a few weeks after the study began. CPH is located in an industrial area close to an iron and steel-works, which emits large quantities of gaseous pollutants. Air pollution readings were unavailable for PNP and HTB, but inspection suggested that smog and SO_2 levels were significantly lower than those at the nearest smog and SO_2 monitoring sites at CPH and MOR, respectively. Patch size and isolation were measured from 1:50 000 topographical maps of each site and adjacent areas (printed by the Government Printer, Pretoria).

Galls were sampled from all the sites once in each of October 1991 and January, February and March 1992. A minimum of 100 galls was collected whenever possible from each site at every visit. However, if gall density at the sites was low (*i.e.* if the collection of 100 galls would result in severe reduction or depletion of galls at the site) smaller samples were collected. A maximum of 10 galls was collected from each tree sampled and a record was kept of the number of galls on sampled trees at each site (gall/resource density). Live galls were weighed. The age of each gall was classed as either 1 - growing galls, 2 - post-growth galls, 3 - lignifying galls, 4 - dead galls and 5 - old galls (Chapter 1). In the laboratory, Lepidoptera larvae were removed from the galls. An estimate was made of the percentage of gall tissue consumed in each gall, and the percentages of occupied galls were calculated for each sampling month. Larvae were identified using the key to larvae compiled (Chapter 2). The time necessary to sample and process material three times each from four sites, within the three month gall growth season, prevented the replication of sampling areas within each of the four localities.

One-way analyses of variance were used to compare each of gall masses, gall

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densities (number of galls on trees sampled), and larval densities in the galls, between sites with data from all sampling pooled. Gall masses and densities required $\log_e$ transformation, and larval densities square-root transformation to render them normally distributed before analysis.

Three indices were calculated to compare moth diversity between sites, because of the differential sensitivity of indices to diversity parameters. α (logseries) has a better discriminant ability than H' (Shannon index) and $1/\lambda$ (Simpson index). $1/\lambda$ is more sensitive to dominance trends than to richness, and H', although sensitive to sample size, has the advantage of associated evenness and t-statistic values (Magurran 1988).

The relationships between site characteristics, species relative abundances, Shannon's indices (H'), and larval densities (n/g), were investigated at each site for each month (*i.e.* n=12) using Spearman rank correlation coefficients (r_s). However, calculations involving physical disturbance, vegetation structural diversity, patch size and isolation, were done using a single value for each site (*i.e.* n=4), because these characters remained constant between months.

RESULTS

Habitat quality, based on the 7 site characteristics, was poorest at MOR, followed by CPH, and comparatively better at the 2 sites on either end of the spectrum, *i.e.* PNP and HTB (Table 4.1).

Galls collected in October were from the previous summer season (age-category 5) and contained no live Lepidoptera. From this collection it was determined that between 91% and 99% of the galls at each site had been occupied by Lepidoptera during the previous season (Table 4.2), as evidenced by silk-lined burrows, frass, exuviae and old pupal cases. Gall density was lower at the sites during the 1992 season possibly as a result of poor rainfall. No galls were found at Moreleta (site C) in March 1992.

Gall mass (sampling months pooled) differed significantly between sites and was highest at CPH ($F = 14.52$; df = 3, 618; $P<0.001$, Table 4.3). Gall mass at MOR was also significantly lower than at CPH (Table 4.3). Although gall masses were not significantly different at HTB and PNP, gall density (sampling months pooled) at PNP was significantly lower than at HTB ($F=29.97$; df = 3, 214; $P<0.001$, Table 4.3). The percentage of gall tissue consumed by the larvae was generally lowest at CPH, and more than double that of the other sites at MOR in January and February. The highest percentage of live galls

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containing Lepidoptera (*i.e.* between January and March) also occurred at MOR (Table 4.2).

Eight Lepidoptera species were recorded: 1. *Cydia (Cydia) victrix* (Meyrick) (Tortricidae), 2. *Ascalenia pulverata* (Meyrick) (Cosmopterigidae), 3. *Anarsia gravata* Meyrick (Gelechiidae), 4. *Characoma submediana* Wiltshire (Noctuidae), 5. *Euzophera* sp. nr. *verrucicola* Hampson (Pyralidae), 6. Phycitinae sp., 7. *Eublemma brachygonia* Hampson (Noctuidae), 8. *Cryptophlebia peltastica* (Meyrick) (Tortricidae). Two gelechiid species were collected at Pienaarspoort and identified as *Anarsia* sp. 1 and *Anarsia* sp. 2. For the purpose of this comparison these species were grouped with *A. gravata.*

The mean number of species per gall was similar at all sites, whereas the mean numbers of individuals per gall were particularly high at MOR and CPH in January and February respectively (Table 4.4). The number of larvae per 1.0 g of gall tissue (n/g = division of the number of individuals per gall by the gall mass), provided a comparison independent of the differences in mean gall mass between the sites (Table 4.4). After this correction MOR had a significantly higher larval density than the other sites ($F=16.91$; d.f. $=3, 301$; $P<0.001$, Table 4.3), whereas in contrast to the number of individuals CPH had the lowest larval density of all sites (sampling months pooled).

C. (C.) victrix had the highest absolute abundance at all sites in all months (Table 4.5). It was relatively most abundant at MOR (Fig. 4.1), and had the highest mean number of individuals per gall at this site (Table 4.6). *A. pulverata* and *A. gravata* were alternatively second and third most abundant at PNP and MOR, and HTB and CPH respectively, and *C. submediana* ranked fourth in relative abundance at all the sites (Fig. 4.1). The rarest species at each site, *i.e.* those with the lowest relative abundance - the pyralid species, *E. brachygonia*, and *C. peltastica*, showed no trends between sites. *C. peltastica* was recorded only at HTB. *C. peltastica* is a recorded pest species of fruit crops (Anneke & Moran 1982), although it does have a number of indigenous host plants. Fruit crop plantations occur in the vicinity of HTB which may account for the presence of *C. peltastica* in the gall-inhabiting community. The pyralid species was not found at HTB and MOR. *Euzophera* sp. nr. *verrucicola* was also not recorded from MOR (Table 4.5). Numerical dominance switches only occurred between *A. pulverata* and *A. gravata. A. pulverata* was the second most numerous species at the two western sites, whereas *A. gravata* was the second most numerous species at the two eastern sites (Fig. 4.1).

The ranked relative abundances of species at each site (Fig. 4.1) show a more even

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distribution of abundances at HTB and PNP than at CPH and MOR (supported by Shannons' evenness (E) values (Table 4.7)). All 3 diversity indices showed HTB and MOR as having the highest and lowest moth diversities respectively (Table 4.7). The α index however, in contrast to H' and $1/\lambda$, showed CPH to be more diverse than PNP. The difference in diversity between HTB and PNP was not significant (H' t-statistic, Table 4.7), but the differences between these and the other sites were highly significant (Table 4.7). The diversity difference between MOR and CPH was also significant, but less so than between these sites and HTB and PNP.

The correlation tests used were non-independent and because of the large number of comparisons done, some of the significant results may occur by chance. However, the trends in the data are evident. Resource density, physical disturbance and vegetation structural diversity were highly correlated with each other, although not significantly so, possibly as a result of small sample sizes (Table 4.8a). Air pollution levels were significantly correlated with moth diversity (H'), whereas rainfall, and to a lesser extent site size and isolation were the site characteristics most strongly correlated with larval density (n/g) (Table 4.8a).

The relative abundance of *C. submediana* was significantly positively correlated with those of *A. gravata*, *E.* sp.nr. *verrucicola*, *E. brachygonia*, and the abundance of *E.* sp. nr. *verrucicola* was significantly negatively correlated with *C. (C.) victrix* (Table 4.8b). The abundances of *C. submediana* and *E.* sp.nr. *verrucicola* were most strongly and significantly correlated with moth diversity, and the abundance of *C. (C.) victrix* was significantly correlated with larval density (n/g) (Table 4.8b). When species relative abundances and diversity values for the three sampling months were combined for each site (n=4), the abundance of *C. (C.) victrix* (sp. 1) was also significantly correlated with diversity (H') (r_s=-1.0, $P<0.001$).

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Table 4.1. Site characteristics for Hartebeespoort (HTB), Proclamation Hill (CPH), Moreleta Nature Reserve (MOR) and Pienaarspoort (PNP).

Character[a]	HTB	CPH	MOR	PNP
1a	<2.92	12.16	2.92	<2.92
b	<12.33	20.16	12.33	<12.33
2	135.40	105.50	136.30	142.20
3	5.2±5.7	6.9±5.2	1.8±1.3	2.4±2.0
4	3	2	5	3
5	3	4	2	2
6	4	2	3	4
7	1	5	3	1

[a] 1. Air pollution readings, yearly mean smog expressed by a soiling index (S/m^3) (a) and SO_2 ($\mu g/m^3$) (b).

2. Rainfall totals (mm) for each of the sites from January to March 1992, obtained from the Weather Bureau of the Department of Environment Affairs, Pretoria.
3. Resource density, mean density (± S.D.) of galls on trees at the site over the season.
4. Physical disturbance, including human and animal (cattle) movement through site, dust as a result of vehicle movement on dirt roads in the vicinity, and fire. Scored from 1 (low) to 5 (high).
5. Vegetation structural diversity, scored from 1 (low) to 5 (high).
6. Patch size, size of the area/site containing *Acacia karroo*. Scored from 1 (± 600 m^2) to 5 (± 1800 m^2).
7. Site isolation, degree of isolation of the site from other such vegetated areas/sites with *Acacia karroo*. Scored from 1(< 1 km) to 5 (> 5 km) (see methods).

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Table 4.2. Gall resource information for Hartebeespoort (HTB), Proclamation Hill (CPH), Moreleta Nature Reserve (MOR) and Pienaarspoort (PNP); n = number of galls.

Month Site	n	Gall Mass (g)	% Gall Consumed	Gall Age	% Galls
		mean±S.D.	median; range	median; range	used by Lepidoptera
October					
HTB	100		32; 0-90	5; 0	93
CPH	100		25; 0-70	5; 0	91
MOR	100		30; 0-70	5; 0	99
PNP	100		32; 0-70	5; 0	93
January					
HTB	50	1.93±2.58	12; 0-80	1; 1-4	70
CPH	50	5.17±3.42	5; 0-60	1; 1-4	56
MOR	22	3.47±2.99	35; 0-80	1; 1-4	91
PNP	50	3.68±3.49	14; 0-60	1; 1-4	88
February					
HTB	50	7.99±8.11	12; 0-60	1; 1-4	78
CPH	50	7.38±6.18	16; 0-70	1; 1-3	88
MOR	26	1.59±1.36	40; 0-70	1; 1-4	65
PNP	50	5.48±7.62	16; 0-60	1; 1-4	86
March					
HTB	100	3.51±6.69	28; 0-70	3; 1-5	37
CPH	100	4.54±4.27	8; 0-60	3; 1-5	24
MOR	0	-	-	-	-
PNP	98	2.92±2.86	16; 0-60	3; 1-5	23

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Table 4.3. Mean ± S.D. and $\log_e$ mean ± Tukey's 95% H.S.D. confidence intervals for gall mass and density of galls on *A. karroo* trees, and the square-root transformed mean ± Tukey's 95% H.S.D. confidence intervals for larval density (n/g) (sample month data pooled); n = number of galls or trees.

Sites	mean±S.D.	transformed mean±H.S.D	n
Gall mass (g)			
HTB	3.92±5.01	0.84±0.12	200
CPH	5.27±4.99	1.33±0.13	200
MOR	2.52±2.52	0.47±0.25	48
PNP	3.77±4.76	0.88±0.12	198
Gall density			
HTB	5.22±5.68	1.18±0.18	54
CPH	6.92±5.24	1.70±0.21	39
MOR	1.80±1.29	0.42±0.28	21
PNP	2.42±1.96	0.57±0.13	104
n/g			
HTB	2.03±3.45	1.15±0.12	108
CPH	0.98±1.16	0.88±0.14	69
MOR	3.78±3.23	1.86±0.21	33
PNP	1.53±1.42	1.12±0.12	98

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Table 4.4. The number of individuals and species per gall, and the number of larvae per 1.0 g of gall tissue (n/g) at the four study sites (HTB, CPH, MOR, PNP) in each of the summer sampling months; n = number of galls containing larvae.

Month Site	n	No. Individuals	Per 1.0 g Gall: n/g	No. Species
		mean±S.D.	mean±S.D.	mean±S.D.
January				
HTB	34	3.09±2.09	4.57±5.26	1.62±0.74
CPH	28	2.86±2.62	0.53±0.31	1.29±0.54
MOR	21	13.00±11.13	4.76±3.62	1.76±0.70
PNP	41	5.05±4.33	1.80±1.57	1.88±0.98
February				
HTB	39	4.87±3.93	0.76±0.80	1.92±0.73
CPH	21	11.96±12.63	1.83±1.72	1.91±0.97
MOR	12	3.36±3.05	2.07±1.25	1.36±0.63
PNP	39	5.62±5.22	1.62±1.40	2.07±1.07
March				
HTB	35	2.37±1.80	0.98±0.69	1.49±0.70
CPH	20	4.00±4.58	0.72±0.59	1.55±0.99
MOR	-	-	-	-
PNP	18	2.22±1.83	0.73±0.60	1.22±0.55
Total/ Mean				
HTB	108	3.50±3.00	2.03±3.45	1.69±0.74
CPH	69	6.04±8.57	0.98±1.16	1.56±0.86
MOR	33	9.14±9.97	3.78±3.23	1.60±0.69
PNP	98	4.78±4.55	1.53±1.42	1.84±0.99

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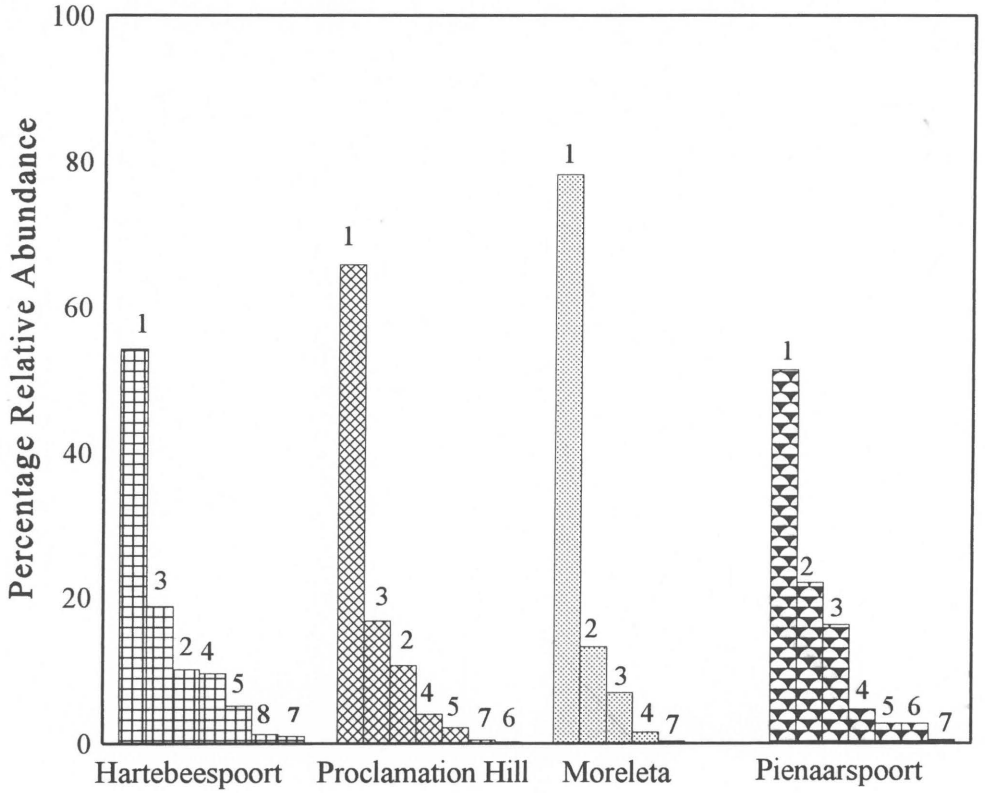

Fig. 4.1. The ranked relative abundances of Lepidoptera species: 1, *Cydia (Cydia) victrix*, 2, *Ascalenia pulverata*, 3. *Anarsia gravata*, 4, *Characoma submediana*, 5, *Euzophera* sp. nr. *verrucicola*, 6, Phycitinae sp., 7, *Eublemma brachygonia*, 8, *Cryptophlebia peltastica*, from four sites.

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Table 4.5. Absolute abundances of species during January (J), February (F) and March (M) at each of the study sites (HTB, CPH, MOR, PNP).

Sites / Species	HTB			CPH			MOR			PNP		
	J	F	M	J	F	M	J	F	M	J	F	M
1. *C.(C.) victrix*	62	106	43	58	195	26	217	33	-	128	100	19
2. *A. pulverata*	24	12	3	17	28	0	40	2	-	15	88	3
3. *A. gravata*	10	53	10	5	34	32	16	6	-	48	24	6
4. *C. submediana*	11	17	9	2	6	9	0	5	-	11	8	3
5. *E.* sp.nr. *verrucicola*	4	1	15	0	0	9		-		0	11	2
6. Phycitinae sp.		-		0	0	1		-		3	3	7
7. *E. brachygonia*	1	3	0	0	0	2	0	1	-	0	2	0
8. *C. peltastica*	0	1	4		-			-			-	

Table 4.6. Mean (± S.D.) number of individuals per gall of species 1 to 8 (species numbered as in text) at each study site (HTB, CPH, MOR, PNP) over the summer sampling months.

Sites / Species	HTB	CPH	MOR	PNP
1. *C. victrix*	2.58±2.13	5.60±7.69	8.07±8.27	2.99±2.69
2. *A. pulverata*	1.50±0.81	2.14±1.91	3.00±2.35	3.00±2.13
3. *A. gravata*	2.21±1.54	3.23±2.79	3.14±3.13	1.86±2.01
4. *C. submediana*	1.44±0.71	2.11±1.27	1.67±1.16	1.92±1.51
5. *E.* sp.nr. *verrucicola*	1.25±1.00	2.25±1.50	-	2.60±2.07
6. Phycitinae sp.	-	1.00±0.00	-	1.30±0.95
7. *E. brachygonia*	1.33±0.58	1.00±0.00	1.00±0.00	2.00±0.00
8. *C. peltastica*	1.25±0.50	-	-	-

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Table 4.7. Indices of moth diversity (S = species richness; N = number of larvae) at the four study sites (HTB, CPH, MOR, PNP), and H' t-statistics (below the diagonal), d.f., and P values (above the diagonal) for paired Shannon diversity index comparisons between sites (according to Magurran 1988).

Sites / Index		HTB	CPH	MOR	PNP
S		7	7	5	7
N		389	424	320	481
α logseries		1.21	1.19	0.84	1.16
Simpson $1/\lambda$		2.86	2.11	1.58	2.88
Shannon H'		1.42	1.06	0.85	1.33
Shannon E		0.73	0.55	0.53	0.68
Variance H'		0.0018	0.0019	0.0023	0.0014
				d.f.; P	
	HTB	*	813; <0.001	674; <0.001	828; >0.1
t	CPH	5.87	*	706; <0.01	863; <0.001
	MOR	8.92	3.28	*	664; <0.001
	PNP	1.58	4.65	7.9	*

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Table 4.8a. Spearman rank correlation coefficients (r_s) (values for each month (3) at each site (4), *i.e.* n=12) for site characteristics (1 to 7 as in Table 4.1), Shannon's index (H'), and larval density in the galls (n/g). Correlation coefficients (r_s) given in the top line (*e.g.* [1]) and probability values (P<) below (*e.g.* [2]). Figures in bold were calculated from a single value for each site, *i.e.* n=4; rain. = rainfall, resd. = resource density, dist. = physical disturbance, vegst. = vegetation structural diversity, size = patch size, isol. = patch isolation.

a. Character	1a	1b	2	3	4	5	6	7
1a. smog	*							
1b. SO^2	[1].97 [2].00	*						
2. rain.	-.06 .83	.03 .91	*					
3. resd.	.14 .63	.17 .57	-.36 .23	*				
4. dist.	**-.33** **.56**	**-.33** **.56**	**.63** **.27**	**-.95** **.10**	*			
5. vegst.	**.50** **.39**	**.50** **.39**	**-.95** **.10**	**.95** **.10**	**-.83** **.15**	*		
6. size	**-1.0** **.00**	**-1.0** **.00**	**.63** **.27**	**-.32** **.58**	**.33** **.56**	**-.50** **.39**	*	
7. isol.	**1.0** **.00**	**1.0** **.00**	**-.63** **.27**	**.32** **.58**	**-.33** **.56**	**.50** **.39**	**-1.0** **.00**	*
H'	-.59 .05	-.57 .06	-.27 .37	.53 .08	**-.32** **.58**	**-.11** **.86**	**.74** **.20**	**-.74** **.20**
n/g	-.22 .46	-.06 .83	.80 .01	-.22 .46	**.32** **.58**	**-.63** **.27**	**.94** **.10**	**-.74** **.10**

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Table 4.8b. Spearman rank correlation coefficients (r_s) (values for each month (3) at each site (4), *i.e.* n=12) for moth species (1 to 8 as in text), Shannon's index (H'), and larval density in the galls (n/g). Correlation coefficients (r_s) given in the top line (*e.g.* [1]) and probability values (P<) below (*e.g.* [2]); C.v., *Cydia* (*Cydia*) *victrix*; A.p., *Ascalenia pulverata*; A.g., *Anarsia gravata*; C.s., *Characoma submediana*; E.v., *Euzophera* sp. nr. *verrucicola*; PH, Phycitinae sp.; E.b., *Eublemma brachygonia*; C.p., *Cryptophlebia peltastica*.

b. Species	1	2	3	4	5	6	7	8
1.C.v.	*							
2.A.p.	[1].46 [2].13	*						
3.A.g.	-.15 .61	-.39 .19	*					
4.C.s.	-.30 .31	-.33 .27	.59 .05	*				
5.E.v.	-.61 .04	-.13 .67	.37 .22	.68 .02	*			
6.PH	-.41 .17	.02 .93	.51 .08	.17 .59	.37 .22	*		
7.E.b.	-.26 .39	-.21 .48	.44 .15	.66 .03	.30 .32	.00 1.0	*	
8.C.p.	-.13 .65	-.38 .20	.23 .44	.40 .18	-.44 .14	-.31 .31	.04 .91	*
H'	-.48 .12	-.02 .95	.54 .07	.75 .01	.91 .00	.57 .06	.29 .33	.34 .25
n/g	.64 .04	.48 .11	-.08 .78	-.00 .99	-.22 .47	-.20 .51	.09 .76	-.12 .68

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DISCUSSION

This study indicates that the moth community in *R. macowaniana* galls is useful for monitoring local habitat changes in urban areas. Not only were the galls relatively simple to sample, but eight moth species regularly occupied the galls, usually with seven species present at each site. The sole exception was MOR where only five species were recorded. This site was, however, severely disturbed by fire shortly after the initiation of sampling. Because resources often limit insect populations (Beaver 1977; Dempster 1983; Dempster & Pollard 1981), high disturbance may cause high insect mortalities through dramatic reduction of resource availability, and this was probably the case at MOR. Excessive larval density per unit gall mass at the site supports this contention. It seems likely that without the effects of fire, larval density and moth diversity would have been entirely different.

Although disturbance obviously played a major role in influencing larval density at MOR, rainfall and site size and isolation were most strongly correlated with the differences in larval density between sites. Because *R. macowaniana* galls are an ephemeral resource augmented by rainfall (high humidity facilitates germination of the rust-fungus spores (Alexopoulos & Mims 1979)), and because gall density and larval density appear to be inversely related (Table 4.3), the influence of between-site differences in rainfall is not surprising, although the high disturbance at MOR may have enhanced the strength of the relationship. The strong relationship between site size and isolation, and larval density, although not significant (possibly as a result of small sample size), is consistent with habitat fragmentation theory (Dempster 1991; Fahrig & Merriam 1985; Wilcox & Murphy 1985), *i.e.* a decrease in abundance and diversity resulting from habitat loss and insularization, and serves to illustrate the utility of the moth community for demonstrating the effects of increasing urbanization (see also Wilcox & Murphy 1985).

The significant inverse relationship between moth diversity and smog and SO_2 levels shows that the *R. macowaniana*-gall moth community may be potentially useful for monitoring air pollution. This study therefore also supports Sheehan's (1984a) contention that toxic pollutants usually bring about a reduction in diversity. At CPH, the significantly lower diversity may have been due to the direct effects of SO_2 on adult moths (see *e.g.* Kroupa *et al.* 1990), or due to the indirect effects of acid rain on soil and plant tissue pH (Sheehan 1984b). Although the relationships between moth diversity, and air pollution and resource density were significant, the correlation coefficients were relatively low, and this emphasizes the multiplicity of factors determining the moth diversity in a particular habitat.

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Community properties such as evenness, overall diversity and larval density not only differed between sites, but differed in accordance with the habitat quality of each site. In addition, the two sites on either end of the east-west spectrum (PNP and HTB), both with better habitat qualities, were more similar to each other than to the sites closest to them (MOR and CPH respectively), which had poorer habitat qualities. Between-site differences in species richness and dominance were insignificant in this study, however, and, contrary to similar studies (Winner *et al.* 1980), are therefore not considered useful for monitoring environmental quality. Despite the utility of overall diversity and larval density, it should be noted that these properties were markedly influenced by just three species. The relative abundance of *Cydia (Cydia) victrix* was significantly correlated with larval density, and those of *Characoma submediana* and *E.* sp. nr. *verrucicola* with overall diversity. Although the remaining species obviously also contributed to these community properties, the high r_s of *C. (C.) victrix*, and *C. submediana* and *E.* sp. nr. *verrucicola* with larval density and diversity, respectively, indicate that these species may be important 'key indicators' for the system (see Chapter 6 for further discussion).

In conclusion, despite small sample sizes (i.e. n=12 and n=4), moth community properties, *i.e.* 'key measures' provided clear estimates of environmental quality, although three "key indicator" species may also be useful. Unlike other studies of the effects of changes in environmental quality on faunal communities, which usually have a marked temporal component, this study relied on a spatial 'snapshot' technique (see Diamond 1986). This approach may explain why rare species were too inconsistently present to make them useful indicators, and why changes in numerical dominance were also of little utility (see also Chapter 6).

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REFERENCES

Alexopoulus, C.J. & Mims, C.W. 1979. *Introductory Mycology*. Third edition. John Wiley & Sons, New York.

Anneke, D.P. & Moran, V.C. 1982. *Insects and Mites of Cultivated Plants in South Africa*. Butterworths, Durban.

Beaver, R.A. 1977. Non-equilibrium 'island' communities: Diptera breeding in dead snails. *Journal of Animal Ecology* **46**, 783-98.

Berkman, H.E., Rabeni, C.F. & Boyle, T.P. 1986. Biomonitors of stream quality in agricultural areas: fish versus invertebrates. *Environmental Management* **10**, 413-19.

Chessman, B.C. 1995. Rapid assessment of rivers using macroinvertebrates: a procedure based on habitat-specific sampling, family level identification and a biotic index. *Australian Journal of Ecology* **20**, 122-129.

Clark, T. 1991. The dragonfly (Odonata) fauna as indicators of water characteristics in the rivers of the Kruger National Park. In *Proceedings of the Eighth Congress of the Entomological Society of Southern Africa*. Bloemfontein, p. 134.

Dempster, J.P. 1983. The natural control of populations of butterflies and moths. *Biological Review* **58**, 461-481.

Dempster, J.P. 1991. Fragmentation, isolation and mobility of insect populations. In Collins, N.M. & Thomas, J.A. (Eds). *The Conservation of Insects and their Habitats*. Academic Press, London, pp. 143-153.

Dempster, J.P. & Pollard, E. 1981. Fluctuations in resource availability and insect populations. *Oecologia* **50**, 412-416.

den Boer, P.J. 1990. The survival value of dispersal in terrestrial arthropods. *Biological Conservation* **54**, 175-192.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. In Diamond, J. & Case, T.J. (Eds). *Community Ecology*. Harper and Row, New York, pp. 3-22.

Erhardt, A. & Thomas, J.A. 1991. Lepidoptera as indicators of change in the semi-natural grasslands of lowland and upland Europe. In Collins, N.M. and Thomas, J.A. (Eds). *The Conservation of Insects and their Habitats*. Academic Press, London, pp. 213-236.

Fahrig, L. & Merriam, G. 1985. Habitat patch connectivity and population survival. *Ecology* **66**, 1762-1768.

Hellawell, J. M. 1991. Development of a rationale for monitoring. In Goldsmith, F.B. (Ed.). *Monitoring for Conservation and Ecology*. Chapman & Hall, London, pp. 1-14.

Holloway, J.D. 1980. Insect surveys - an approach to environmental monitoring. In *Atti XII Congr. Naz. Ital. Entomol.*, Roma, pp. 239-261.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**, 203-217.

Kremen, C, Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F. & Sanjayan, M.A. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**, 796-808.

Kroupa, M., Spitzer, K. & Novak, I. 1990. The heavy metal content in melanic and typical forms of *Biston betularia* (Lepidoptera, Geometridae) and its bioindicator significance. *Acta Entomologica Bohemoslovaca* **87**, 249-52.

Lenhard, S.C. & Witter, J.A. 1977. Insects as biological indicators of environmental change. *Bulletin of the Entomological Society of America* **23**, 191-192.

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Magurran, A.E. 1988. *Ecological Diversity and Its Measurement*. Croom Helm, London.

New, T.R., Pyle, R.M., Thomas, J.A. Thomas, C.D. & Hammond, P.C. 1995. Butterfly conservation management. *Annual Review of Entomology* **40**, 57-83.

Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4**, 355-364.

Pearson, D.L. & Cassola, F. 1992. World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology* **6**, 376-391.

Pollard, E. 1991. Monitoring butterfly numbers. In F. B. Goldsmith (Ed.). *Monitoring for Conservation and Ecology*. Chapman & Hall, London, pp. 87-111.

Pressey, R.L. & Nicholls, A.O. 1991. Scores and score classes for evaluation criteria: a comparison based on the cost of reserving all natural features. *Biological Conservation* **56**, 281-294.

Samways, M.J. 1989. Insect conservation and landscape ecology: a case-history of bush crickets (Tettigoniidae) in Southern France. *Environmental Conservation* **16**, 217-26.

Samways, M.J. 1994. *Insect Conservation Biology*. Chapman & Hall, London.

Sheehan, P.J. 1984a. Effects on community and ecosystem structure and dynamics. In Sheehan, P.J., Miller, D.R., Butler, G.C. & Bourdeau, P. (Eds). *Effects of Pollutants at the Ecosystem Level*. John Wiley and Sons, New York, pp. 51-100.

Sheehan, P.J. 1984b. Functional changes in the ecosystem. In Sheehan, P.J., Miller, D.R., Butler, G.C. & Bourdeau, P. (Eds). *Effects of Pollutants at the Ecosystem Level*. John Wiley and Sons, New York, pp. 101-146.

Swartz, P.P. 1982. 'n Numeriese-taksonomiese evaluering van die takson *Acacia karroo* Hayne in Suidelike Afrika. MSc thesis, University of Pretoria, Pretoria.

Thomas, J.A. 1984. The conservation of butterflies in temperate countries: past efforts and lessons for the future. In Vane-Wright, R.I. & Ackery, P.R. (Eds). *The Biology of Butterflies*. Academic Press, London, pp. 333-335.

Usher, M.B. 1986. Wildlife conservation evaluation: attributes, criteria and values. In Usher, M.B. (Ed.). *Wildlife Conservation Evaluation*. Chapman & Hall, London, 3-44.

Wilcox, B.A. & Murphy, D.D. 1985. Conservation strategy: the effects of fragmentation on extinction. *The American Naturalist* **125**, 879-887.

Williams, K.A., Green, D.W.J., Pascoe, D. & Gower, D.E. 1986. The acute toxicity of Cd to different larval stages of *Chironomus riparius* (Diptera: Chironomidae) and its ecological significance for pollution regulation. *Oecologia* **70**, 362-366.

Winner, R.W., Boesel, M.W. & Farrell, M.P. 1980. Insect community structure as an index of heavy-metal pollution in lotic ecosystems. *Canadian Journal of Fisheries and Aquatic Science* **37**, 647-55.

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CHAPTER 5

A regional comparison of the diversity and structure of the Lepidoptera community

Climate is a major determinant of ecosystem functioning at chemical, physical and biotic levels, and changes in the patterns of global climate, therefore, have major implications for the structure and functioning of ecosystems (Field *et al.* 1992). Global climate changes are presently predicted to be occurring at a rate far higher than climate changes of the past, and general circulation models (GCM's) predict a global increase in mean temperature of between 1.5°C to 4.5°C in the next century (Schneider 1992). Changes in rainfall quantity, rainfall seasonality and variability are also predicted (Schneider 1992). In addition, although predictions of the frequency and magnitude of severe weather events (*e.g.* droughts and floods, sporadic temperature extremes) are particularly uncertain, these are likely to have the most serious short-term consequences on ecosystems (Dennis & Shreeve 1991; Joubert 1994). A further problem associated with climate change predictions, and attempts to determine possible ecosystem responses, are that GCM's are large scale models that cannot provide credible information at regional, subregional or smaller scales, *i.e.* scales at which local ecosystems function (Schneider 1993; Root & Schneider 1993). This makes it almost impossible to predict the responses of local communities, populations and individuals to short or long-term changes in climate. Some attempt to do this, however, has to be made as the viability of natural resources and regional agricultural productivity are dependent on our being able, at least to some extent, to foresee and plan for future climate scenarios (Kingsolver *et al.* 1993; Mooney & Chapin 1994; Sugden 1992).

Best estimates of predicted climate changes in Southern Africa include a fairly certain increase in mean annual temperature of between 4°C and 6°C with a doubling in atmospheric carbon dioxide concentration (Joubert 1994; Tyson 1993). Simulated changes for total rainfall are far less certain as GCM's demonstrate little agreement on possible changes, and the patterns of precipitation change for most of the region are patchy (Joubert 1994). However, a 10% to 15% decrease in annual rainfall is expected for the summer rainfall regions (mostly the eastern and inland central parts of South Africa) with the onset of the rainy season beginning earlier (B.C. Hewitson, personal communication). A shorter rainfall season is expected for the winter rainfall regions (western Cape region of South Africa), with a mid-

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winter increase in rainfall (B.C. Hewitson, personal communication). Initial indications are that there may be a year-round increase in rainfall in the comparatively aseasonal regions of the south-eastern Cape (B.C. Hewitson, personal communication). In spite of the caution accompanying these predictions of future regional climates, there is no doubt that changes are occurring and that it is imperative that we attempt to predict the responses of biotic communities to these changes (Kingsolver *et al.* 1993).

Because plant-insect interactions are one of the dominant interaction types in terrestrial ecosystems (Strong *et al.* 1984), the impact of climate change on insect herbivores and the nature of their interaction with their host plants deserve particular attention. Insect herbivores consume large quantities of plant material in terrestrial ecosystems and have the potential to modify ecosystem structure and function (Carpenter *et al.* 1993; Naeem *et al.* 1994; Pitelka 1994). In addition, insect herbivores are important crop pests world wide and climate change is likely to affect insect pest complexes, as well as the extent of their damage to crop plants (Cammel & Knight 1992; Wolfe & Erickson 1993).

Temperature and moisture availability are two of the most important abiotic factors affecting the distribution and abundance of organisms (Walter & Breckle 1985) and their effects are manifest at the biotic ecosystem level in a number of ways, *i.e.* directly on the physiology of individual organisms, mediated through the organisms resource base, and on the interactions between individuals and between species (Field *et al.* 1992; Kingsolver 1989; Wolda 1988; Carpenter *et al.* 1993). Increases in temperature, in the presence of an adequate moisture regime, are likely to result in, for example, the expansion of the geographic ranges of many insects, increased population growth rates, increased number of annual generations, extended length of the developmental season, and changing synchrony in insect - host plant relationships (Gates 1993). Drier climatic conditions will result in decreased fecundity, and higher mortality of organisms as weather conditions begin to fall beyond the physiological tolerances of the species (Gates 1993). The carbon to nitrogen ratios of plants are also altered under higher CO_2 levels and in many plants this ratio increases, thereby lowering the nutritional quality of plant tissue for the majority of herbivorous insects (Fajer *et al.* 1992; Lincoln *et al.* 1993). Consequently insect growth rate may be retarded, the period of exposure to predation and parasitism extended, and life-cycle asynchrony with host-plant phenology and optimal seasonal developmental conditions, may occur. In combination these resource-based, physiological and interactive effects are liable to alter species distributions

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and population abundances, and the structure of, and interactions within, herbivore insect communities (Kingsolver 1989).

Changes in individual organisms and populations affect interactions between and within trophic levels that eventually determine the functioning, productivity and integrity of communities and ecosystems (Cammel & Knight 1992; Carpenter *et al.* 1993). A fairly extensive knowledge base exists on the responses of individual organisms and populations to temperature, moisture and host-plant quality (Cammel & Knight 1992). However, the responses of communities and ecosystems is less well understood and documented (Bazzaz 1990; Pitelka 1994; Sugden 1992). In addition, the responses of individual organisms may not be good predictors of the responses of communities (Bazzaz 1990). It is clear, therefore, that although studies on the effects of climate change on communities are essential, the inadequacy of GCM resolutions at small scales poses considerable problems. One way to address these problems is to conduct regional, large-scale, comparative studies between the structural parameters of matched communities across present climate gradients. Information from such comparative studies can then be used to predict the types of community changes that may occur under a shift in climate regime, *e.g.* from colder to warmer, wetter to drier, aseasonal to more seasonal conditions, and *vice versa* (Harrison 1993; Holloway 1990).

Community structure is generally described and quantified by one or more measures of the diversity of the community. Measures of diversity include species richness, the evenness of the species relative abundance distributions, and density (absolute abundance or number of individuals or biomass per unit habitat). These parameters are often combined, for greater comparative ease, into one of numerous possible diversity indices, particularly when communities are being compared over time or across a spatial gradient (Magurran 1988). An additional feature important to community structure, and not included in diversity indices, is the species composition of the community. Numerical classification techniques and multivariate analyses of communities, however, provide comparisons between communities that incorporate both species composition and diversity and provide measures of similarity between communities over time or across spatial gradients (Clarke & Warwick 1994; Eyre *et al.* 1986; Gauch 1982). These techniques are, thus, particularly useful for examining the relationships between communities and environmental gradients when the intention is to select indicator assemblages for monitoring the impact of climate change on terrestrial ecosystems (Kremen 1992).

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The community of Lepidoptera that inhabit fungus galls on *Acacia karroo* Hayne lends itself to a study of this nature because *A. karroo*, *Ravenelia macowaniana* Pazschke and the resident Lepidoptera community are widely distributed in South Africa and represented across a gradient of climatic conditions (see Chapter 1). The aim of this study was, therefore, to determine the structure of Lepidoptera communities from different localities in South Africa, using diversity parameters and multivariate ordination techniques, and to relate the differences in community structure between localities to climate data. The final objective was to predict possible shifts in community structure under the climate changes that have been forecast for southern Africa.

STUDY SITES and METHODS

Galls were sampled from nine localities in four regions, *i.e.* Boekenhoutskloof, Hartebeespoort and Pienaarspoort in the Gauteng Province, Parys and Bloemfontein in the Orange Free State, Richards Bay in Kwazulu-Natal and Grahamstown, Sundays River Valley and Aston Bay in the Eastern Cape (see Table 1.1, Fig. 1.2, Chapter 1). (Data from Moreleta Nature Reserve and Proclamation Hill (Gauteng Region) were not included in this comparison because of the highly disturbed nature of these localities (see Chapter 4)). Of the former localities, five were classified as inland localities (> 100km from sea) and four were classified as coastal (< 100 km from the sea). The months during which these localities were sampled are listed in Table 1.2, Chapter 1. Six of the nine localities were sampled in more than one month (temporally replicated) (*i.e.* Boekenhoutskloof, Hartebeespoort, Pienaarspoort, Parys, Bloemfontein and Aston Bay), whereas the remaining three localities were sampled only once, during the 1994 season (Table 1.2, Chapter 1). Of the former localities, only Aston Bay was sampled during winter as it was only at this locality that larval activity in the galls continued during winter.

Climatic conditions at each locality were quantified using, 1. percentage coefficient of variation (% CV) in mean monthly maximum temperatures (°C) (1984 to 1994), 2. % CV in mean monthly minimum temperatures (°C) (1984 to 1994), 3. altitude (metres above sea level), 4. long-term mean annual precipitation (mm) and, 5. % CV in long-term median monthly precipitation (mm). This information was obtained from the Computing Centre for Water Research (CCWR), University of Natal, and coefficients of variation were calculated from the raw data provided.

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Gall sampling, measurement and description, larval extraction from the galls, identification and preservation were performed as outlined in Chapters 1 and 2.

Community analysis

Percentage relative abundances of species in the community were calculated for each sampling month from each locality. Percentage relative abundances of species in the community were also calculated for each locality with the absolute totals for each month (temporal replicates) combined. The mean number of individuals and species per gall were calculated for each locality (sampling months pooled) and each sampling month separately. Larval density was determined by calculating the number of individual larvae per gram of gall tissue. Differences in these means between localities (sampling months pooled) and between each sampling month were determined using Kruskal-Wallis one-way analyses by ranks and Dunn's distribution free multiple comparison tests (Siegel 1956; Zar 1984). The relationship between gall mass (see Chapter 1) and the number of individuals per gall was tested with Spearman rank correlation coefficients for each locality (sampling months pooled). This non-parametric method was used because the number of individuals per gall and gall mass data for a number of localities were not normally distributed.

The number of species in the community (S), evenness of the community (E) (Pielou's measure; Pielou 1975) and Shannon's diversity index (H') (chosen because it is one of the most widely used indices) were calculated for each locality and for each monthly sample (Magurran 1988). The Shannon diversity index for each locality was calculated with the inclusion of data only from the summer sampling months (*i.e.* January, February & March). Significant differences between the Shannon diversity indices for each locality were determined by calculating the variance of H', and 't', according to Magurran (1988, pp. 35-36). A linear regression of evenness on species richness was done on logarithmic transformed data.

The species richness, mean number of individuals, density and mean number of species per gall of the nine localities, were chosen to represent 'non-index measures' of community diversity. These measures were used in addition to Shannon's diversity index because of the differences between the enormous range of diversity indices available as a result of the relative weighting given to richness and evenness (Magurran 1988). In addition, although it is common practise to measure communities using a diversity index, the

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components of diversity, mentioned above, are usually of greater interest. Each locality was, thus, ranked from lowest (rank 1) to highest (rank 9) for each of the non-index diversity measures. The ranks for each measure for each locality were then summed to give a total rank, non-index diversity measure for each locality.

Multivariate community analyses were performed using PRIMER v4.0 1994 (Plymouth Routines in Multivariate Ecological Research), developed by the Plymouth Marine Laboratory, U.K.

The absolute abundances of species from each locality and sampling date were first standardized to percentage relative abundance because of unequal gall sample sizes between localities. A double square-root transformation was used to give an equal weighting to common and rare species (Clarke and Warwick 1994). The similarity matrices were calculated using Bray-Curtis coefficients (Bray and Curtis 1957). This similarity coefficient is considered to be one of the most robust coefficients (*e.g.* insensitive to joint species absences) and is widely used in ecology (Faith *et al.* 1987). From this similarity matrix a cluster analysis, using hierarchical agglomerative clustering and group-average linking, was performed and a dendrogram produced (Clarke & Warwick 1994). Non-metric multidimensional scaling (MDS) (Kruskal and Wish 1978, Clarke 1993) was used to map the sample (each locality at each sampling date) inter-relationships in an ordination of specified number of dimensions.[1] The dimensionality (*i.e.* 2 or 3 dimensions) of the MDS ordinations plotted were chosen according to the acceptability of their associated stress values (stress $<$ 0.1 gives a good ordination with little risk of misinterpretation, stress $<$ 0.2 still acceptable but not as reliable (Clarke 1993)).

The differences in community structure between winter and summer month samples, between January, February and March samples, between localities, between samples from each region (northern - Boekenhoutskloof, Hartebeespoort, Pienaarspoort; central - Parys,

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[1] For obtaining simple ordinations, MDS has a number of advantages over techniques such as principal co-ordinates analysis, reciprocal averaging and correspondence analysis and has been recommended as one of the best ordination techniques for ecological data because of it's flexibility and lack of assumptions (Field *et al.* 1982; Kenkel and Orloci 1986; Clarke 1993). The MDS similarity matrix is calculated using a measure most suited to the type of data to be analyzed (*e.g.* community data that frequently have many zero values and which therefore do not meet assumptions of normality) and a general monotonic transformation is then applied to sample distances. MDS also has good distance preserving properties because, unlike principal components based ordination methods, the 2-dimensional plot is not a projection of 3-dimensional data onto a 2-dimensional plane, but rather a separate minimization of stress (measure of distortion between ranked dissimilarities and corresponding distances on the plot) for each ordination of different dimensionality (Field *et al.* 1982).

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Bloemfontein; and southern localities - Grahamstown, Sundays River Valley, Aston Bay) and between coastal (< 100 km from the sea, *i.e.* Richards Bay, Grahamstown, Sundays River Valley, Aston Bay) and inland locality samples (> 100 km from the sea, *i.e.* Boekenhoutskloof, Hartebeespoort, Pienaarspoort, Parys, Bloemfontein) were tested using ANOSIM (analysis of similarity) on the similarity matrix of each sampling month and locality (Clarke & Green 1988).[2]

Linking of community data with climate variables

Of the five climatic variables, only mean annual precipitation required (logarithmic) transformation. All the variables were normalized to a common scale (for each climate variable the mean of that variable was subtracted across sites and each divided by the standard deviation) and a dissimilarity matrix of Euclidean distances was compiled (Clarke and Warwick 1994). Because the climate variables chosen were univariate and did not vary between replicates within a site, the temporal replicates of the community data for each locality were combined to give single species abundance values for each locality.

Matching of the species abundance patterns to climate variables was then done using PRIMER's BIOENV procedure (Clarke and Ainsworth 1993; Clarke and Warwick 1994) on the species matrix and climate matrices. In this procedure the among-locality species matrix is constructed only once, whereas the climate matrix is computed for every combination of climate variables, singly and in groups of two, three and four (Clarke and Ainsworth 1993).[3] Weighted Spearman rank correlation coefficients (p_w) (Spearman rank correlation coefficient down-weighted to be less sensitive to distances and more sensitive to similarities between the two matrices) were calculated for every match between the species matrix and numerous climate matrices (Clarke and Ainsworth 1993). The best explanatory climate variable, or set

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[2] This is a non-parametric permutation procedure applied to the rank similarity matrix underlying the ordination of samples (Clarke & Green 1988). The Global R in ANOSIM is a test statistic indicating the degree of discrimination between groups or clusters and falls between 0 and 1 (R = 1 if all samples within a cluster are more similar to each other than any samples between clusters, and R approximates 0 when similarities between and within samples are similar on average) (Clarke & Green 1988). If R is significantly different from zero then there are significant differences between clusters within the similarity matrix (Clarke & Green 1988).

[3] The advantages associated with this method of constructing separate biotic and environmental matrices and only linking them by 'pattern matching' are that different best-suited, among-locality similarity measures (*i.e.* Bray-Curtis and Euclidean distance) can be used, and that there are few constraints on the nature of the relationship between the species and the climate variables (*e.g.* no assumptions of linearity between the biotic and abiotic variables) (Clarke and Ainsworth 1993).

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of variables, was then determined (Clarke and Ainsworth 1993). An MDS ordination was done on the condensed species matrix and a Principal Component Analysis (PCA) on the best correlated climate variables. These climate variables were then each superimposed, as symbols of increasing size with increasing value of the variable, onto the species MDS ordination to illustrate the correlation between the climate variables and the Lepidoptera communities from different localities (Clarke & Warrick 1994).

RESULTS

Climate variables

The localities with the highest annual minimum and maximum temperature variation and highest altitude were Bloemfontein and Parys (Table 5.1). Aston Bay and Richards Bay had the lowest temperature variation and Sundays River Valley, Richards Bay and Aston Bay the lowest altitude (Table 5.1). Total annual rainfall was lowest at Sundays River Valley, Bloemfontein and Parys and highest at Richards Bay and Aston Bay. Annual variation in rainfall was highest at Boekenhoutskloof, Hartebeespoort and Pienaarspoort and lowest at Aston Bay, Sundays River Valley and Richards Bay (Table 5.1). The inland localities were therefore the most seasonal with regard to temperature and rainfall variation, whereas the coastal localities were comparatively aseasonal. The central localities had the highest temperature variation and altitude, followed by the northern and then southern localities. The northern localities, however, had the highest rainfall variation and the southern localities the lowest.

Abundance and diversity patterns

The combined percentage relative abundances of species at the 11 localities are presented in Figs 5.1 a - i, and the relative abundances of species in different months and years at each locality are presented in Tables 5.2.1 - 5.2.5. Differences in dominance, evenness and species composition of the nine localities are apparent in the relative abundance distributions (Figs 5.1 a - i). Within season fluctuations in the percentage composition of species in the community, *i.e.* changes in the relative abundances of species between January, February and March also occurred. However, these were not consistent between years or between localities (Tables 5.2.1 to 5.2.5). Sundays River Valley was unique with respect to the fact that the two pest species in the community, *Cryptophlebia peltastica* and *Lobesia*

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stericta, were second and third most abundant. Larval activity in the galls was restricted to late December through to March at Boekenhoutskloof, Hartebeespoort, Pienaarspoort, Parys and Bloemfontein. Aston Bay was the only temporally replicated locality where the community was present in galls as early as November and where Lepidoptera larvae were still active after March (Table 5.2.4). Larval activity was often shorter than the average four month period and the 1994 season at Parys, for example, extended only from early January until late February (Table 5.2.3). By March of 1994 all galls at Parys were dead and no larvae were present. The seasonality of larval activity in the galls is therefore variable between localities and within localities between years.

Table 5.1. Climatic conditions at each locality, *i.e.* percentage coefficient of variation (% CV) in mean monthly maximum temperatures (°C) [T max.], % CV in mean monthly minimum temperatures (°C) [T min.], altitude (metres above sea level) [Alt.], long-term mean annual precipitation (mm) [T Rain] and, % CV in long term median monthly precipitation (mm) [Rain].

Locality	T max. % C.V.	T min. % C.V.	Alt. m.a.s.l.	T Rain (mm)	Rain % C.V.
Boekenhoutskloof	12.14	52.37	1220	661	89.25
Hartebeespoort	11.79	40.44	1170	671	89.03
Pienaarspoort	13.37	48.74	1360	692	88.25
Parys	14.29	57.40	1430	595	84.07
Bloemfontein	18.81	69.61	1430	554	77.62
Richards Bay	9.11	14.11	79	1436	29.86
Grahamstown	10.67	20.83	645	673	34.13
Sundays River Valley	9.72	33.59	51	328	25.68
Aston Bay	8.18	14.66	152	907	18.56

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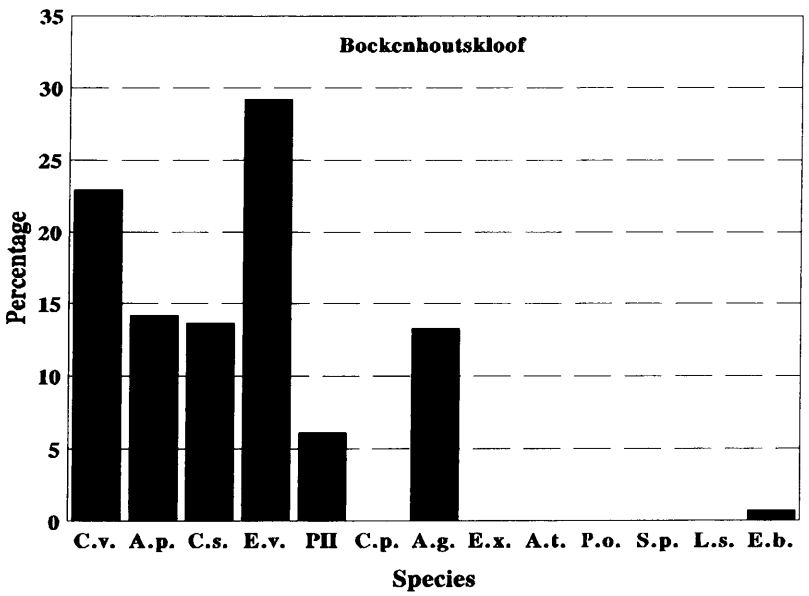
a.



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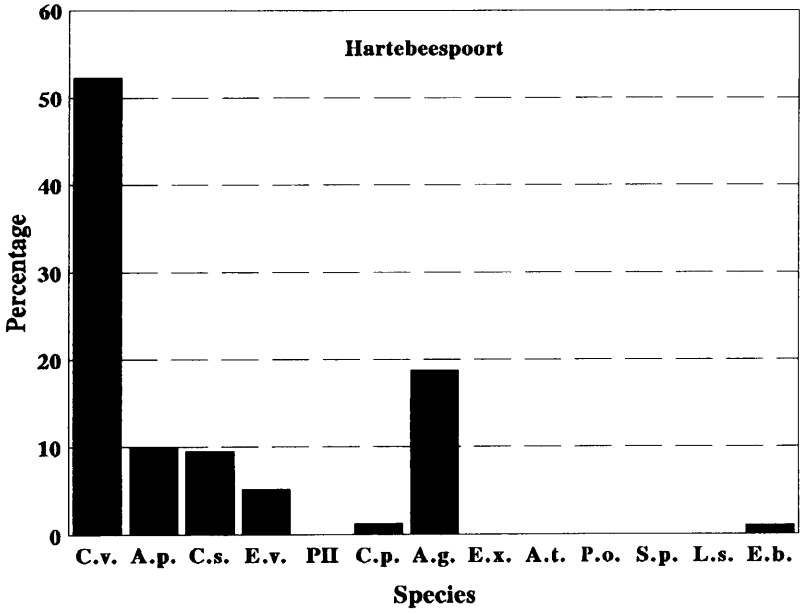

(Figure 5.1 a-b)

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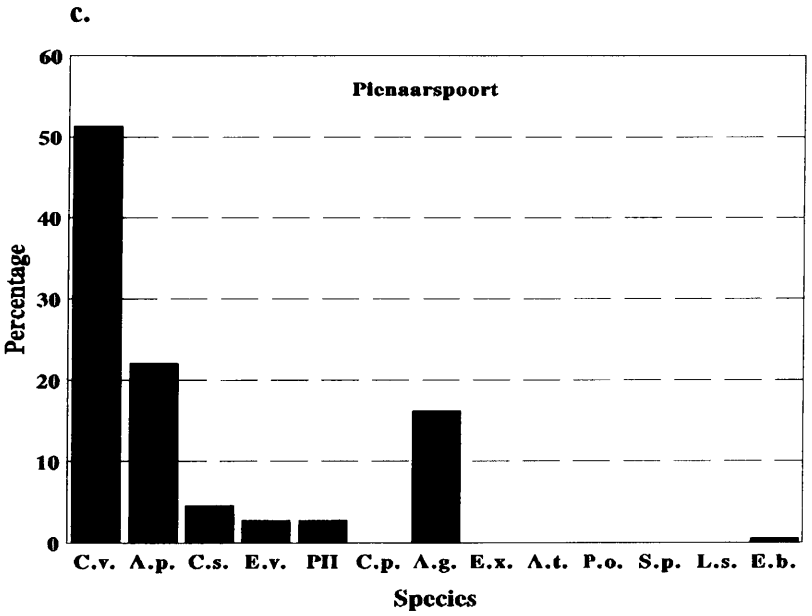

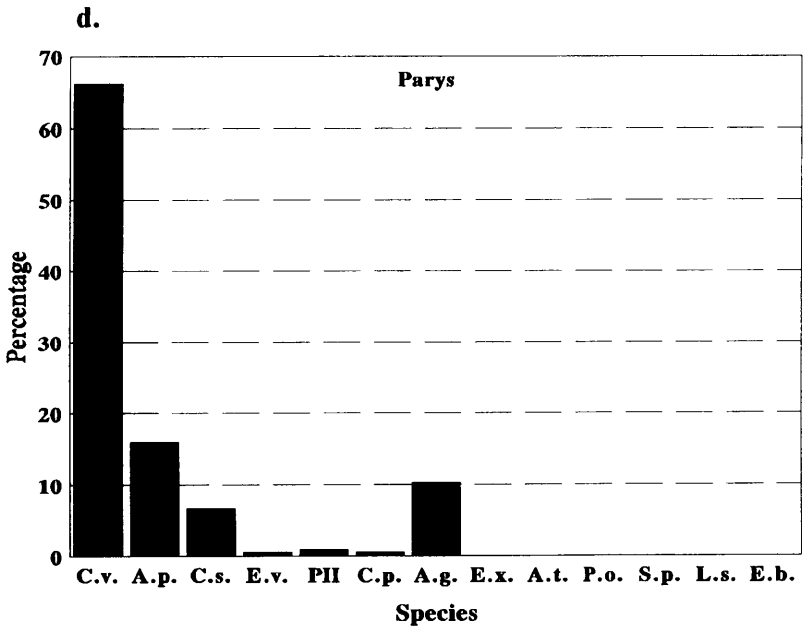

(Figure 5.1 c-d)

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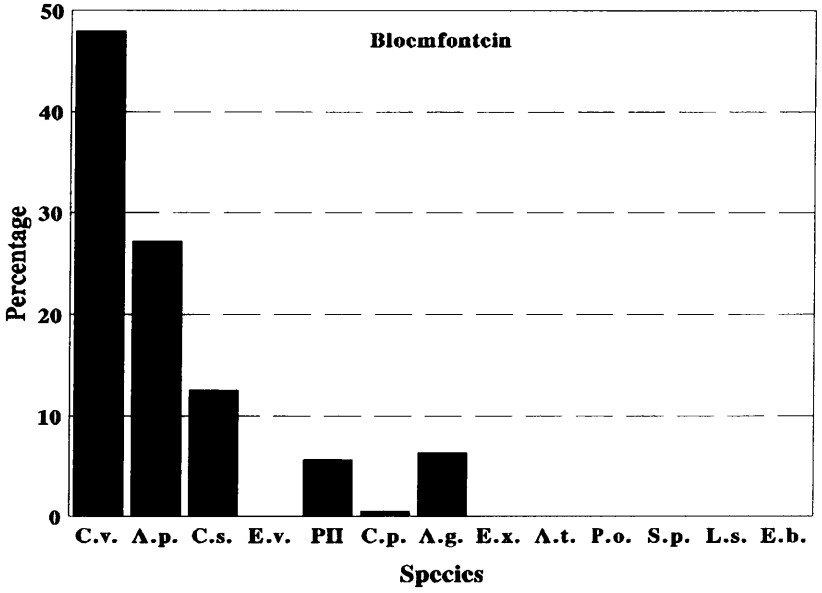
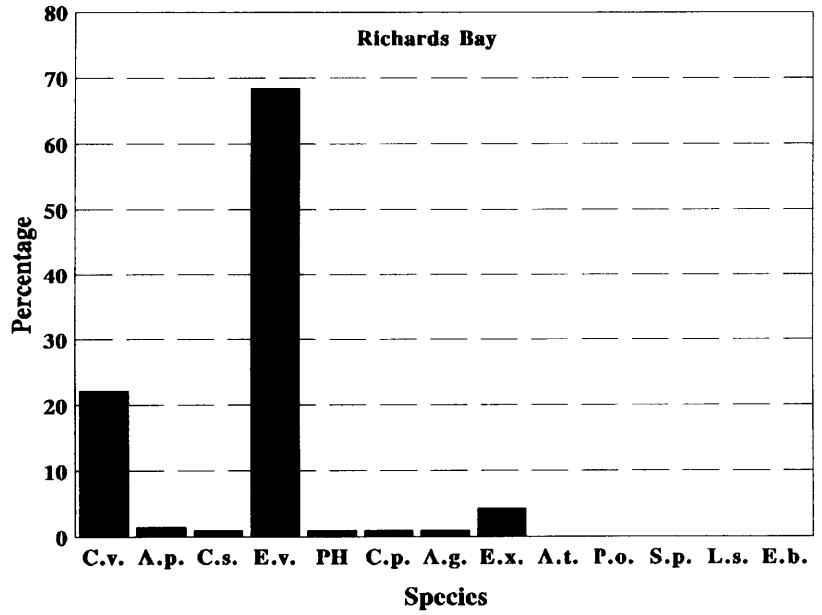
e.



f.



(Figure 5.1 e-f)

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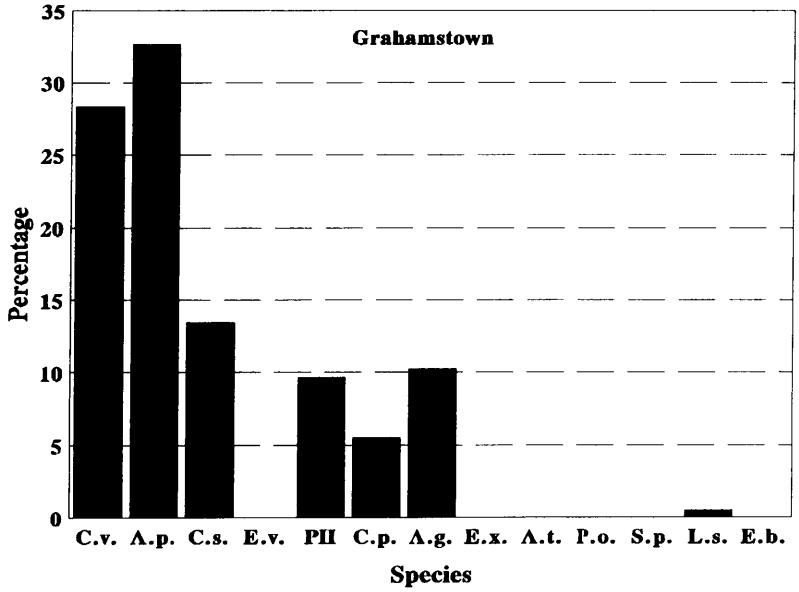
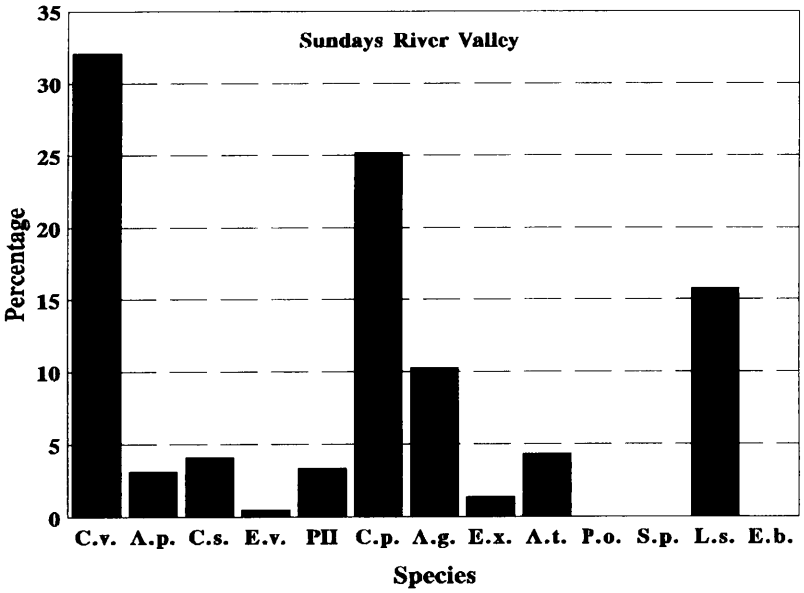
g.



h.



(Figure 5.1 g-h)

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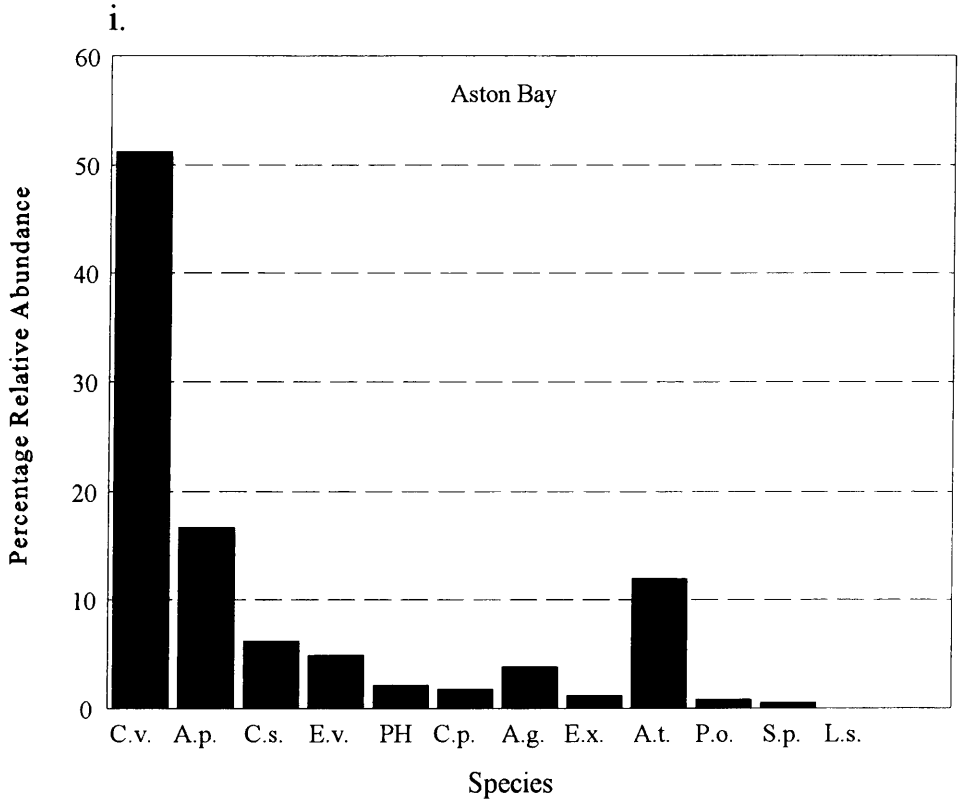

Fig. 5.1.a-i. Total relative abundances of species in the Lepidoptera communities from nine localities; C.v., *Cydia (Cydia) victrix*; A.P., *Ascalenia pulverata*; C.s., *Characoma submediana*; E.v., *Euzophera* sp.nr. *verrucicola*; PH, Phycitinae complex; C.p., *Cryptophlebia peltastica*; A.g., *Anarsia gravata*; E.x., *Encolpotis xanthoria*; A.t., *Anatrachyntis tripola*; P.o., *Phthoropoea oenochares*; S.p., *Schiffermuelleria pedicata*; L.s., *Lobesia stericta*; E.b., *Eublemma brachygonia*.

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Table 5.2.1. Percentage relative abundances of species; **C.v.**, *Cydia victrix*; **A.p.**, *Ascalenia pulverata*; **C.s.**, *Characoma submediana*; **E.v.** *Euzophera* sp.nr. *verrucicola*; **PH**, Phycitinae complex; **C.p.**, *Cryptophlebia peltastica*; **A.g.**, *Anarsia gravata*; **E.x.**, *Encolpotis xanthoria*; **A.t.**, *Anatrachyntis tripola*; **P.o.**, *Phthoropoea oenochares*; **S.p.**, *Schiffermuelleria pedicata*; **L.s.**, *Lobesia stericta*; **E.b.**, *Eublemma brachygonia*.

	Boekenhoutskloof			**Hartebeespoort**		
Species	92 Jan.	92 Feb.	92 Mar.	92 Jan.	92 Feb.	92 Mar.
C.v.	33.91	15.79	14.29	55.36	54.92	51.19
A.p.	16.96	13.88	9.24	21.43	6.22	3.57
C.s.	10.43	18.88	11.76	9.82	8.81	10.71
E.v.	17.83	29.19	51.26	3.57	0.52	17.86
PH	5.65	4.31	10.08	0	0	0
C.p.	0	0	0	0	0.52	4.76
A.g.	14.78	17.22	3.36	8.93	27.46	11.90
E.x.	0	0	0	0	0	0
A.t.	0	0	0	0	0	0
P.o.	0	0	0	0	0	0
S.p.	0	0	0	0	0	0
L.s.	0	0	0	0	0	0
E.b.	0.43	1.44	0	0.89	1.55	0

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Table 5.2.2. Percentage relative abundances of species; **C.v.**, *Cydia victrix*; **A.p.**, *Ascalenia pulverata*; **C.s.**, *Characoma submediana*; **E.v.** *Euzophera* sp.nr. *verrucicola*; **PH**, Phycitinae complex; **C.p.**, *Cryptophlebia peltastica*; **A.g.**, *Anarsia gravata*; **E.x.**, *Encolpotis xanthoria*; **A.t.**, *Anatrachyntis tripola*; **P.o.**, *Phthoropoea oenochares*; **S.p.**, *Schiffermuelleria pedicata*; **L.s.**, *Lobesia stericta*; **E.b.**, *Eublemma brachygonia*.

	Pienaarspoort			**Bloemfontein**			
Species	92 Jan.	92 Feb.	92 Mar.	92 Feb.	93 Jan.	93 Mar.	94Jan.
C.v.	62.44	42.37	47.50	69.97	43.15	5.88	45.03
A.p.	7.32	37.29	7.50	0	37.40	0	29.08
C.s.	6.37	3.39	7.50	14.76	11.39	32.35	12.27
E.v.	0	4.66	5.00	0	0	0	0
PH	1.46	1.27	17.50	3.56	3.23	58.82	7.48
C.p.	0	0	0	0	0.20	0	0.12
A.g.	23.41	10.17	15.00	11.7	4.64	2.94	6.01
E.x.	0	0	0	0	0	0	0
A.t.	0	0	0	0	0	0	0
P.o.	0	0	0	0	0	0	0
S.p.	0	0	0	0	0	0	0
L.s.	0	0	0	0	0	0	0
E.b.	0	0.85	0	0	0	0	0

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Table 5.2.3. Percentage relative abundances of species; **C.v.**, *Cydia victrix*; **A.p.**, *Ascalenia pulverata*; **C.s.**, *Characoma submediana*; **E.v.** *Euzophera* sp.nr. *verrucicola*; **PH**, Phycitinae complex; **C.p.**, *Cryptophlebia peltastica*; **A.g.**, *Anarsia gravata*; **E.x.**, *Encolpotis xanthoria*; **A.t.**, *Anatrachyntis tripola*; **P.o.**, *Phthoropoea oenochares*; **S.p.**, *Schiffermuelleria pedicata*; **L.s.**, *Lobesia stericta*; **E.b.**, *Eublemma brachygonia*.

	Parys					
Species	93 Jan.	93 Feb.a	93 Feb.b	93 Mar.	94 Jan.	94 Feb.
C.v.	18.47	52.27	49.31	97.89	87.64	75.76
A.p.	56.69	20.64	21.31	0	6.75	1.52
C.s.	3.82	9.28	15.78	2.11	0.16	0
E.v.	0.64	0	0	0	0	4.55
PH	2.55	0.19	0.69	0	0.41	0
C.p.	0	0	0.12	0	0	4.55
A.g.	17.83	17.61	12.79	0	5.02	13.64
E.x.	0	0	0	0	0	0
A.t.	0	0	0	0	0	0
P.o.	0	0	0	0	0	0
S.p.	0	0	0	0	0	0
L.s.	0	0	0	0	0	0
E.b.	0	0	0	0	0	0

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Table 5.2.4. Percentage relative abundances of species; **C.v.**, *Cydia victrix*; **A.p.**, *Ascalenia pulverata*; **C.s.**, *Characoma submediana*; **E.v.** *Euzophera* sp.nr. *verrucicola*; **PH**, Phycitinae complex; **C.p.**, *Cryptophlebia peltastica*; **A.g.**, *Anarsia gravata*; **E.x.**, *Encolpotis xanthoria*; **A.t.**, *Anatrachyntis tripola*; **P.o.**, *Phthoropoea oenochares*; **S.p.**, *Schiffermuelleria pedicata*; **L.s.**, *Lobesia stericta*; **E.b.**, *Eublemma brachygonia*.

	Aston Bay						
Species	91 Nov.	92 Feb.	93 Jan.	93 Mar.	93 May	94 Jan.	94 Feb.
C.v.	50.49	51.71	71.91	7.85	0	42.20	50.57
A.p.	14.39	28.73	9.14	0.29	0	36.35	19.06
C.s.	29.76	9.29	1.50	0.29	0	10.21	3.55
E.v.	0	2.08	5.90	11.63	0	2.87	10.34
PH	0	0.12	3.63	2.91	3.90	0.46	1.78
C.p.	0	5.26	0.82	1.45	0	1.72	2.75
A.g.	2.20	2.20	5.42	1.74	0.26	4.93	3.72
E.x.	0.49	0.61	1.60	0	0	1.26	1.94
A.t.	2.68	0	0.10	73.55	91.69	0	6.30
P.o.	0	0	0	0	4.16	0	0
S.p.	0	0	0	0.29	0	0	0
L.s.	0	0	0	0	0	0	0
E.b.	0	0	0	0	0	0	0

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Table 5.2.5. Percentage relative abundances of species; **C.v.**, *Cydia victrix*; **A.p.**, *Ascalenia pulverata*; **C.s.**, *Characoma submediana*; **E.v.** *Euzophera* sp.nr. *verrucicola*; **PH**, Phycitinae complex; **C.p.**, *Cryptophlebia peltastica*; **A.g.**, *Anarsia gravata*; **E.x.**, *Encolpotis xanthoria*; **A.t.**, *Anatrachyntis tripola*; **P.o.**, *Phthoropoea oenochares*; **S.p.**, *Schiffermuelleria pedicata*; **L.s.**, *Lobesia stericta*; **E.b.**, *Eublemma brachygonia*.

	Grahamstown	**Richards Bay**	**Sundays River Valley**
Species	94 Feb.	94 Feb.	94 Feb.
C.v.	28.35	22.17	32.09
A.p.	32.64	1.42	3.15
C.s.	13.42	0.94	4.13
E.v.	0	68.40	0.39
PH	9.68	0.94	3.35
C.p.	5.53	0.94	25.20
A.g.	10.24	0.94	10.24
E.x.	0	4.25	1.38
A.t.	0	0	4.33
P.o.	0	0	0
S.p.	0	0	0
L.s.	0.14	0	15.75
E.b.	0	0	0

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Regional diversity patterns

The highest mean number of individuals per gall occurred at Aston Bay and Grahamstown (Table 5.3) and density of individuals (number of larvae per gram of gall tissue) was highest at Grahamstown, Richards Bay and Aston Bay (Table 5.4). Although the number of individuals per gall was low at Hartebeespoort, larval density was comparatively high at this locality. At Boekenhoutskloof and Pienaarspoort both the number of larvae per gall and gall density were low (Tables 5.3 & 5.4). There was a significantly positive correlation between gall mass and the number of larvae in galls at all 9 localities (Table 5.5). The mean number of species per gall ranged between 1.72 and 2.64 and was highest at Grahamstown, Sundays River Valley and Aston Bay and lowest at Hartebeespoort, Richards Bay and Pienaarspoort (Table 5.6). Gall occupancy (in terms of individuals and species) was thus highest in communities at two of the southern localities (Aston Bay and Grahamstown) and lowest at the northern localities (Boekenhoutskloof, Hartebeespoort and Pienaarspoort).

Species richness was also highest at Aston Bay, Sundays River Valley and Richards Bay, and lowest at Bloemfontein (Table 5.7). The species richnesses of the coastal Lepidoptera communities were, therefore, mostly higher than the richness of inland communities. Five of the localities had the same species richness, *i.e.* seven species (Table 5.7). The evenness of the species relative abundance distributions was greatest at Boekenhoutskloof followed by Grahamstown, Sundays River Valley and Bloemfontein (Table 5.7). The evenness of communities at Richards Bay and Parys were low (Table 5.7). Species richness and evenness were, however, significantly correlated ($Y = -1.75X + 0.69$, d.f. = 28, $r = 0.57$, $P<0.001$) and evenness tended to increase with species richness.

The Shannon indices of diversity were highest at Sundays River Valley, Boekenhoutskloof and Grahamstown and lowest at Richards Bay and Parys (Table 5.7). The non-index based measures of diversity show that Aston Bay and Grahamstown rank highest (Table 5.8), whereas the diversity index measure (H') gives Sundays River Valley, Boekenhoutskloof and Grahamstown the highest diversity. Correspondingly Boekenhoutskloof, Hartebeespoort and Pienaarspoort have the lowest non-index diversity ranks (Table 5.8), whereas Parys and Richards Bay have the lowest diversity indices (Table 5.7). According to the non-index diversity measure, therefore, the southern and northern localities have the highest and lowest diversities respectively, whereas there is no such latitudinal trend in the H' index diversity of the localities.

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Table 5.3. Mean ± S.E. of the number of individual larvae per gall; H = 55.58, P<0.001; n = number of galls; different letters denote a significant difference of P < 0.05 between localities.

Localities	n	Individuals	
Aston Bay	658	8.19±0.44	a
Grahamstown	102	7.23±0.70	a
Parys	421	6.94±0.41	b
Bloemfontein	398	5.75±0.33	c
Sundays River Valley	92	5.56±0.62	c
Pienaarspoort	101	4.78±0.45	d
Richards Bay	101	4.49±0.37	e
Boekenhoutskloof	150	4.29±0.37	f
Hartebeespoort	110	3.59±0.29	f

Table 5.4. Mean ± S.E. of the number of larvae per 1.0 g of fresh gall tissue (density); H=176.44, P<0.001; n = number of galls; different letters denote a significant difference of P < 0.01 between localities.

Localities	n	Larval Density	
Grahamstown	94	2.60±0.28	a
Richards Bay	100	2.46±0.24	b
Aston Bay	661	2.16±0.15	cd
Hartebeespoort	107	1.99±0.33	e
Parys	423	1.72±0.10	f
Sundays River Valley	80	1.66±0.21	gd
Bloemfontein	397	1.12±0.07	h
Boekenhoutskloof	150	1.02±0.10	i
Pienaarspoort	100	0.62±0.03	j

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Table 5.5. Spearman rank correlation coefficients (r_s) of gall mass (g) and the number of larvae per gall for each locality; n = number of galls with larvae.

Localities	n	r_s	P<
Boekenhoutskloof	127	0.48	0.001
Hartebeespoort	98	0.45	0.001
Pienaarspoort	109	0.41	0.001
Parys	388	0.45	0.001
Bloemfontein	376	0.52	0.001
Richards Bay	100	0.24	0.02
Grahamstown	102	0.67	0.001
Sundays River Valley	81	0.52	0.001
Aston Bay	446	0.47	0.001

Table 5.6. Mean ± S.E. of the number of species per gall; H=42.72, P<0.001; n = number of galls; different letters denote a significant difference of P < 0.05.

Localities	n	Species	
Grahamstown	102	2.64±0.14	ab
Sundays River Valley	92	2.32±0.14	cd
Aston Bay	672	2.23±0.05	eb
Parys	356	2.09±0.05	f
Bloemfontein	399	2.05±0.05	gd
Boekenhoutskloof	151	1.97±0.10	hi
Pienaarspoort	101	1.87±0.10	j
Richards Bay	100	1.77±0.09	k
Hartebeespoort	111	1.72±0.07	li

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Table 5.7. Total species richness, evenness and diversity (H') of the Lepidoptera communities at each locality; H' values with no letters in common denote a significant difference between the pair of $P < 0.01$.

Locality	Richness (S)	Evenness (J')	Shannon (H')	
Sundays River Valley	10	0.79	1.81	a
Boekenhoutskloof	7	0.88	1.74	a
Grahamstown	7	0.83	1.62	ab
Aston Bay	11	0.65	1.41	bc
Pienaarspoort	7	0.68	1.29	c
Hartebeespoort	7	0.70	1.28	cd
Bloemfontein	6	0.73	1.28	cd
Parys	7	0.53	1.03	de
Richards Bay	8	0.46	0.96	e

Table 5.8. Ranks (1 - 9) for each locality of species richness (S), mean number of individuals, mean density and mean number of species per gall, and sum total of the ranks of each of these parameters.

Locality	S	No. Ind.	Density	No. Spp	Total
Aston Bay	9	9	7	7	32
Grahamstown	4	8	9	9	30
Sundays River Valley	8	5	4	8	25
Parys	4	7	5	6	22
Richards Bay	7	3	8	2	20
Bloemfontein	1	6	3	5	15
Pienaarspoort	4	4	1	3	12
Hartebeespoort	4	1	6	1	12
Boekenhoutskloof	4	2	2	4	12

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Seasonal diversity patterns

Within seasons the mean number of individuals per gall showed a tendency to peak in January and February and to drop towards the end of the gall growth season (late February to March) (Table 5.9). Larval density in most instances showed a similar trend, except that density appeared to reach a peak slightly later than number of individuals per gall (this may be attributed to the consistent decline in gall mass after the gall growth stage, Chapter 1) (Table 5.9). The number of species per gall was also, almost consistently, highest during mid-season (Table 5.9). Once again, however, these trends are clouded by interseasonal and interlocality variability in gall phenology (Chapter 1).

Within seasons at each locality species richness was lowest either early and or late in the season (January and March) and generally highest during mid-season (Table 5.10). Because of the interseasonal variation in gall phenology (see Chapter 1), however, early, mid- and late gall season do not always correspond to the months of January, February and March and this results in some distortion of the pattern. At Aston Bay, however, the old-gall inhabiting, winter community (May) had the lowest species richness of samples from that locality (Table 5.10). No patterns were apparent in the changes in evenness between sampling months within localities (Table 5.10). The species diversity of the Aston Bay winter community, however, was low, as were the diversities of most communities during March, *i.e.* late in the gall development season (Table 5.10). The highest within-month species diversities occurred at Boekenhoutskloof (1.68, January 1992) and Aston Bay (1.56, February 1994). Therefore both Shannon's diversity and the non-index diversity measures were highest mid-way through the gall development season.

Seasonal community patterns

The species relative abundance composition of the winter, old-gall inhabiting moth community was significantly different from the summer, live-gall inhabiting moth community (ANOSIM Global R = 0.992, P=0.034, permutations = 29 [all possible permutations]) (Fig. 5.2). Communities across all localities were also significantly different in March, compared to January and February (ANOSIM Global R = 0.117, P=0.033, permutations = 5000 [random sample from total possible number of permutations]) (Fig 5.3; Table 5.11). These results support the temporal trends in density and diversity observed by inspection (see previous section).

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Table 5.9. Mean ± S.E. of the number of individuals and number of species per gall, as well as the number of individuals per gram of gall tissue (density); number of galls containing larvae in parentheses; different letters within a locality denote a significant difference of $P < 0.05$ between monthly means.

Boekenhoutskloof Date		Individuals	Larval Density	Species
1992	January	3.86±0.45 (69) **a**	0.69±0.07 (69) **a**	1.85±0.13 (69) **a**
	February	4.34±0.64 (58) **a**	1.12±0.13 (58) **a**	2.07±0.17 (58) **a**
	March	5.48±1.23 (23) **a**	1.76±0.49 (23) **b**	2.00±0.26 (23) **a**
H; P<		**0.18; 0.91**	**10.59; 0.005**	**0.53; 0.76**
Hartebeespoort				
1992	January	3.20±0.37 (35) **ab**	4.52±0.92 (33) **a**	1.65±0.13 (35) **a**
	February	5.00±0.61 (40) **a**	0.81±0.14 (39) **b**	2.03±0.13 (40) **b**
	March	2.37±0.30 (35) **b**	0.92±0.11 (35) **b**	1.44±0.11 (36) **a**
H; P<		**14.63; 0.001**	**28.22; 0.001**	**10.72; 0.005**
Pienaarspoort				
1992	January	5.05±0.68 (41) **a**	0.57±0.05 (41) **a**	1.90±0.15 (41) **a**
	February	5.62±0.81 (42) **a**	0.59±0.05 (42) **a**	2.11±0.18 (42) **a**
	March	2.22±0.43 (18) **b**	0.76±0.07 (17) **b**	1.22±0.13 (18) **b**
H; P<		**9.77; 0.008**	**3.27; 0.195**	**10.95; 0.004**
Parys				
1993	January	2.29±0.24 (65) **c**	0.76±0.11 (65) **a**	-
early	February	5.40±0.62 (99) **a**	1.09±0.09 (99) **b**	2.16±0.09 (99) **a**
late	February	8.75±0.71 (100) **b**	1.77±0.14 (100) **c**	2.80±0.11 (100) **b**
	March	2.90±0.52 (33) **d**	1.00±0.15 (33) **d**	1.03±0.03 (33) **c**
1994	January	11.79±1.20 (103) **b**	3.41±0.33 (103) **e**	1.82±0.07 (103) **d**
	February	2.47±0.51 (21) **a**	0.37±0.12 (23) **f**	1.42±0.16 (21) **e**
H; P<		**123.34; 0.001**	**144.32; 0.001**	**100.77; 0.001**
Bloemfontein				
1992	February	8.53±1.77 (49) **a**	1.29±0.22 (49) **ab**	1.76±0.13 (49) **a**
1993	January	6.05±0.45 (166) **a**	1.25±0.09 (165) **a**	2.14±0.08 (166) **b**
	March	1.74±0.29 (23) **c**	0.70±0.12 (23) **c**	1.09±0.06 (23) **c**
1994	January	5.18±0.39 (5.18) **a**	0.99±0.11 (160) **bc**	2.17±0.09 (161) **b**
H; P<		**25.06; 0.001**	**15.10; 0.002**	**29.22; 0.001**
Aston Bay				
1991	November	3.28±0.29 (64) **b**	1.44±0.14 (64) **a**	1.29±0.06 (75) **a**
1992	February	10.30±1.37 (80) **a**	2.55±0.31 (80) **b**	2.44±0.13 (80) **b**
1993	January	11.89±1.17 (174) **a**	1.13±0.11 (174) **c**	2.28±0.10 (174) **c**
	March	4.71±0.62 (76) **c**	2.00±0.48 (76) **d**	1.53±0.10 (78) **d**
	May	5.35±0.59 (72) **d**	2.44±0.56 (75) **a**	1.35±0.07 (72) **e**
1994	January	9.34±1.40 (94) **a**	4.29±0.43 (94) **e**	3.52±0.14 (94) **f**
	February	6.81±0.62 (98) **e**	2.03±0.19 (98) **f**	2.66±0.15 (99) **g**
H; P<		**46.61; 0.001**	**126.07; 0.001**	**204.90; 0.001**

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Table 5.10. Species richness, evenness and diversity of the Lepidoptera communities at each locality for each sampling month.

Date		Richness (S)	Evenness (J')	Shannon (H')
Boekenhoutskloof				
1992	January	7	0.86	1.68
	February	7	0.89	1.73
	March	6	0.80	1.44
Hartebeespoort				
1992	January	6	0.70	1.26
	February	7	0.61	1.19
	March	6	0.79	1.41
Pienaarspoort				
1992	January	5	0.65	1.04
	February	7	0.68	1.32
	March	6	0.83	1.48
Parys				
1993	January	6	0.67	1.19
early	February	5	0.75	1.20
late	February	6	0.71	1.27
	March	2	0.15	0.10
1994	January	5	0.29	0.48
	February	5	0.51	0.83
Bloemfontein				
1992	February	4	0.65	0.90
1993	January	6	0.69	1.24
	March	4	0.68	0.95
1994	January	6	0.75	1.35
Aston Bay				
1991	November	6	0.67	1.19
1992	February	8	0.62	1.28
1993	January	9	0.49	1.08
	March	9	0.44	0.96
	May	4	0.26	0.35
1994	January	8	0.66	1.36
	February	9	0.71	1.56

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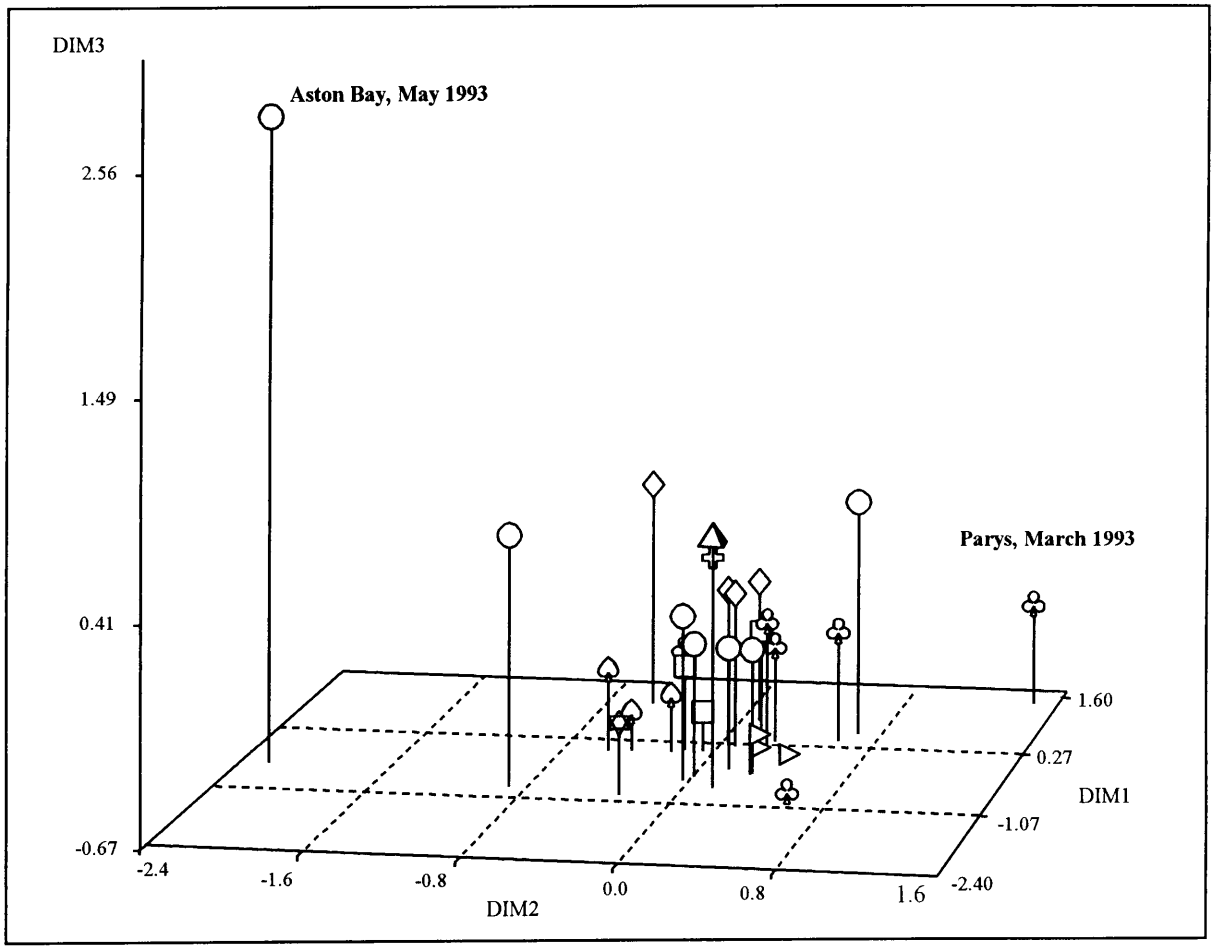

Figure 5.2. Three dimensional non-metric multidimensional scaling ordination of the relative abundances of species in the Lepidoptera community of each sample from nine localities, the main cluster includes January, February and March locality samples, whereas the two outliers are Aston Bay, May 1993 and Parys, March 1993;

Boekenhoutskloof = ♤ , Hartebeespoort = ▷ , Pienaarspoort = □ , Parys = ♧ , Bloemfontein = ◇ , Richards Bay = ▲ , Grahamstown = ✚ , Sundays River Valley = ✡, Aston Bay = ○ ; stress = 0.08.

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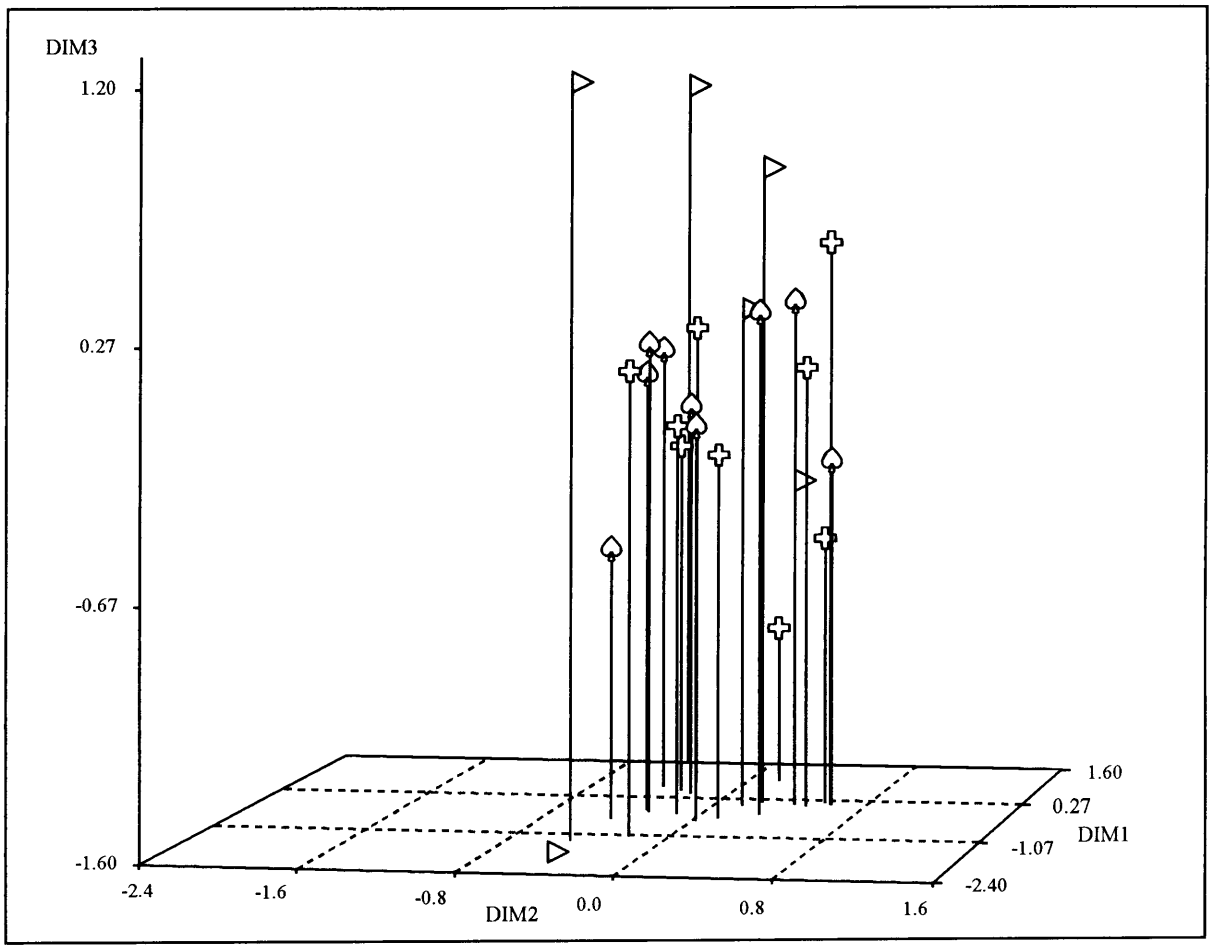

Figure 5.3. Three dimensional non-metric multidimensional scaling ordination of the relative abundances of species in the Lepidoptera community from six temporally replicated localities;

January = ♤ , February = ✚ , March = ▷ ; stress = 0.07.

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Table 5.11. Probability values of analyses of similarity (ANOSIM) of Lepidoptera communities between the sampling months of January, February and March across all localities.

P=	January	February	March
January	*		
February	n.s.	*	
March	0.01	0.05	*

Regional community patterns

The dendrogram of the percentage similarity of samples from each locality clearly illustrates the separation of the three coastal localities, Aston Bay, Sundays River Valley and Richards Bay from the inland localities (Fig. 5.4). Grahamstown, however, fell within the inland locality grouping. A number of the late season March samples and the Aston Bay May and November samples were less similar to the January and February samples (Fig. 5.4). The dendrogram also shows that the level of similarity between the communities from different localities is relatively high, with all the localities being separated above a similarity level of approximately 74 % (Fig. 5.4).

The MDS ordination of the January to March samples illustrates the position of the temporally unreplicated localities (Richards Bay, Grahamstown and Sundays River Valley) in relation to the other localities, where Grahamstown (icon = cross) lies between the inland and coastal clusters (Fig. 5.5). The structure of the summer Lepidoptera community at Aston Bay was significantly different from the communities at all the other temporally replicated sampling localities, *i.e.* Bloemfontein, Parys, Hartebeespoort, Pienaarspoort and Boekenhoutskloof (Table 5.12, Fig. 5.6). The Lepidoptera community at Bloemfontein was also significantly different from the communities at Boekenhoutskloof and Hartebeespoort (Table 5.12). Therefore, although the communities in general have a high level of similarity (around 74 %, Fig. 5.4), there were significant differences between them. The three most northern localities (in the Gauteng Province) were significantly different from the central localities (those in the Orange Free State) and from the southern localities (Eastern Cape) (Table 5.13) and the central localities were significantly different from the southern localities (Table 5.13). Communities from coastal localities and inland localities were also significantly

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different (ANOSIM Global R = 0.33, P = 0.007, permutations = 5000 [random sample from total possible number of permutations]).

Linking of community data with climate variables

The climate variables that were individually most highly correlated with the species matrix of communities from the nine localities were total annual rainfall, altitude and percentage coefficient of variation in rainfall (Table 5.14). These three variables in combination also provided the best correlation between the species matrix and all the climate matrices of climate variable combinations (Table 5.14). Figure 5.7a shows the MDS ordination of the species matrix of nine localities. In this ordination Aston Bay, Sundays River Valley and Richards Bay are separated on the right hand side of the ordination. The three northern localities (Boekenhoutskloof, Hartebeespoort and Pienaarspoort) are grouped in the upper left side of the ordination (Fig. 5.7a). The central localities (Parys and Bloemfontein) are below these and Grahamstown is positioned in the bottom left corner of the ordination. Figure 5.7b shows the two dimensional PCA of localities according to the three best matching climate variables (the first two principal component axes explained 98.21% of the variation). The positions of the localities on this environmental ordination (Fig. 5.7b) and on the species ordination (Fig 5.7a) are well matched. The only locality that is not positioned similarly on both ordinations is Grahamstown, *i.e.* positioned in the centre of the climate variable ordination (Fig. 5.7b).

Fig 5.8 a, b and c clearly illustrate that higher total annual rainfall, lower intra-annual rainfall variability and low altitude are largely associated with the Lepidoptera communities from coastal localities, and that lower total annual rainfall, high intra-annual variability in rainfall and higher altitude are associated with the Lepidoptera communities at inland localities. Once again, however, the Lepidoptera community from Grahamstown appears to have a structure more associated with inland than coastal conditions. The community structure at Sundays River Valley was different than expected from the low total rainfall at this locality (Fig 5.8b). The climate variables did not discriminate between the inland (northern and central) localities.

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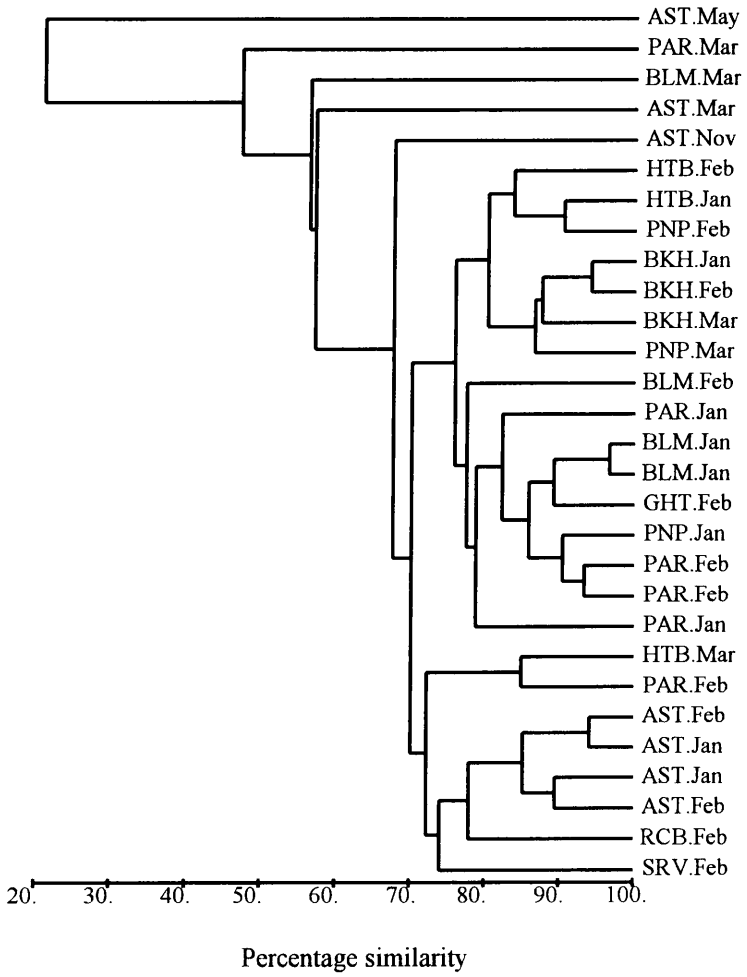

Fig. 5.4. Dendrogram of Bray-Curtis percentage similarities between the nine sampling localities in each month; BKH, Boekenhoutskloof; HTB, Hartebeespoort; PNP, Pienaarspoort; PAR, Parys; BLM, Bloemfontein; RCB, Richards Bay; GHT, Grahamstown ; SRV, Sundays River Valley; AST, Aston Bay; Jan, January; Feb, February; Mar, March; Nov, November.

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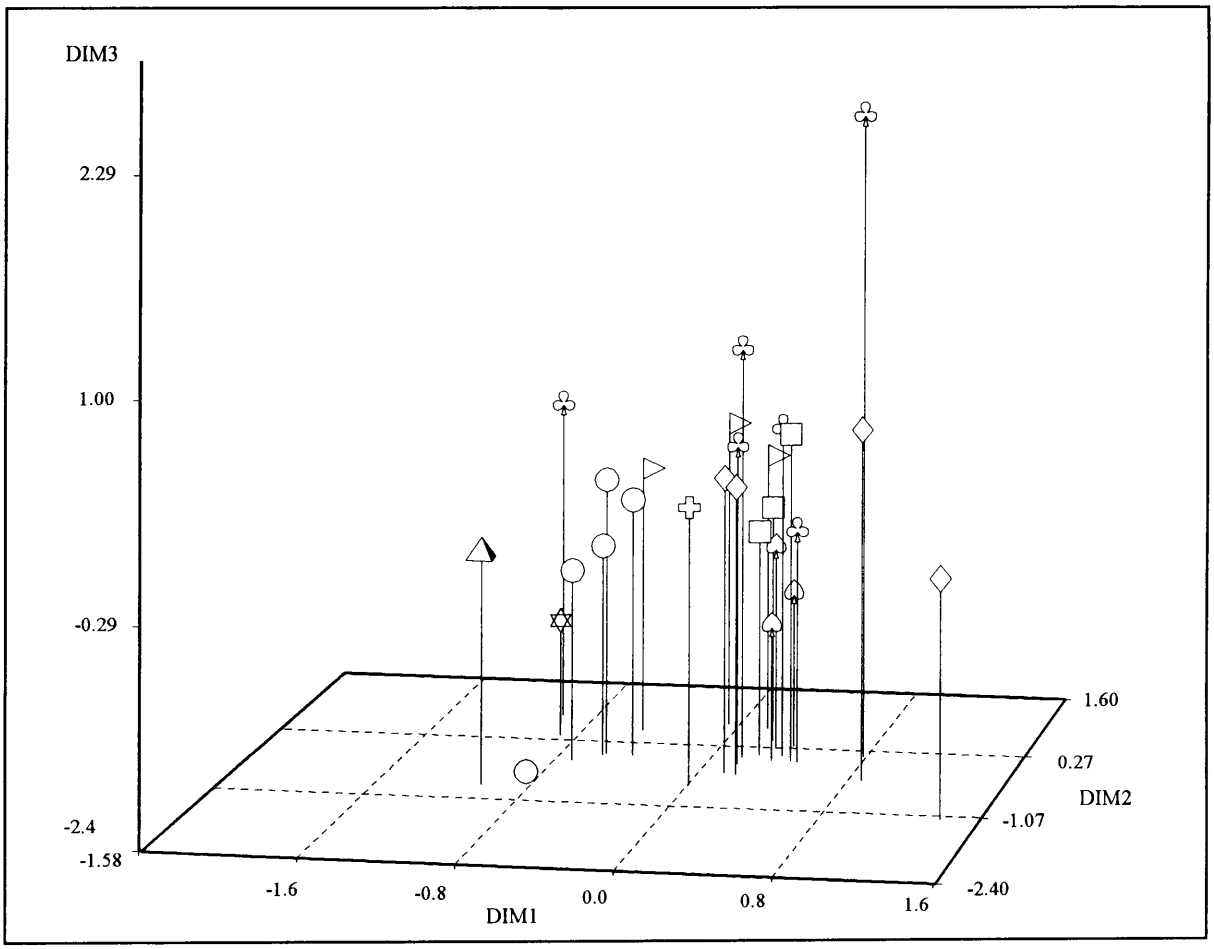

Figure 5.5. Three dimensional non-metric multidimensional scaling ordination of the relative abundances of species in the Lepidoptera communities at all nine localities for the months January, February and March;

Boekenhoutskloof = ♤ , Hartebeespoort = ▷ , Pienaarspoort = □ , Parys = ♧ , Bloemfontein = ◊ , Richards Bay = ▲ , Grahamstown = ✚ , Sundays River Valley = ✡, Aston Bay = ○ ; stress = 0.08.

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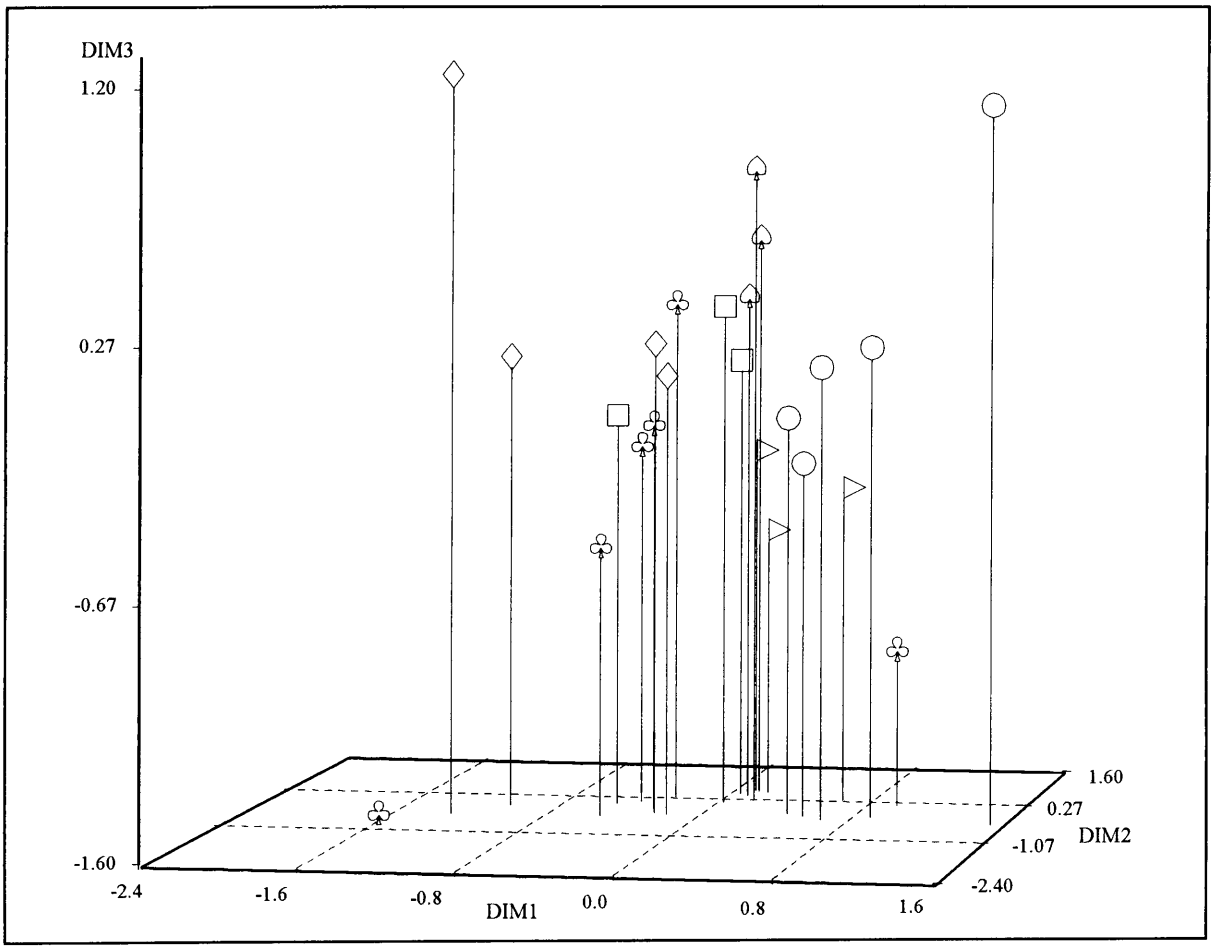

Figure 5.6. Three dimensional non-metric multidimensional scaling ordination of the relative abundances of species in the Lepidoptera community from the six temporally replicated localities;

Boekenhoutskloof = ♤ , Hartebeespoort = ▷ , Pienaarspoort = □ , Parys = ♧ , Bloemfontein = ◊ , Aston Bay = ○ ; stress = 0.07.

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Table 5.12. Probability values of analyses of similarity (ANOSIM) of Lepidoptera communities between localities.

P=	BKH	HTB	PNP	PAR	BLM	AST
BKH	*					
HTB	n.s.	*				
PNP	n.s.	n.s.	*			
PAR	n.s.	n.s.	n.s.	*		
BLM	0.029	0.029	n.s.	n.s.	*	
AST	0.018	0.036	0.036	0.017	0.008	*

Table 5.13. Probability values of analyses of similarity (ANOSIM) of Lepidoptera communities between regions.

P=	Northern	Central	Southern
Northern	*		
Central	0.04	*	
Southern	0.001	0.01	*

Table 5.14. Weighted rank correlations (p_w) between the species matrix and climate matrices, taking each climate variable on its own and each of the best matching variables in combination (1,2; 1,3; 2,3 and 1,2,3); vertical lines indicate the climate variables listed in the first column and included in the correlation.

Climate variable	p_w	p_w 1,2	p_w 1,3	p_w 1,2,3
1. Total annual rainfall (mm)	0.601			
2. Altitude (m.a.s.l.)	0.564	0.754	0.740	0.762
3. % Covariation: rainfall	0.464			
4. % Covariation: minimum temperature	0.127			
5. % Covariation: maximum temperature	0.010			

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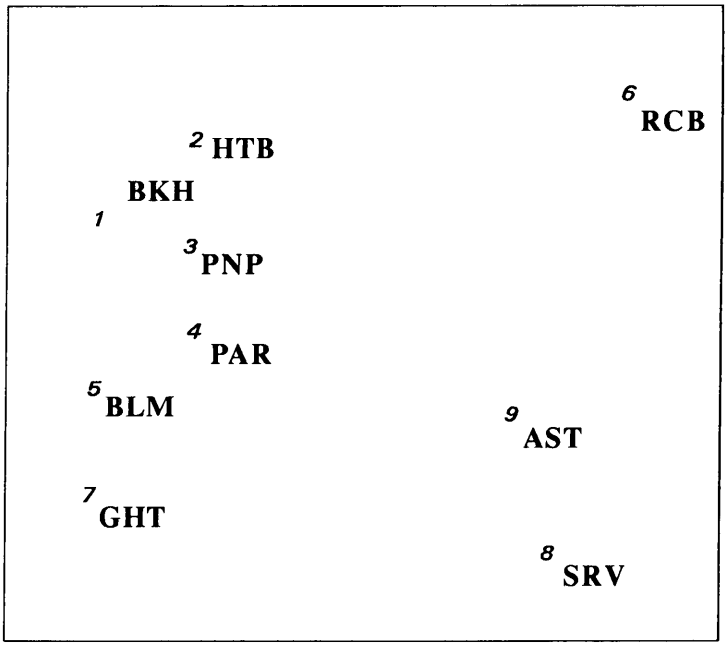
a.



b.

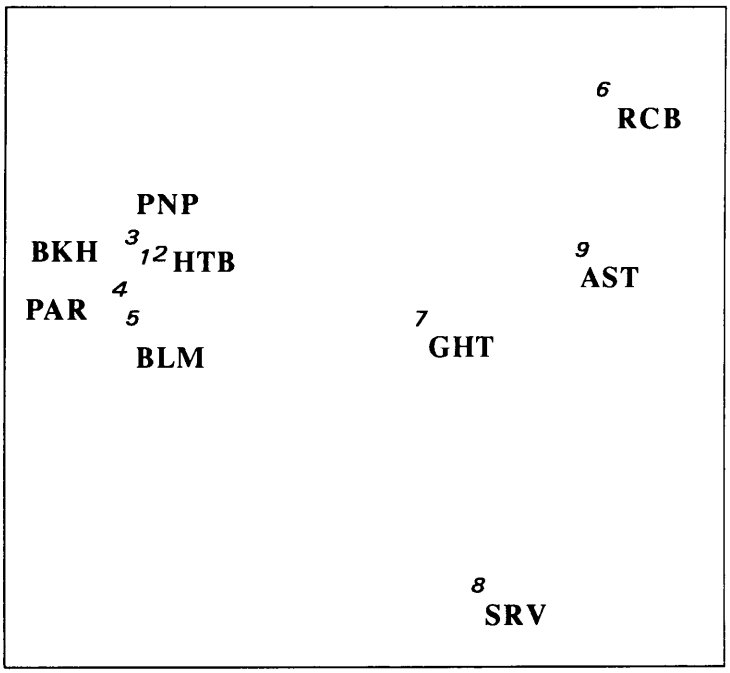


Fig. 5.7a and b. Ordinations of the nine sampling localities based on a. MDS of the species in the Lepidoptera community (stress = 0.07) and b. two dimensional PCA of the best matching subset of climate varaibles (variation explained = 98 %) (scaled axes of these plots are unnecessary as the absolute distance between every pair of points on the ordination is a relative measure of their similarity).

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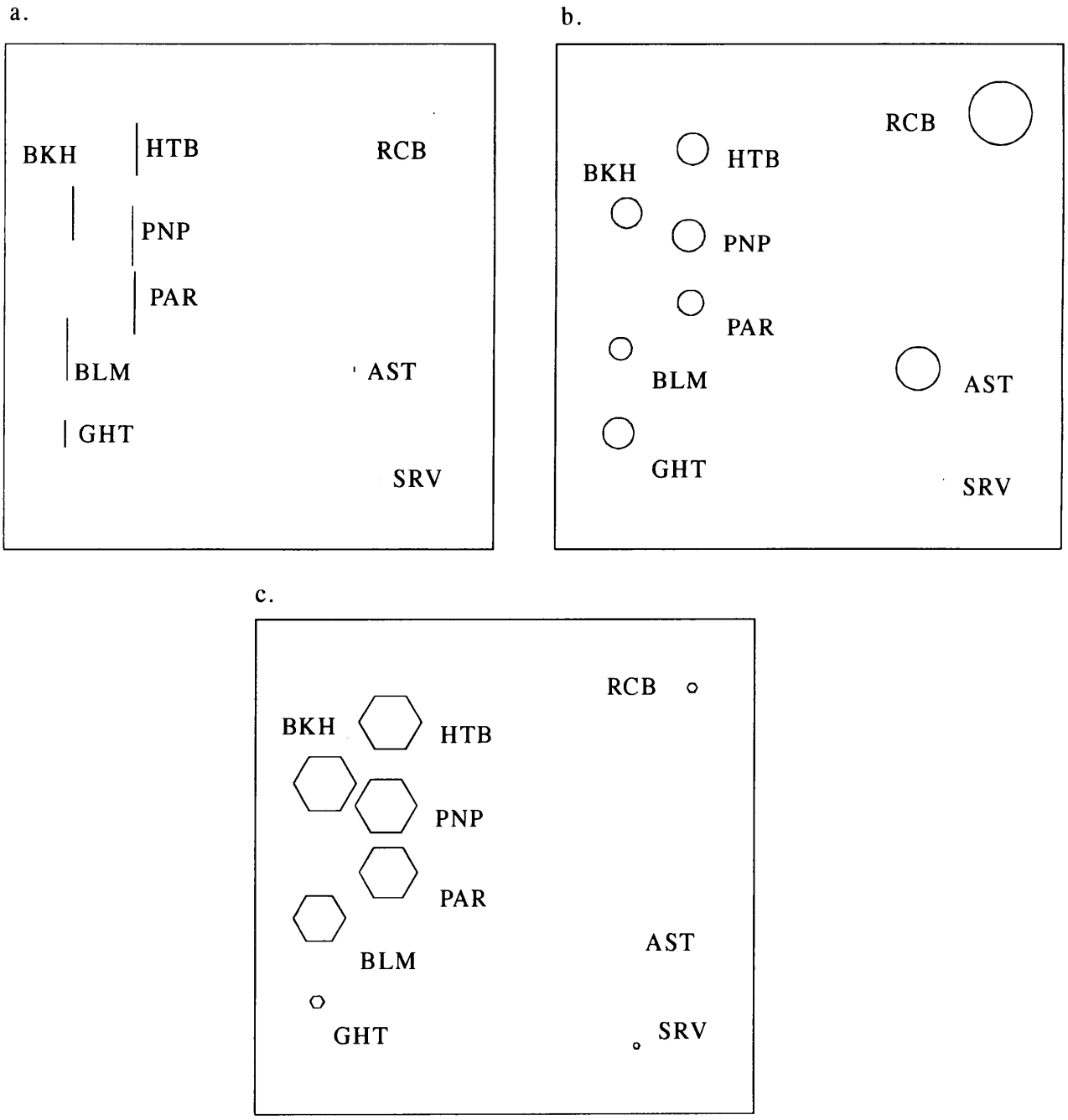

Fig. 5.8 a - c. Species MDS ordination (as in Fig. 5.6 a) with superimposed symbols of a. altitude (longer lines with increasing altitude), b. total rainfall (larger circles with higher rainfall) and c. rainfall variability (larger hexagons with higher variability in intra-annual rainfall) (scaled axes are of these plots are unnecessary as the absolute distance between every pair of ponts on the ordination is a relative measure of their similarity).

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DISCUSSION

The seasonality of larval activity in the galls is dependent on the duration of the gall development season, as well as on winter climatic conditions. At Aston Bay, where larval activity in the galls occurred throughout the year, gall development was prolonged (Chapter 1) and winter climate conditions at this locality are mild with rainfall. Although larvae are present in dead galls during winter months at Aston Bay, this Lepidoptera community consists of fewer, and mostly different, species to the summer gall-inhabiting community. In comparison to Aston Bay, the other temporally replicated localities (Bloemfontein, Parys, Hartebeespoort, Pienaarspoort and Boekenhoutskloof) have cold, dry winters. They also have short summer gall-development periods, and larval activity is restricted to this rainy, summer season and to the duration of available live gall tissue. The other localities with climatic conditions most similar to Aston Bay (*i.e.* Richards Bay, Sundays River Valley and Grahamstown) were not sampled during winter and larval activity at these localities may also be aseasonal.

In addition to the extended duration of larval activity in galls at Aston Bay, gall occupancy (number and density of individuals per gall) was highest here, and at Grahamstown and Sundays River Valley (the southern localities). Gall densities at these localities were, however, similar to the other localities (see Chapter 1) and the high larval densities were therefore not a result of lower gall densities. Mean gall mass at Grahamstown and Sundays River Valley was significantly lower than gall mass at Aston Bay (Chapter 1, Table 1.4). Other localities with higher mean gall masses than the former two localities (*e.g.* Boekenhoutskloof), however, had larval densities lower than Sundays River Valley and Grahamstown. It therefore appears that although there is a positive relationship between gall mass and number of occupant larvae (Table 5.5), differences in mean gall mass between localities were not entirely responsible for differences in mean larval density between localities. This could unfortunately not be tested because of the non-normal distributions (that did not respond sufficiently to transformation) and inequality of variances of the data from most localities. Possible explanations of the different larval densities between localities may be that the species population sizes at the mentioned localities are larger, or that alternative host-plant material of a similarly high quality is available. In addition, the high species densities at Aston Bay and Sundays River Valley are probably a result of the high species richnesses at these localities.

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Species richness trends, globally, show a tendency to increase with decreasing latitude (Pianka 1966), and galling species richness and abundance has been shown to be higher in xeric than in mesic habitats (Fernandes & Price 1988; Fernandes & Price 1992). (Although this community of Lepidoptera are merely gall inhabitants and not gall inducers, the same advantages of gall habitation would appear to apply, see Chapter 1). In contrast, species richness and abundance in this Lepidoptera community were highest in habitats receiving most rainfall and were greater at higher, and not lower, latitudes. Sundays River Valley was an apparent exception as total annual rainfall at this locality was extremely low considering its high species richness. This locality is under citrus cultivation and is intensively irrigated and total precipitation is, therefore, effectively much higher. Interestingly, on the MDS ordination of Lepidoptera community structure the position of the northern and central localities and Grahamstown (all the localities placed left in the ordination) is an exact reflection of the order of their latitudes from north to south (see Fig. 1.2, Chapter 1). Ichneumonid species-richness has also been shown to be richer in temperate regions than in the tropics (Gauld 1986). These studies of latitudinal gradients in species richness, however, address patterns in higher level taxa, from family level upwards, whereas the gall inhabiting Lepidoptera community is a small subset of regional Lepidoptera species richness.

Although correlated with rainfall and altitude, the mechanisms behind the patterns of species richness in this community are unclear. However, a number of models have been proposed to explain the asymptotic recruitment curves and equilibrium (dynamic) number of herbivore species in communities (Cornell 1993; Lawton & Strong 1981). These will be discussed in detail in a further chapter (see Chapter 7). The maximum species richness recorded for the Lepidoptera community between January and February was nine species at Aston Bay (with a local total of 11 species), whereas the communities from the majority of other localities had only six or seven species. A number of these localities were sampled over two or three years and the species richness remained constant. Although the dominant species appear established in the community (they are most abundant and most widespread and were consistently so during the sampling period), it is likely that there will be some turnover over time among the least dominant species as new species attempt to colonize the community (Cornell & Lawton 1992; Ricklefs 1987) (see Chapter 6).

The total diversity of each locality was dependent on the measure of diversity used, and there were differences in the diversity ranking of each locality as determined by the non-

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index diversity measures and Shannon's diversity. The only unique parameter in the calculation of H' is evenness, and this was shown to be correlated with species richness. This positive correlation between richness and abundance is a common occurrence in communities (Cotgreave & Harvey 1994) and evenness is often less useful than species richness for detecting differences between communities (Magurran 1988). In this Lepidoptera community evenness may be more useful for monitoring local habitat quality where local communities have similar species richnesses (as was shown in Chapter 4), rather than for comparisons across climatic gradients between communities with wide ranging numbers of species. The non-index diversity measure for this community is, therefore, considered a better measure of differences in community diversity between localities because each of the paramaters is a direct measurement or quantification of a single aspect of community structure, and not a relative parameter as in Shannon's index. The southern localities (Aston Bay, Grahamstown and Sundays River Valley), therefore, had the highest diversity in terms of species richness, abundance and density measures, followed by the central (although the community at Bloemfontein had the lowest species richness it had comparatively higher species abundances and densities than the northern localities) and then the northern localities.

The results of the multivariate analysis of differences between temporally replicated localities correspond largely with the diversity ranking of these localities. Aston Bay (the most southern of the localities) was significantly different from all other localities, whereas the northern localities, and the most northern of the central localities (Parys), were all similar. Bloemfontein (central locality) was also different from two of the three northern localities, as well as from Aston Bay (southern locality). Differences in the species composition and species relative abundances were therefore in accordance with differences in diversity between localities. Both community diversity and community structural differences were thus strongest between the southern and low altitude communities and the central and northern higher altitude communities.

Lepidoptera community structure was best correlated with total rainfall, altitude and rainfall variability. Elsewhere, species richness for birds, mammals, amphibians and reptiles has been shown to be well explained by annual potential evapotranspiration, *i.e.* the amount of water that evaporates from a saturated surface and is therefore dependent on ambient energy and relative humidity (Currie 1991). British butterfly and moth species richness were also shown to be best correlated with sunshine and temperature (explaining nearly 80 % of

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the variance in diversity) (Turner *et al.* 1987). In contrast to Britain, South Africa's climate is dominated by high thermal and radiant energy and comparatively low, often highly seasonal, rainfall (Tyson 1986). It therefore seems plausible that Lepidoptera species richness in South Africa will not be explained as well by sunshine and temperature variables, but that rainfall is likely to play a more significant role. Larval development also occurs during that part of the season when both minimum and maximum daily temperatures are highest and larval development is, therefore, even less likely to be limited by low temperatures. Indeed rainfall, and not temperature, variables were shown to be best correlated with the structure of the gall-inhabiting moth community. Although no causal relationship can be inferred between rainfall patterns and moth community structure, rainfall has both a direct and indirect effect on the Lepidoptera community because gall development is also highly dependent on rainfall (Chapter 1). Although annual potential evapotranspiration (PET) figures for the localities and regions of South Africa included in this study were unavailable, PET is also correlated with net primary productivity (Currie 1991) and is probably an important determinant of gall productivity, and hence duration of larval activity and larval density in the galls. Total precipitation has also been shown to be the best predictor of plant species richness in the south-western Cape Province of South Africa (Linder 1991) and to be more important than temperature in the morphological adaptations of certain small mammal species in southern Africa (Ellison *et al.* 1993).

Species richness is only one parameter of community structure and, in this study, rainfall variables were correlated with the entire abundance distribution of the species in the community and not only with species richness. The species richness pattern was, however, similar to the differences in abundance distributions between localities, *i.e.* the community structures of all the temporally replicated localities with the same species richness were not significantly different from each other, whereas Aston Bay and Bloemfontein (having different species richnesses) were significantly different from the former localities.

In the light of the predicted regional climate changes, *i.e.* a decrease in precipitation and an earlier onset of rainfall in summer rainfall regions, and an increase in year-round rainfall in the south-eastern Cape (B.C. Hewitson, personal communication), a number of predictions can be made concerning their potential effect on this Lepidoptera community. A decrease in summer rainfall at the Gauteng and Orange Free State localities (see Table 1.1, Chapter 1) will retard and inhibit gall development and, therefore, have an indirect negative

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effect on the Lepidoptera community. Low gall abundance and low mean gall mass that will result from decreased rainfall, may be expected to increase the level of larval competition in galls and may even result in loss of species from the community, *e.g. Euzophera* sp. nr. *verrucicola* that was absent in the community from Bloemfontein, *i.e.* the locality with the lowest total rainfall (without irrigation, see below). However, earlier rainfall may result in earlier gall formation and change the seasonality of the Lepidoptera community. An increase in annual rainfall at Aston Bay may result in an even longer gall development season, an increase in the duration of the activity period of the live-gall community and a further increase in the species richness of the live-gall community. Species such as *Encolpotis xanthoria*, that was present only in communities at high rainfall localities, may increase in abundance at Aston Bay.

Intensive irrigation at Sundays River Valley increased the effective total precipitation and the community at this locality was similar to a high rainfall community. Increased conversion of land for agricultural cultivation may see a concomitant increase in the invasion of pest species into natural communities, as occurred at Sundays River Valley where the two pest species, *Cryptophlebia peltastica* and *Lobesia stericta*, were second and third most abundant in the community.

The evenness of species relative abundance distributions do not appear to be determined predominantly by climatic variables and possible evenness changes due to climate changes cannot, therefore, be predicted. Larval abundances, however, may decrease as a result of lower total rainfall, but may increase at Aston Bay as a result of the predicted increase in yearly rainfall.

Although temperature variables were not well correlated with community structure, higher temperatures, in the presence of sufficient water and nutrients, may increase the growth rate of Lepidoptera larvae in the galls (Casey 1994). In addition, galls have been shown to attain temperatures several degrees higher than ambient air temperature (Layne 1991; Layne 1993).

Gall tissue quality is also likely to change under higher atmospheric carbon dioxide concentrations (Fajer *et al.* 1989; Lincoln *et al.* 1993). The predicted increase in carbon to nitrogen ratios for many plant tissues may mean that gall tissue quality will decrease and that the larvae will have to consume greater quantities of gall tissue to assimilate sufficient nutrients (Fajer *et al.* 1989; Lincoln *et al.* 1993). Intra and interspecific resource-mediated

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competition between the larvae may then become more severe (see Chapter 3). This negative effect may, however, be ameliorated if higher rainfall improves gall productivity, as well as by higher temperatures increasing larval growth rate.

Clearly the impact of regional climate change on the structure of this gall-inhabiting moth community is dependent on abiotic variables, on biotic resource factors and on community interactions. This study has thus identified regional factors that are likely to be important determinants of future community structure and functioning, although the combined impact of these variable and their interactions remains uncertain.

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REFERENCES

Bazzaz, F.A. 1990. The response of natural ecosystems to the rising global CO_2 levels. *Annual Review of Ecology and Systematics* **21**, 167-196.

Bray, J.R. & Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* **27**, 325-349.

Cammell, M.E. & Knight, J.D. 1992. Effects of climatic change on the population dynamics of crop pests. *Advances in Ecological Research* **22**, 117-162.

Carpenter, S.R., Frost, T.M., Kitchell, J.F. & Kratz, T.K. 1993. Species dynamics and global environmental change: a perspective from ecosystem experiments. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland, pp. 267-279.

Casey, T.M. 1994. Effects of temperature on foraging caterpillars. In Stamp, N.E. & Casey, T.M. (Eds). *Caterpillars Ecological and Evolutionary Constraints on Foraging*. Chapman & Hall, New York, pp. 5-28.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117-143.

Clarke, K.R. & Ainsworth, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**, 205-219.

Clarke, K.R. & Green, R.H. 1988. Statistical design and analysis for a biological effects study. *Marine Ecology Progress Series* **46**, 213-226.

Clarke, K.R. & Warwick, R.M. 1994. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Natural Environmental Research Council, United Kingdom.

Cornell, H.V. 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. In Ricklefs, R.E. & Schluter, D. (Eds). *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago, pp. 243-252.

Cornell, H.V. & Lawton, J.H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**, 1-12.

Cotgreave, P. & Harvey, P.H. 1994. Evenness of abundance in bird communities. *Journal of Animal Ecology* **63**, 365-374.

Currie, D.J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist* **137**, 27-49.

Dennis, R.L.H. & Shreeve, T.G. 1991. Climate change and the British butterfly fauna: opportunities and constraints. *Biological Conservation* **55**, 1-16.

Ellison, G.T.H., Taylor, P.D., Nix, H.A., Bronner, G.N. & McMahon, J.P. 1993. Climatic adaptation of body size among pouched mice (*Saccostomus campestris*: Cricetidae) in the southern African subregion. *Global Ecology and Biogeography* **3**, 41-47.

Eyre, M.D., Rushton, S.P., Luff, M.L., Ball, S.G., Foster, G.N. & Topping, C.J. 1986. *The Use of Invertebrate Community Data in Environmental Assessment*. Agricultural Environmental Research Group, The University, Newcastle upon Tyne.

Faith, D.P., Minchin, P.R. & Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**, 57-68.

Fajer, E.D., Bower, M.D. & Bazzaz, F.A. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Science* **243**, 1198-1200.

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Fajer, E.D., Bower, M.D. & Bazzaz, F.A. 1992. The effects of nutrients and enriched CO_2 environments on production of carbon-based allelochemicals in *Plantago*: a test of the carbon/nutrient balance hypothesis. *The American Naturalist* **140**, 707-723.

Fernandes, G.W. & Price, P.W. 1988. Biogeographical gradients in galling species richness: tests of hypotheses. *Oecologia* **76**, 161-167.

Fernandes, G.W. & Price, P.W. 1992. The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats. *Oecologia* **90**, 14-20.

Field, C.B., Chapin III, F.S., Matson, P.A. & Mooney, H.A. 1992. Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annual Review of Ecology and Systematics* **23**, 201-235.

Field, J.G., Clarke, K.R. & Warwick, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* **8**, 37-52.

Gates, D.M. 1993. *Climate Change and its Biological Consequences*. Sinauer Associates, Massachusetts.

Gauch, H.G. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.

Gauld, I.D. 1986. Latitudinal gradients in ichneumonid species-richness in Australia. *Ecological Entomology* **11**, 155-161.

Harrison, S. 1993. Species diversity, spatial scale, and global change. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland, pp. 388-401.

Holloway, J.D. 1990. Norfolk Island and biogeography for the nineties: ideas from a dot on the map. *Journal of Biogeography* **17**, 113-115.

Joubert, A. 1994. Simulations of southern African climatic change by early generation general circulation models. *Water SA* **20**, 315-322.

Kenkel, N.C. & Orloci, L. 1986. Applying metric and nonmetric multidimensional scaling to some ecological studies: some new results. *Ecology* **67**, 919-928.

Kingsolver, J.G. 1989. Weather and the population dynamics of insects: integrating physiological and population ecology. *Physiological Zoology* **62**, 314-334.

Kingsolver, J.G., Huey, R.B. & Kareiva, P.M. 1993. An agenda for population and community research on global change. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland, pp. 480-486.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural area monitoring. *Ecological Applications* **2**, 203-217.

Kruskal, J.B. & Wish, M. 1978. *Multidimensional Scaling*. Sage Publications, London.

Lawton, J.H. & Strong, D.R. 1981. Community patterns and competition in folivorous insects. *The American Naturalist* **118**, 317-338.

Layne, J.R. 1991. Microclimate variability and the eurythermic nature of goldenrod gallfly *Eurosta solidaginis* larvae (Diptera: Tephritidae). *Canadian Journal of Zoology* **69**, 614-617.

Layne, J.R. 1993. Winter microclimate of goldenrod spherical galls and its effects on the gall inhabitant *Eurosta solidaginis* (Diptera: Tephritidae). *Journal of Thermal Biology* **18**, 125-130.

Lincoln, D.E., Fajer, E.D. & Johnson, R.H. 1993. Plant-insect herbivore interactions in elevated CO_2 environments. *Trends in Ecology and Evolution* **8**, 64-68.

Digitised by the Department of Library Services in support of open access to information, University of Pretoria, 2021

Linder, H.P. 1991. Environmental correlates of patterns of species richness in the south-western Cape Province of South Africa. *Journal of Biogeography* **18**, 509-518.

Magurran, A.E. 1988. *Ecological Diversity and its Measurement*. Croom Helm, London.

Mooney, H.A. & Chapin III, F.S. 1994. Future directions of global change research in terrestrial ecosystems. *Trends in Ecology and Evolution* **9**, 371-372.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**, 734-737.

Pianka, E.R. 1966. Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist* **100**, 33-46.

Pielou, E.C. 1975. *Ecological Diversity*. Wiley & Sons, New York.

Pitelka, L.F. 1994. Ecosystems response to elevated CO_2. *Trends in Ecology and Evolution* **9**, 204-207.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**, 167-171.

Root, T.L. & Schneider, S.H. 1993. Can large-scale climatic models be linked with multiscale ecological studies? *Conservation Biology* **7**, 256-270.

Schneider, S.H. 1992. The climatic response to greenhouse gases. *Advances in Ecological Research* **22**, 1-32.

Schneider, S.H. 1993. Scenarios of global warming. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland, pp.9-23.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioural Sciences*. McGraw Hill, New York.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Publications, Oxford.

Sugden, A.M. 1992. Using biotic interactions to forecast the consequences of global climate change. *Trends in Ecology and Evolution* **7**, 35-36.

Turner, J.R.G., Gatehouse, C.M. & Corey, C.A. 1987. Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos* **48**, 195-205.

Tyson, P.D. 1986. *Climate change and variability in southern Africa*. Oxford University Press, Cape Town.

Tyson, P.D. 1993. Recent developments in the modelling of the future climate of southern Africa. *South African Journal of Science* **89**, 494-505.

Walter, H. & Breckle, S-W. 1985. *Ecological systems of the geobiosphere*. Springer-Verlag, Berlin.

Wolda, H. 1988. Insect seasonality: why? *Annual Review of Ecology and Systematics* **19**, 1-18.

Wolfe, D.W. & Erickson, J.D. 1993. Carbon dioxide effects on plants: uncertainties and implications for modelling crop response to climate change. In Kaiser, H.M. & Drennen, T.E. (Eds). *Agricultural Dimensions of Global Climate Change*. St Lucie Press, Florida, pp. 153-178.

Zar, J.H. 1984. *Biostatistical Analysis*. Prentice-Hall, New Jersey.

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CHAPTER 6

The contribution of individual Lepidoptera species to community structure and function: an analysis of commonness, rarity, typicality and discriminant ability

Species conservation and the maintenance of ecosystem integrity and functioning are seen as complementary approaches to the conservation of biodiversity (Simberloff 1988; Walker 1992). It appears possible (although controversial, Ehrlich & Ehrlich 1981), however, that certain species in communities are ecologically redundant and superfluous to the functioning of communities and ecosystems (Walker 1992). Ecological redundancy is difficult to test as all possible spatial and temporal scales of the ecosystem have to be examined before it can be established that a particular species makes no significant contribution to ecosystem functioning (Carpenter *et al.* 1993, Rahel 1990, Walker 1992).

Rare species (species with low abundance and/or narrow ranges (Gaston 1994)) have historically received much conservation attention, because of their apparent high vulnerability to extinction (Gaston 1994) and rare species have often been regarded as useful indicators of the state of the environment (Samways 1994; Usher 1986). However, the position and role of rare species in the structure and functioning of communities is poorly known (Gaston 1994). Focus has also been directed at pivotal species, keystone species and indicator species in communities. The identification of these species has been highlighted as a top priority in order to be able to anticipate ecological change, to evaluate the state of ecological resources and to communicate the consequences of habitat degradation to decision makers and the public (Carpenter *et al.* 1993; Kingsolver *et al.* 1993; Noss 1990; Power & Mills 1995; Quinn & Karr 1993).

In spite of the acknowledged importance of rare, pivotal and indicator species, few practical guidlines exist for their identification and selection (Kremen 1992). Identifying rare, pivotal and indicator species involves determining the links between community structure (quantified as species abundances, and composition in terms of rare, common, widespread and narrow range species, and the spatial and temporal dynamics of these) and function (Simberloff 1988). There are two approaches aimed at elucidating this relationship. The first is to establish the spatial and temporal concordance and variability in the relative abundance rankings of species within a defined community (Gaston 1990; Gaston 1994, Rahel 1990).

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Gaston (1994, p. 78) recommended a number of "numerical resolutions of spatial concordance". These include determining to what extent, across a geographical range, "individual species tend to fall consistently within the same rare category; the species composition of the rare category remains constant; the rank abundances of the rare species remain the same; and the rank abundances of all species in the community remain the same". A second approach to examining the relationship between community structure and function is to identify typical and discriminant species in communities (Clarke 1993; Clarke & Warwick 1994). Typical species are those that contribute most consistently to the local integrity of a community or to its similarity over time, whereas discriminant species are those that contribute most consistently to the dissimilarity between communities across a spatial gradient (Clarke 1993; Clarke & Warwick 1994). Identifying typical and discriminant species in the community identifies species that may be important determinants of community functioning and responsible for the spatial concordance (or lack thereof) and structural variability of the community over time or a geographic range. There may also be some relationship between typical and discriminant species and pivotal and indicator species. If pivotal species are removed from a community substantial changes occur to the functioning of the community and ecosystem (Carpenter *et al.* 1993). This is similar to the recently revised keystone species concept (Paine 1969; Power & Mills 1995). During this recent debate on keystone species it was argued that the term should not be restricted to a particular trophic level, and that it is important to determine whether or not keystone species can be identified *a priori* (before experimental confirmation) (Power & Mills 1995). The revised definition of a keystone adopted is "a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance" (Power & Mills 1995). Pragmatically defined this is a species " whose loss from or addition to a system would change community composition, structure or function enough to arouse concern" (Power & Mills 1995). This is in essence similar to pivotal species as defined by Carpenter *et al.* (1993). If typical species are those with the highest temporal and spatial consistency within a community, it is these species that if perturbed will have the greatest impact on community structure and function, and therefore qualify as pivotal, if not keystone, species (Carpenter *et al.* 1993). In contrast to pivotal and keystone species, indicator species are those that change before functional changes in the community and ecosystem begin to occur (Carpenter *et al.* 1993). Discriminant species are those with a consistent turnover along

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spatial gradients and are, by definition, good indicators of environmental change.

These concepts of the roles of species in communities have a number of parallels with Hanski's (1982) core and satellite species, where core species are widespread and locally abundant and satellite species have small ranges and low abundances. The core-satellite species hypothesis is a null model to explain regional rarity and predicts a bimodal distribution between geographic range (frequency of patch occupancy) and number of species, as well as change in species status between core and satellite classes (Hanski 1982). Three explanations have been proposed to explain the positive relationship between distribution and abundance, *i.e.* sampling artefacts (McArdle 1990), ecological specialization (Brown 1984), and metapopulation dynamics (Hanski *et al.* 1993). Elucidating which of these mechanisms is responsible for the observed community patterns has important implications for assessing the vulnerability of rare species and the degree of confidence that can be placed in species identified as pivotal and indicator species.

The Lepidoptera in *Ravenelia macowaniana* galls are an ideal community for examining the roles of species in community structure and functioning as the gall-inhabiting community is easily defined, relatively discrete and regionally widespread. In this chapter both local and regional data are incorporated to determine the spatial concordance and variation in the community. The rare, common, typical and discriminant species in the Lepidoptera community are identified from the above analysis with a view to examining the roles of species in the community and to identifying regionally and locally consistent indicator and pivotal species. These community patterns are discussed with regard to the predictions made by Hanski's core-satellite hypothesis and with regard to the possible mechanisms responsible for the patterns. Predictions are also made concerning the use of species in the community for widespread environmental monitoring, the possible temporal persistence of the community, and the vulnerability of the rare species.

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STUDY SITES and METHODS

The results of the data collection and collation described in Chapter 5 were used in the analyses in this Chapter.

Species range and abundance

Tables 5.2.1 - 5.2.5 (Chapter 5) were used to extract information on species ranges, commonness and rarity. Samples from March and May were excluded from this analysis because communities from both these months showed seasonal succession effects and were significantly different from the summer-month (January and February) communities (Chapter 5). This separation of seasonal temporal effects from spatial effects is recommended in studies of the relationship between distribution and abundance (Hanski *et al.* 1993). The January and February samples for each year were, therefore, non-seasonal temporal replicates for each locality. Simple linear regressions of mean relative abundances of species from each locality (mean calculated from summer (January and February) replicates) on the number of recorded localities for each species were done on log transformed data, as well as on the mean relative abundances of species from all localities (regional mean calculated from all summer temporal replicates and localities). The variance of $\log_e$ relative abundance of each species was calculated using January and February samples from all localities to give a comparative measure of the variability in relative abundance between species (Lewontin 1966). The variation in mean relative abundance was then compared for each common, moderate and rare species pair using an F-test (Lewontin 1966). In these analyses means and variances were calculated for each species only at those localities where the species was present (Hanski *et al.* 1993). Frequency distributions of the ranks of the relative abundances of each species in the community were compiled using data from all localities. The Kendall coefficient of concordance was used to determine the degree of association between species rankings across localities (Siegel 1956). Separate Kendall coefficients were calculated for 1. the temporal replicates (each January and February sample) from each locality combined, 2. for these separately, 3. for all species in the community, and 4. with the rare species excluded. Where the number of species (N) was below eight, critical values for s (sum of squares of the deviation from the mean sum of ranks) were used, and when N was larger than seven chi-square critical values were used (Siegel 1956). A coefficient of concordance

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could not be calculated for the rare species separately as these species were present at too few localities.

Typical and discriminant species

PRIMER's SIMPER ('similarity percentages') procedure was used to determine the percentage contribution by each species, and the consistency of contribution, to the similarity within localities (typical species), as well as to the dissimilarities between localities (discriminant species) (Clarke & Warwick 1994)[1]. The species matrix used in SIMPER was the same matrix used for the MDS and ANOSIM procedures (Chapter 5). The percentage contribution of each species to the dissimilarity between each pair of localities was ranked and the ranks for each species between one locality and all its locality pairs were summed. This gave the summed rank contribution (Σr) of each species for each locality against all other localities. A similar procedure was carried out for the species with the highest consistency ratios across all paired localities. The species with the highest value for the summed consistency ranks (sum of the ranked consistency values for locality x paired with each other locality in turn) therefore contributed most consistently to the difference between a particular locality and all others.

RESULTS

Species ranges

Four species were widespread and present in communities from all sampled localities (total of nine localities, Table 6.1). These were *Cydia* (*Cydia*) *victrix*, *Ascalenia pulverata*, *Characoma submediana* and *Anarsia gravata* (Table 6.1; see also Tables 5.2.1 - 5.2.5, Chapter 5). Three other species were present at most, but not all localities. These were

[1] The SIMPER procedure computes the average similarity between each sample within a locality (to determine typical species) and average dissimilarity between each pair of between locality samples (to determine discriminant species) from the species similarity matrix. It then divides this average into contributions by each species to the dis/similarity between localities/samples (Clarke 1993). In addition to the percentage contribution by each species, a measure of how consistently a species contributes to the dis/similarities between or within localities (*i.e.* across all between, or within, locality sample pairs), is the standard deviation of the calculated average dis/similarity. If the ratio of the average contribution from species 1 to the standard deviation of that contribution is high, then species 1 consistently contributes a large proportion to the dis/similarities and is a typical, or good discriminant, species (Clarke & Warwick 1994).

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Euzophera verrucicola (absent from Grahamstown and Bloemfontein), the Phycitinae complex (absent from Hartebeespoort) and *Cryptophlebia peltastica* (absent from Boekenhoutskloof and Pienaarspoort) (Table 6.1; Tables 5.2.1 - 5.2.5). The remaining species were recorded only from a single sub-region. *Eublemma brachygonia* was only present at localities in the Gauteng Region (Boekenhoutskloof, Hartebeespoort and Pienaarspoort) (Tables 5.2.1 and 2). *Anatrachyntis tripola* was recorded from Aston Bay and Sundays River Valley and *Encolpotis xanthoria* from Aston Bay, Sundays River Valley and Richards Bay (Tables 5.2.4 and 5.2.5). *Lobesia stericta* was only recorded from Sundays River Valley and Aston Bay (Table 5.2.5). Of the community of 11 Lepidoptera species in galls in January and February there were, therefore, four widespread species, three species with a medium range and four species with small (localized) ranges. As a result there were two peaks in the distribution of the number of species recorded at the number of localities and the distribution therefore appeared bimodal (Fig. 6.1).

Table 6.1. Mean ± S.E., and the standard deviations of $\log_e$, relative abundances of Lepidoptera species across all localities; N = number of localities from which species were recorded; N = 9 are widespread species, 4 ≥ N < 9 are medium-range species. N ≤ 3 are narrow-range species; species in parentheses are winter species not included in this analysis; N in parentheses are the total number of spatial and temporal replicates in which the species was present.

Species and Rank	N	Mean ± S.E.	$S^2(\log_e)$
1. *Cydia (Cydia) victrix*	9 (23)	47.99±3.87	0.19
2. *Ascalenia pulverata*	9 (22)	20.06±3.09	1.07
3. *Characoma submediana*	9 (22)	9.35±1.47	1.26
4. *Anarsia gravata*	9 (14)	10.50±1.48	0.16
5. Phycitinae complex	8 (19)	2.82±0.61	1.41
6. *Cryptophlebia peltastica*	7 (13)	3.98±1.93	3.02
7. *Euzophera verrucicola*	7 (23)	11.61±5.05	2.43
8. *Eublemma brachygonia*	3 (5)	1.03±0.18	0.21
9. *Encolpotis xanthoria*	3 (7)	1.65±0.44	0.39
10. *Lobesia stericta*	2 (2)	7.94±5.51	4.98
11. *Anatrachyntis tripola*	2 (6)	3.35±1.14	2.35

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Species relative and ranked abundances

Species range and local mean relative abundance were significantly positively correlated at seven of the nine localities (Table 6.2). Regional mean relative abundance was also significantly associated with species range (Table 6.2). The variation (variance of $\log_e$ data) in relative abundances of all the widespread species was lower than the variation in the relative abundances of the medium range species and in most instances significantly so (Tables 6.1 and 6.3). Variation in the small range category was low for some species and high for others (Table 6.1), although in 20 (asterisks in Table 6.3) of the 27 instances where the variances in abundances between species were significantly different, the less abundant species was more variable than the more abundant species (Table 6.3).

The four species that were most widespread (present at all nine localities) were also the most abundant species and were therefore categorized as common (Table 6.1). On similar grounds, rankings five to seven were classed as 'moderate' and species occupying ranks eight onwards were classed as 'rare'. Thus categorized, the most widespread species in the community showed a slightly greater tendency to remain common or moderate than the rare species to remain rare (Fig. 6.2). One widespread species was consistently common (Fig. 6.2 a) and only one of the four widespread species extended into the rare category (Fig. 6.2 b). In Fig. 6.3 the frequency distributions of the seven widespread and medium range species are combined. Here it is evident that the six most abundant species each had a ranking in the distribution at which it was uniquely most frequent, thus *C* (*C.*) *victrix* most commonly ranked first most abundant, *A. pulverata* second *etc.*. The frequency peaks of these species therefore each corresponded successively with the relative abundance ranks one to six (Fig. 6.3). The seventh species, *E. verrucicola*, did not peak distinctly at any one rank, and the frequency distribution of this species was spread most uniformly along the x axis below the frequency distribution peaks of the other six species (Fig. 6.2 g, Fig. 6.3). The relative abundances of the localized species, however, extended across the abundance range between common, moderate and rare categories (Figs 6.2 e - k). The rank frequency distributions of the species with localized ranges were mostly distributed widely along the x axes without distinct rank frequency peaks (Figs 6.2 h - k). The relative abundance rankings of the common and moderate species in the community therefore remained relatively constant, whereas the relative abundance ranks of the rare species did not.

Kendall's coefficients of concordance showed that the species relative abundance

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rankings between localities and temporal replicates were significantly similar to each other, particularly when the rare species were excluded from the analysis (Table 6.4). The relative abundance rankings between localities were, however, different (*i.e.* no significant association between the rankings using the Kendall coefficient of concordance) in the analysis where the rare species were included and the temporal replicates from each locality combined (Table 6.4). The species relative abundance structure of this community therefore remains constant across localities, although the level of variability among the rare species is high. In addition, there is circumstantial evidence for temporal concordance in the community, as the spatial concordance of the community remained significant with the inclusion of temporal replicates (Table 6.4).

Table 6.2. Simple linear regressions of mean local relative abundance and distribution (number of sites occupied) of species and of mean regional relative abundance and distribution.

Locality	Y = a + bX	d.f.	r	P <	
Boekenhoutskloof	Y = -0.89 + 0.39X	10	0.93	0.001	
Hartebeespoort	Y = -0.80 + 0.33X	10	0.69	0.02	
Pienaarspoort	Y = -0.92 + 0.35X	10	0.74	0.008	
Parys	Y = -1.06 + 0.37X	10	0.77	0.004	
Bloemfontein	Y = -1.12 + 0.38X	10	0.76	0.006	
Richards Bay	Y = 0.17 + 0.15X	10	0.34	0.29	n.s
Grahamstown	Y = -1.14 + 0.42X	10	0.87	0.001	
Sundays River Valley	Y = 1.03 + 0.12X	10	0.31	0.35	n.s.
Aston Bay	Y = -0.33 + 0.29X	10	0.73	0.01	
Regional mean	Y = -0.11 + 0.29X	10	0.86	0.001	

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Table 6.3. F-tests of the variance (s^2) in $\log_e$ mean relative abundance between widespread and medium-range species in the community; d.f., degrees of freedom; ns, not significant; * or ¥, $P<0.05$; ** or ¥¥, $P<0.01$; asterisks denote significant differences where the more common species of the pair has a lower variance than the less common species in the pair; common species in upper-left part of the Table and rare species in the lower-right part of the Table; Cv, *Cydia (Cydia) victrix*; Ap, *Ascalenia pulverata*; Cs, *Characoma submediana*; Ag, *Anarsia gravata*; PH, Phycitinae complex; Cp, *Cryptophlebia peltastica*; Ev, *Euzophera verrucicola*; Eb, *Eublemma brachygonia*; Ex, *Encolpotis xanthoria*; Ls, *Lobesia stericta*; At, *Anatrachyntis tripola*.

Sp	df	s^2	Cv	Ap	Cs	Ag	PH	Cp	Ev	Eb	Ex	Ls	At
Cv	22	0.19	-										
Ap	21	1.07	**	-									
Cs	21	1.26	**	ns	-								
Ag	13	0.16	**	ns	ns	-							
PH	18	1.41	**	ns	ns	ns	-						
Cp	12	3.02	**	*	*	**	ns	-					
Ev	22	2.43	**	*	ns	**	ns	ns	-				
Eb	7	0.21	ns	¥	¥	ns	¥¥	¥¥	¥¥	-			
Ex	4	0.39	ns	ns	ns	ns	ns	¥	¥	ns	-		
Ls	2	4.98	**	*	*	**	ns	ns	ns	**	**	-	
At	4	2.35	**	ns	ns	*	ns	ns	ns	**	ns	ns	-

Table 6.4. Kendall's coefficients of concordance between the ranked relative abundances of species from each locality, with the temporal replicates from each locality combined (k = 9) and separate (k = 22), and with all species (N = 11) and with rare species excluded (N = 7); k = number of localities; N = number of species; W = Kendall coefficient of concordance; s = sum of squares of deviations from mean sum of ranks.

Samples and species used:	k	N	W	s	χ^2	P
Samples combined, all species	9	11	0.16	-	14.58	n.s.
Samples combined, rare species excluded	9	7	0.41	952.93	-	<0.01
Samples separate, all species	22	11	0.21	-	45.51	<0.01
Samples separate, rare species excluded	22	7	0.26	3534.85	-	<0.01

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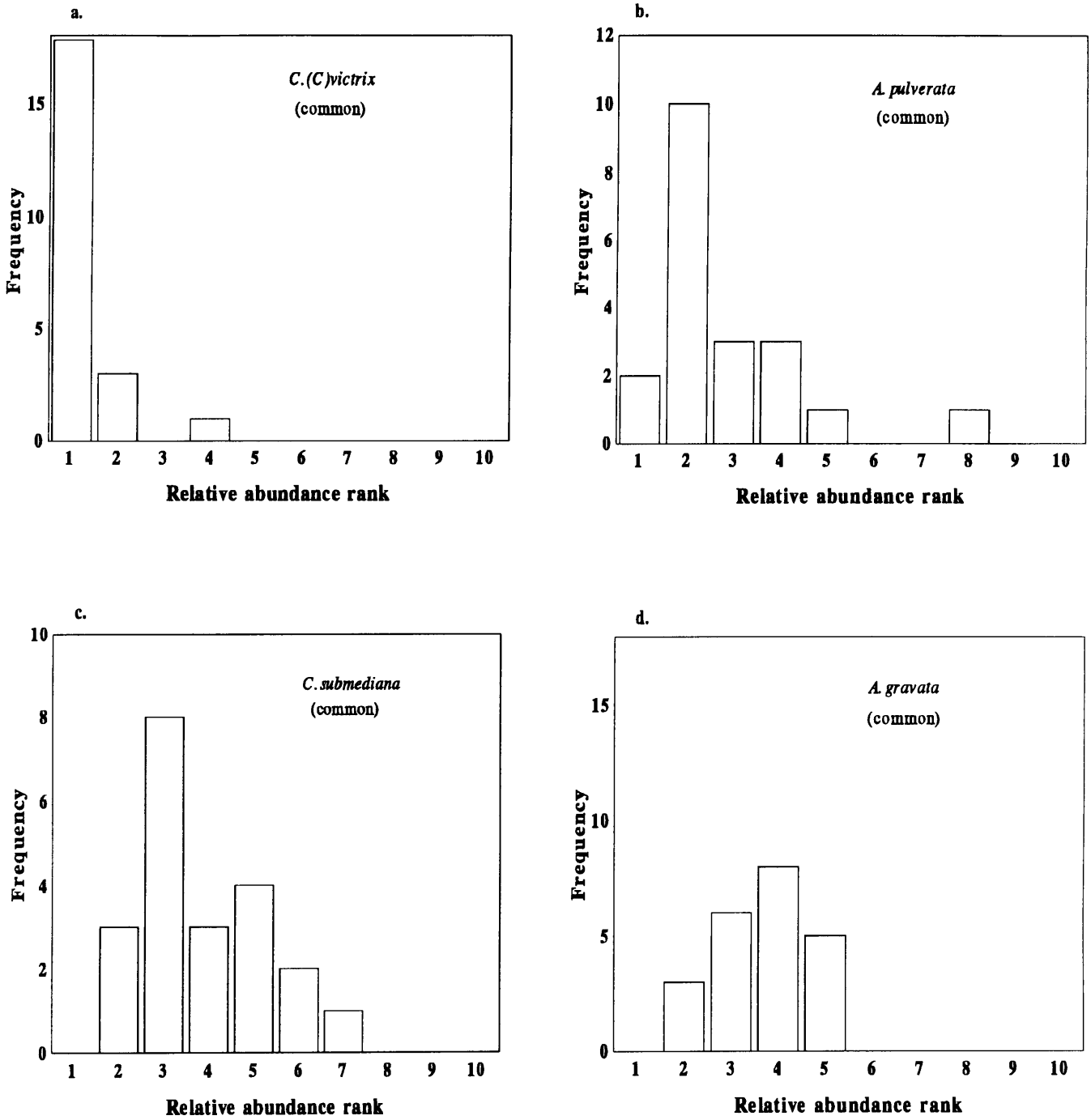

(Fig. 6.2 a - d)

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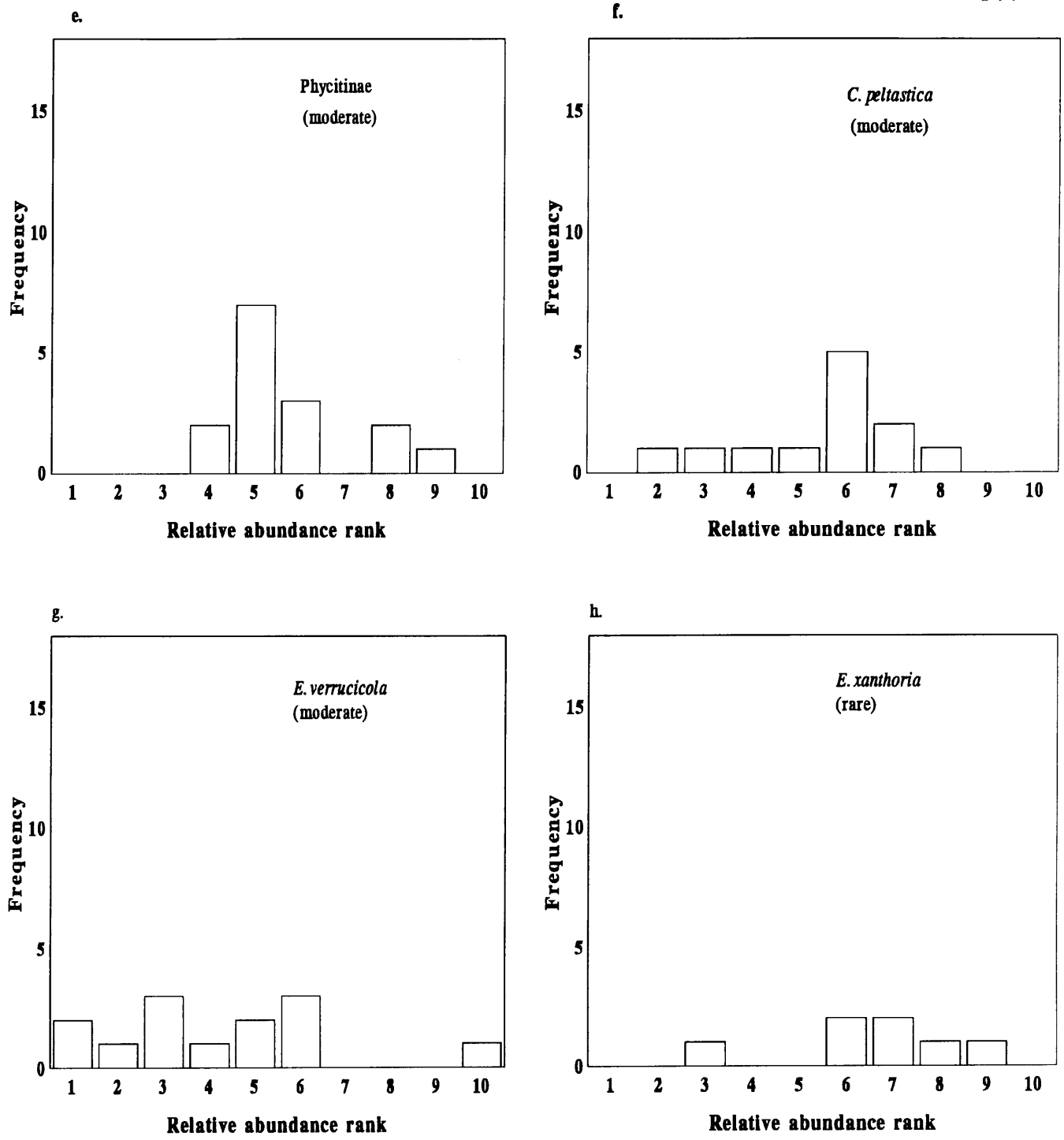

(Fig. 6.2 e - h)

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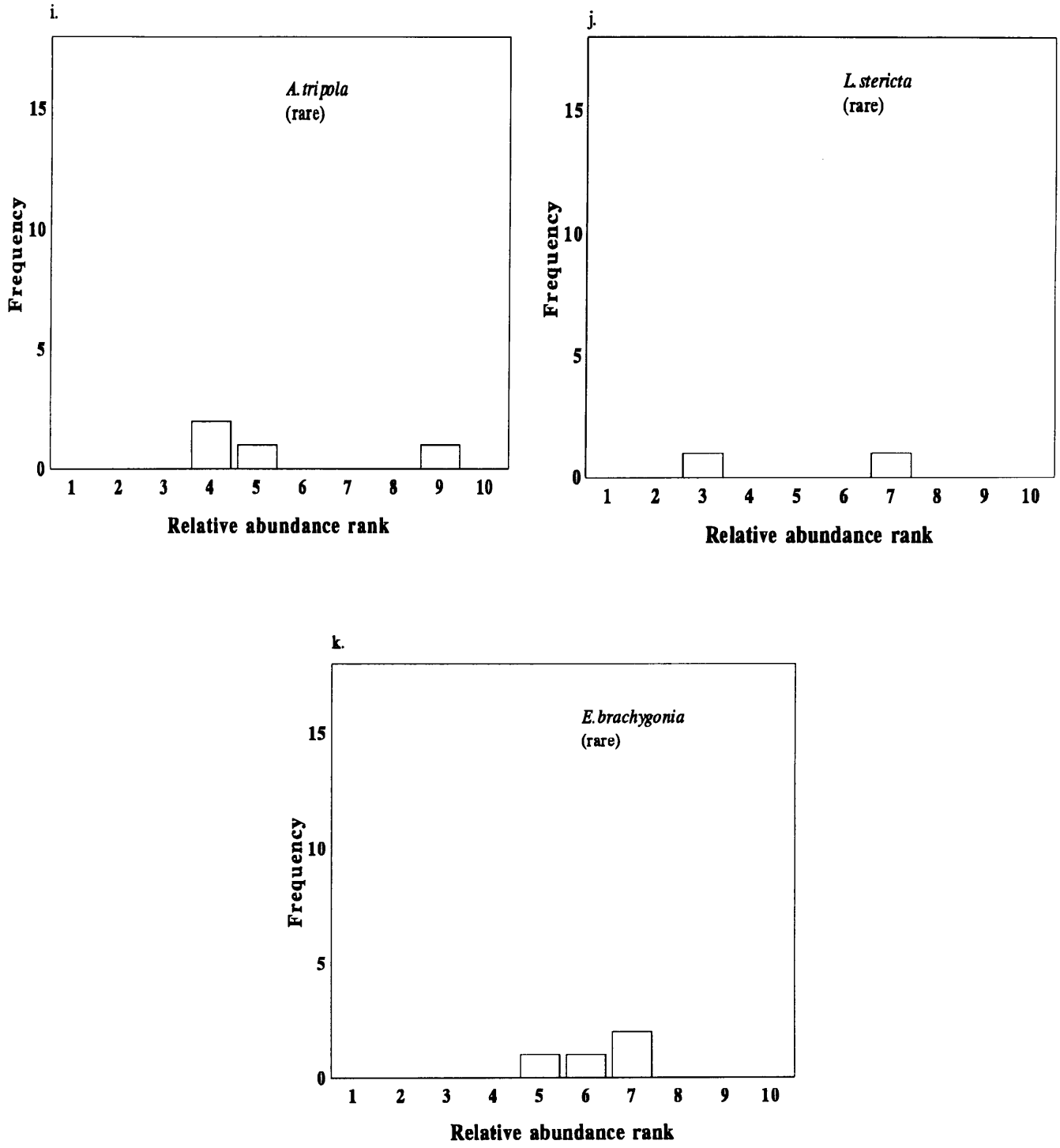

Fig. 6.2 a - k. Frequency distributions of the relative abundance rankings for each common, moderate and rare species in the Lepidoptera community.

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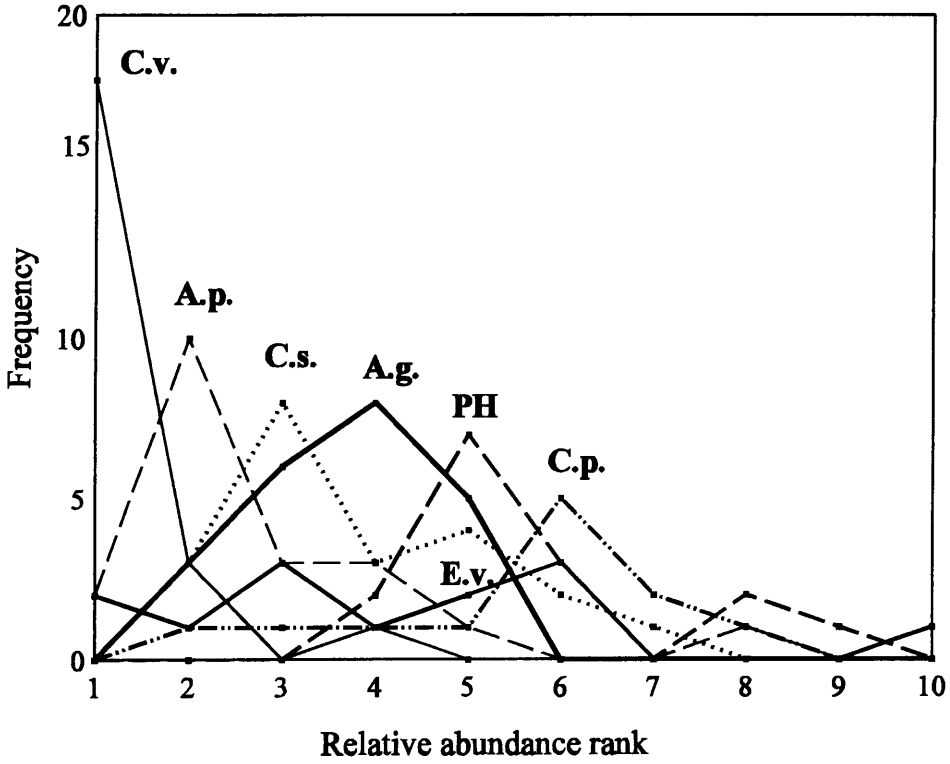

Fig. 6.3. The relative abundance rank frequency distribution of the common and moderate Lepidoptera species in the community; C.v., *Cydia (Cydia) victrix*, A.p., *Ascalenia pulverata*, C.s., *Characoma submediana*, A.g., *Anarsia gravata*, PH, Phycitinae complex, C.p., *Cryptophlebia peltastica*, E.v., *Euzophera verrucicola*.

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The core-satellite species hypothesis

According to Hanski (1982) the four common and four rare species in the community qualified as core and satellite species respectively. The species in this community also either had narrow distributions (present at three or fewer localities) or were widespread (present at seven or more localities) and the distribution of the frequency of site occupancy was, therefore, bimodal (Fig. 6.1). A single example of regional switching was found in the Lepidoptera community. At Sundays River Valley there was a switch between *A. pulverata* (a core species at all other localities) and *L. stericta* (a satellite species) (Tables 5.2.1 - 5.2.5). In the community at this locality *A. pulverata* ranked eighth and *L. stericta* was ranked third in the relative abundance distribution, effectively switching between common and rare categories (Fig 6.2 b & j).

Typical species

The species with the highest percentage contribution to the typicality of communities at each locality (calculated from species relative abundances at that locality over time) were often not those that contributed most consistently (Table 6.5). Because the consistency ratio takes both percentage contribution and its variation into account, the species contributions highlighted in superscript as 1, 2 and 3 in Table 6.5 were the most typical species in the community at each locality. All the localities had a different set of typical species (*i.e.* the species with the most consistent and greatest contribution to the typicality of the locality) (Table 6.5). At Boekenhoutskloof *Ascalenia pulverata*, *Euzophera verrucicola* and *Characoma submediana* were the most typical species (Table 6.5). Similarly, at Hartebeespoort *Characoma submediana* and *Anarsia gravata* were most typical, at Pienaarspoort *Anarsia gravata* and *Ascalenia pulverata* were most typical, at Parys *Cydia (Cydia) victrix* and *Anarsia gravata* were most typical, at Bloemfontein the Phycitinae complex, *Characoma submediana* and *Anarsia gravata* were most typical, and at Aston Bay *Anarsia gravata*, *Cydia (Cydia) victrix*, and *Ascalenia pulverata* were most typical (Table 6.5). Two of these localities, therefore, had typically unique species, *i.e. Euzophera verrucicola* at Boekenhoutskloof and the Phycitinae complex at Bloemfontein (Table 6.5). Among the other species *Anarsia gravata* was typical to five of the six localities, *Characoma submediana* to four, *Ascalenia pulverata* to three and *Cydia* (*Cydia*) *victrix* to two localities.

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Table 6.5. Percentage contribution of the Lepidoptera species that contributed most (cut off at 90% cumulative contribution), and contributed most consistently (superscripts), to the typicality of the Lepidoptera community in each of the six temporally replicated sampling localities. The values given are percentage contributions and superscripts denote the species with the three highest consistency ratios over time within each locality; A.g., *Anarsia gravata*; C.s., *Characoma submediana*; A.p., *Ascalenia pulverata*; C.v., *Cydia* (*Cydia*) *victrix*; E.v., *Euzophera verrucicola*; PH, Phycitinae complex; BKH, Boekenhoutskloof; HTB, Hartebeespoort; PNP, Pienaarspoort; PAR, Parys; BLM, Bloemfontein; AST, Aston Bay.

Species	Localities					
	BKH	**HTB**	**PNP**	**PAR**	**BLM**	**AST**
A.g.	41.99	50.85^{2}	51.12^{1}	42.26^{2}	31.99^{3}	23.50^{1}
C.v.	9.40	32.98	39.75	46.46^{1}	43.43	26.74^{2}
C.s.	7.53^{3}	8.14^{1}			11.85^{2}	5.89
A.p.	12.13^{1}		5.01^{2}	9.01		15.64^{3}
E.v.	23.44^{2}					
PH					9.72^{1}	
E.x.						4.53
A.t.						18.10

Discriminant species

Once again, the species that were the most consistent discriminant species were often not those that contributed the highest percentage to the difference between any pair of localities (Tables 6.6.1 - 6.6.9). The best discriminant species at a single locality (determined by SIMPER using species relative abundances and not determined by species presences or absences) varied depending on the locality with which it was being compared (Tables 6.6.1 - 6.6.9). However, for each locality certain species were better discriminants than others. *C.* (*C.*) *victrix* and *A. gravata* were, overall, the two best discriminant species (those with the highest summed rank percentage contribution (Σr column, Tables 6.6.1 - 6.6.9)) and highest summed consistency ranking (superscript in Σr column, Tables 6.6.1 - 6.6.9)) at all the localities that had temporally replicated samples, *i.e.* at Boekenhoutskloof, Hartebeespoort, Pienaarspoort, Parys, Bloemfontein and Aston Bay (Tables 6.6.1- 5 and 6.6.9). The other good discriminant species at these localities included *A. pulverata*, *C. submediana*, and *C. peltastica*. A number of additional species were shown to be good discriminating species at

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the non-temporally replicated localities. At Richards Bay, besides *C.* (*C.*) *victrix* and *A. gravata*, *E. xanthoria* had high ranking consistency ratios. At Grahamstown the best discriminant species were *C. peltastica* and *A. pulverata*, and at Sundays River Valley *C. peltastica*, *Lobesia stericta* and *Anatrachyntis tripola*. More weight should be given to the discriminant species identified from the temporally replicated localities (i.e. Boekenhoutskloof, Hartebeespoort, Pienaarspoort, Parys, Bloemfontein, and Aston Bay, see Tables 6.6.1 - 5 and 6.6.9) as these include internal measures of consistency. Without a measure of temporal consistency at the three remaining localities, the results from these remain preliminary. In summary, all the species identified as both typical within communities and discriminant between communities belonged to the common and moderate (*i.e.* high and medium abundance and distribution range) species categories.

Tables 6.6.1 - 6.6.9. Percentage contribution of the Lepidoptera species that contributed most (up to 90% cumulative contribution), and contributed most consistently, to differences between each pair of the nine localities (discriminant species); Σr = sum of the ranks of the percentage contribution of the species for each locality against all other localities; Σr superscript is the summed ranks of the consistency ratios for the species across all localities; bold superscripts denote species with the three highest consistency ratios for each locality pair; A.g., *Anarsia gravata*; C.s., *Characoma submediana*; A.p., *Ascalenia pulverata*; C.v., *Cydia* (*Cydia*) *victrix*; E.v., *Euzophera verrucicola*; PH, Phycitinae complex; C.p., *Cryptophlebia peltastica*; E.x., *Encolpotis xanthoria*; A.t., *Anatrachyntis tripola*; L.s., *Lobesia stericta*; BKH, Boekenhoutskloof; HTB, Hartebeespoort; PNP, Pienaarspoort; PAR, Parys; BLM, Bloemfontein; RCB, Richards Bay; GHT, Grahamstown; SRV, Sundays River Valley; AST, Aston Bay.

1. BKH	Σr	HTB	PNP	PAR	BLM	RCB	GHT	SRV	AST
A.g.	66^{11}	37.8^{1}	32.9^{3}	39.5^{1}	22.0	38.2	45.6^{3}	11.4	12.91^{1}
C.v.	60^{13}	20.8^{2}	22.9^{1}	23.1^{3}	33.7^{1}	8.5	22.2^{2}	13.4^{2}	17.88^{2}
E.v.	50^{1}	21.3	19.5	14.4	16.2	11.2	9.8	4.3	4.72
A.p.	43^{7}	7.1^{3}	13.6^{2}	12.8^{2}	11.4^{3}	9.8^{2}	6.2	1.2	11.36^{3}
C.s.	34^{4}	5.1	6.5	5.0	9.8^{2}	7.5^{3}	5.9	0.9	6.08
C.p.	20^{3}	0	0	1.2	0	0	7.1^{1}	23.2^{1}	1.63
E.x.	15^{3}	0	0	0	0	17.9^{1}	0	2.8^{1}	5.06
A.t.	14	0	0	0	0	0	0	8.9^{1}	37.00
L.s.	9	0	0	0	0	0	0	32.5^{1}	0

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2. HTB	Σr	BKH	PNP	PAR	BLM	RCB	GHT	SRV	AST
A.g.	75^{12}	37.8^{1}	42.3^{1}	48.2^{2}	31.0^{2}	33.8	52.2	13.0	13.8^{2}
C.v.	70^{14}	20.8^{2}	28.8^{3}	27.0^{3}	35.6^{1}	20.6^{1}	16.4	10.6^{3}	16.5^{1}
A.p.	55^{3}	7.1^{3}	15.3	15.4	10.7	4.5	9.6^{3}	0.7	12.7^{3}
C.s.	47^{7}	5.1	4.2^{2}	4.3^{1}	10.0	3.7	8.3^{2}	0.7	6.8
PH	35^{1}	2.2	3.3	0.6	9.0^{3}	0.4	3.1	1.5	1.5
C.p.	33^{6}	0	0	2.0	0.9	1.0	7.4^{1}	24.8^{1}	1.5
E.v.	30^{2}	21.3	1.7	0.6	0	14.9^{2}	0	0	3.3
E.x.	18^{1}	0	0	0	0	18.7^{3}	0	3.0	5.1
A.t.	16	0	0	0	0	0	0	9.6	36.9
L.s.	14^{2}	0	0	0	0	0	1.0	35.0^{2}	0

3. PNP	Σr	BKH	HTB	PAR	BLM	RCB	GHT	SRV	AST
A.g.	67^{13}	32.9^{3}	42.3^{1}	46.6^{1}	29.0^{3}	31.8^{3}	51.6	12.0^{3}	13.4^{1}
C.v.	63^{17}	22.9^{1}	28.8^{3}	27.8^{2}	34.6^{1}	22.4^{1}	14.0	9.2^{2}	16.3^{1}
A.p.	49^{6}	13.6^{2}	15.3	16.8	14.3	10.5	11.3^{2}	3.3	12.5^{2}
C.s.	40^{6}	6.5	4.2^{2}	3.0^{3}	12.4^{2}	1.1	10.2^{3}	1.2	7.4
E.v.	34	19.5	1.7	1.2	1.4	13.2	0.9	0.3	3.1
C.p.	23^{6}	0	0	1.6	0	0.6	8.1^{1}	24.9^{1}	1.6
E.x.	14^{2}	0	0	0	0	17.2^{2}	0	3.0	5.1
A.t.	14^{4}	0	0	0	0	0	0	9.6^{1}	37.3^{3}
L.s.	13^{3}	0	0	0	0	0	1.0	34.9^{1}	0

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4. PAR	Σr	BKH	HTB	PNP	BLM	RCB	GHT	SRV	AST
A.g.	69^{17}	39.5^{1}	48.2^{2}	46.6^{1}	37.5^{1}	39.9^{2}	50.7	15.9^{3}	20.7^{1}
C.v.	60^{9}	23.1^{3}	27.0^{3}	27.8^{2}	29.8^{3}	19.8^{3}	16.0^{3}	7.3	13.9^{2}
A.p.	50^{5}	12.8^{2}	15.4	16.8	13.8	12.1	12.4^{2}	4.7	11.4^{3}
C.s.	40^{6}	5.0	4.3^{1}	3.0^{2}	10.2^{2}	2.2	9.0	1.5	6.3
C.p.	37^{6}	1.2	2	1.6	1.3	1.5	7.6^{1}	23.5^{1}	1.5
E.v.	27^{3}	14.4	0.6	1.2	0	10.7^{1}	0.1	0.1	3.1
A.t.	15^{2}	0	0	0	0	0	0	9.2^{2}	35.7
E.x.	14^{2}	0	0	0	0	12.9^{2}	0	2.9	4.7
L.s.	13^{2}	0	0	0	0	0	1.0	33.4^{2}	0

5. BLM	Σr	BKH	HTB	PNP	PAR	RCB	GHT	SRV	AST
C.v.	74^{15}	33.7^{1}	35.6^{1}	34.6^{1}	29.8^{3}	31.1^{1}	20.8	7.9	53.3^{2}
A.g.	72^{11}	22.0	31.0^{2}	29.0^{3}	37.5^{1}	19.7^{2}	48.8	12.3^{3}	12.8^{1}
PH	56^{1}	4.8	9.0^{3}	7.2	6.8	7.2	2.8	1.2	3.4
E.v.	50	16.2	0	1.4	0	10.9	0	0.1	3.3
A.p.	37^{3}	11.4^{3}	10.7	14.3	13.8	7.6	10.5^{3}	3.9	12.0^{3}
C.p.	27^{4}	0	0.9	0	1.3	0	7.3^{2}	24.3^{2}	1.5
C.s.	25^{10}	9.8^{2}	10.0	12.4^{2}	10.2^{2}	10.1^{3}	8.6^{1}	3.6	7.7
E.x.	16	0	0	0	0	12.8	0	2.9	4.9
A.t.	16^{3}	0	0	0	0	0	0	9.3^{1}	37.1
L.s.	14^{3}	0	0	0	0	0	0.9	34.0^{1}	0

6. RCB	Σr	AST	BLM	BKH	HTB	PNP	PAR
A.g.	39^{8}	16.1^{1}	19.7^{2}	38.2	33.8	31.8^{3}	39.9^{2}
C.v.	34^{11}	16.4^{3}	31.1^{1}	8.5	20.6^{1}	22.4^{1}	19.8^{3}
E.x.	28^{10}	4.4^{2}	12.8	17.9^{1}	18.7^{3}	17.2^{2}	12.9^{2}
E.v.	21^{5}	3.2	10.9	11.2	14.9^{2}	13.2	10.7^{1}
A.p.	20^{2}	13.3	7.6	9.8^{2}	4.5	10.5	12.1
C.s.	14^{2}	7.6	10.1^{3}	7.5^{3}	3.7	1.1	2.2
A.t.	7	34.9	0	0	0	0	0

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7. GHT	Σr	BKH	HTB	PNP	PAR	BLM	AST
A.g.	47^{3}	45.6^{3}	52.2	51.6	50.7	48.8	24.5^{2}
C.v.	41^{6}	22.2^{2}	16.4	14.0	16.0^{3}	20.8	11.9^{1}
A.p.	33^{7}	6.2	9.6^{3}	11.3^{2}	12.4^{2}	10.5^{3}	8.1^{3}
C.s.	27^{6}	5.9	8.3^{2}	10.2^{3}	9.0	8.6^{1}	5.0
C.p.	22^{14}	7.1^{1}	7.4^{1}	8.1^{1}	7.6^{1}	7.3^{2}	3.0
E.v.	14	9.8	0	0.9	0.1	0	3.0
A.t.	8	0	0	0	0	0	36.4
E.x.	3	0	0	0	0	0	4.5

8. SRV	Σr	BKH	HTB	PNP	PAR	BLM	AST
L.s.	42^{15}	32.5^{1}	35.0^{2}	34.9^{1}	33.4^{2}	34.0^{1}	26.0^{2}
C.p.	35^{17}	23.2^{1}	24.8^{1}	24.9^{1}	9.2^{1}	24.3^{2}	17.8^{1}
A.g.	28^{7}	11.4^{1}	13.0	12.0^{3}	23.5^{3}	12.3^{3}	9.1^{3}
A.t.	24^{10}	8.9	9.6^{2}	9.6^{1}	15.9^{2}	9.3^{1}	24.5
C.v.	21^{5}	13.4^{2}	10.6^{3}	9.2^{2}	7.3	7.9	7.1
A.p.	11	1.2	0.7	3.3	4.7	3.9	6.6
E.v.	6	4.3	0	0.3	0.0	0.0	1.9

9. AST	Σr	BKH	HTB	PNP	RCB	PAR	BLM	GHT	SRV
A.t.	63	37.0	36.9	37.3	34.9	35.7	37.1	36.4	24.5
C.v.	51^{16}	17.8^{2}	16.5^{1}	16.3^{1}	16.4^{3}	13.9^{2}	16.2^{2}	11.9^{1}	7.1
A.g.	49^{20}	12.9^{1}	13.8^{2}	13.4^{1}	16.1^{1}	20.7^{1}	12.8^{1}	24.5^{2}	9.1^{3}
A.p.	38^{7}	11.3^{3}	12.7^{3}	12.5^{2}	13.3	11.4^{3}	12.0^{3}	8.1^{3}	6.6
C.s.	29	6.0	6.8	7.4	7.6	6.3	7.7	5.0	0.9
E.x.	23^{3}	5.0	5.1	5.1^{3}	4.4^{2}	4.7	4.9	4.5	2.8
L.s.	20^{2}	0	0	0	0	0	0	0.5	26.0^{2}
C.p.	9^{3}	1.6	1.5	1.6	1.5	1.5	1.5	3.0	17.8^{1}

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DISCUSSION

Species range and abundance

The regional distributions and biologies of some of the moth species in this community may explain features of their relative abundance distributions. *C. peltastica* and *L. stericta*, for example, have both been recorded as citrus crop pests (de Villiers 1992; C. Erichsen, personal communication). These species had inflated relative abundance rankings at Sundays River Valley, an area under extensive citrus cultivation, compared to the other localities. In addition, although *C. peltastica* was not recorded in galls from Boekenhoutskloof and Pienaarspoort, its distribution is known to be widespread throughout these areas (Chapter 2), and the possibility exists that this species may be recorded from these localities with longer-term sampling. The Phycitinae complex was also not recorded from Hartebeespoort, although it was present at adjacent localities with similar habitat types. It is also notable that *E. xanthoria* was recorded only from coastal localities. *A. tripola* is detritivorous and, although it did occur in live galls in low abundance, has different resource requirements to species in the live-gall inhabiting community. The relative abundances and distributions of certain species in the community can therefore be interpreted in terms of their habits and biologies.

Local and regional species relative abundances were positively correlated with the regional distribution of the species, as has been found in numerous closely related, ecologically similar taxa across all scales (Hanski 1982; Brown 1984; Gaston & Lawton 1988; Gaston & Lawton 1990; Hanski *et al.* 1993; McArdle *et al.* 1990). The distribution of site occupancy frequencies was apparently bimodal with the right hand mode at 100 % site occupancy, as predicted by Hanski's (1982) model. An example of regional switching was also documented in this Lepidoptera community, however this was at a locality where the natural Lepidoptera community was influenced by adjacent agricultural activity, *i.e.* Sundays River Valley. Indeed, species switching from core to satellite status and *vice versa*, as predicted by Hanski's model, has seldom been observed (Gaston & Lawton 1989), and according to Hanski & Gyllenberg (1993) there have been no well documented cases of this phenomenon. Hanski and Gyllenberg (1993) actually suggest that switching is likely to be infrequent and perhaps, as shown here, is more likely a result of some form of disturbance experienced by the community than a periodically intrinsic event in community functioning. The community in *R. macowaniana* galls, therefore, appears to provide limited support for

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Hanski's (1982) core-satellite species hypothesis, although little evidence exists in support of the assumptions of this model or the underlying mechanism of metapopulation dynamics (Gaston & Lawton 1989).

In addition to the positive relationship between distribution and abundance, the community was found to be relatively spatially resilient with significant spatial concordance among the common and medium species. Gaston (1994) predicted that the likelihood of finding high concordance is greater when the species composition of the community is similar and lower when the sites sampled are dissimilar and large distances apart. The species composition of the Lepidoptera community examined here was largely similar between localities, however the localities compared were far apart. The similarity of these localities are high if one considers the actual gall and *A. karroo* tree as the habitat, however the adjacent vegetation and climatic conditions of the localities were markedly different (see Chapter 5). In spite of the large distances apart and different environmental conditions between communities at the localities sampled, the community was highly concordant. This suggests that the constraints on the common and moderate species in the community are similar between localities (Gaston 1994). The rare species, however, were found to be comparatively diffusive (rare at some localities and not at others), as predicted by Gaston (1994). Although an apparently simplistic generalization, species have been considered to attain highest abundances near the centres of their ranges and lower abundances near the margins (Gaston 1994; Hengevel & Haek 1982). Because rare species are considered to have more fragmented geographic ranges than common species (Gaston 1994), a higher variability in their abundances would be detected than for more evenly distributed, common species. A further possible explanation for this dichotomy between common and rare species is that the rare species populations may be behaving in a metapopulation dynamics manner, whereby their populations are continually becoming extinct and being recolonized by founder populations (Hanski 1982, Hanski & Gyllenberg 1993). The common species, alternatively, appear to be widespread generalists and provide more support for Brown's (1984) hypothesis. If, with longer-term sampling, the temporal concordance of the rare species was found to be high, the rare species may then be highly specialized species with narrow distribution ranges (Brown 1984), rather than species behaving according to metapopulation dynamics (Hanski 1982). Data to answer this question is, however, presently unavailable. Finally, it appears unlikely that the observed patterns are an artefact of sampling (as discussed by McArdle

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1990), because the gall sample sizes were large and representative of the locality being sampled. Other studies have shown that similar patterns are not merely sampling artefacts, but intrinsic properties of the species themselves (*e.g.* Bock 1987). The evidence, therefore suggests that both metapopulation dynamics and ecological generalization may be involved in structuring this community, although longer-term monitoring and the establishment of the degree of temporal, in addition to spatial, concordance of the structure of this Lepidoptera community will provide further information.

As discussed, the level of spatial concordance of rarity found in the community was low. Gaston's "numerical resolutions of the concordance of rarity" (Gaston 1994, p. 78) were also negative. That is, although the mean abundances of the species categorized as rare were low, these species occurred in both the medium and common categories on a number of occasions and therefore did not fall consistently within the rare category. The species composition of the rare category was also not consistent and species in the moderate category were sometimes rare, and different species were often rare at different localities. However, despite the low spatial concordance of rare species, the spatial concordance of relative abundance rankings of species for the entire community (*i.e.* inclusion of common, moderate and rare species) was high. In addition, the species identified to most likely be important in community functioning, *i.e.* the typical and discriminant species, were all common and moderate species in the community. Nevertheless, the rare species contribute substantially to the species richness of this Lepidoptera community as well as to its functioning. As shown in Chapter 3, the Lepidoptera larvae in the galls are often resource limited and competition occurs between individuals and species in the community. Every individual in a gall, where the density is on average limited to between 6 and 13 individuals depending on the size of the gall, contributes to the total density and biomass in the gall and exacerbates the level of competition (Chapter 3). The additive abundance of all the rare species also contributes substantially to this non species-specific, density dependent level of competition and, the higher the species richness, the more numerous will be the interspecific interactions in the community. In addition, the low spatial concordance of the rare species and the uncertainty of mechanistic understanding concerning their behaviour in the community makes it difficult to assess their vulnerability. If rare species tend to be rare only in some localities and not in others, they may not be as vulnerable to extinction as initially believed. Some evidence for this can be found from a number of examples of insect species that have been considered

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extinct for several years, whereafter they have been rediscovered and become abundant, *e.g.* the large blue butterfly, *Maculinea arion*, in the United Kingdom thought to be extinct in the late 1880's and reappeared to become locally common in the 1920s and 1930s (Dempster 1989). However, if the temporal concordance of rare species is also found to be low, then their vulnerability remains high. There are a number of examples of species extinctions regardless of population level (Dempster 1983). Therefore, contrary to suggesting that these species may be ecologically redundant, these results suggest that more attention should be given to understanding the dynamics of rare species.

Typical and discriminant species

If typical and discriminant species were to be identified on the basis of the presence or absence of species from each particular locality (rather than on the basis of percentage contribution to relative abundance and temporal consistency, as was the case here), then the four rare species with narrow distribution ranges would be most typical to the localities where they do occur and most discriminant between localities where they are present and absent respectively. However, because the rare species in this community were found to have low spatial concordance, and due to the lack of long-term data on the temporal concordance of these species, little confidence can presently be placed in their utility as typical and discriminant species. In contrast, however, the common and moderate species make more reliable typical and discriminant species. Kremen (1992) also found that the more ubiquitous species in tropical butterfly assemblages showed clear trends, whereas the rare species were highly variable. In Kremen's study, further work was thus required to determine whether rare species were characteristic of the habitats in which they were recorded, whether they were sampled at the edges of their range, or whether they were rare as a result of random sampling error (Kremen 1992).

Using relative abundance data and SIMPER in this study, similar sets of species were identified as having the greatest contribution to community structure within and between localities, although with different rankings of consistency. All of these species were of the seven common and moderate species in the community. Carpenter *et al.* (1993) also stated that the roles of pivotal and indicator species need not be mutually exclusive. In addition, although keystone species should be distinguished from dominants, the effects of keystone species on their communities may also be far more continuously distributed than warrants the

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delineation of 'keystones' and 'non-keystones' (Power & Mills 1995). To detect local changes in habitat quality it would, nevertheless, be most expedient to monitor the typical species in the community at each locality, as changes in these species would indicate significant change to the local environment. Support for this contention is provided by the results of the local-scale analysis of the impact of habitat quality on Lepidoptera community structure (Chapter 4) where *C. (C.) victrix*, *C. submediana* and *E.* sp. nr. *verrucicola* were identified as potential indicator species of local habitat quality changes (see also Table 6.5). The species with the highest and most consistent contribution to local community structure, may be identified *a priori* as possible keystone species and their abundances thereafter monitored to determine the effect of their removal on community structure and functioning.

The discriminant species between localities may be best used to determine the effects of regional climate, or other spatial environmental gradients, on community structure, as it is these species that show consistent turnover across spatial gradients. Typical species can therefore be used in the temporal monitoring of local environmental changes, *e.g.* to determine the impacts of habitat fragmentation or pollution on community structure and function. However, when monitoring a set of species identified as consistently typical, the least consistent of the species within that set may be better indicators of habitat change than the most consistent species in the set. This is because the most consistently typical species (*e.g. A. gravata* and *C. submediana*) may have stronger pivotal or keystone species properties and respond more slowly to changes in habitat quality. The less consistent, faster responding, species (*e.g. A. pulverata* and *C. (C.) victrix*) will therefore be better indicator species. In contrast, the most discriminant species between two localities (*e.g. A. gravata*) may be expected to respond faster to climate changes than the less discriminant species (*e.g. C. peltastica*, *C. submediana* and *A. pulverata*).

The selected indicator and pivotal species, based on their typicality and discriminant values, represent hypotheses of the properties of these species in relation both to their behaviour in the community and to environmental gradients (see also Kremen 1992) and future spatial and temporal sampling of the community should be used to provide replicates with which to determine the reliability of these choices.

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REFERENCES

Bock, C.E. 1987. Distribution-abundance relationships of some Arizona landbirds: a matter of scale? *Ecology* **68**, 124-129.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* **124**, 255-279.

Carpenter, S.R., Frost, T.M., Kitchell, J.F. & Kratz, T.K. 1993. Species dynamics and global environmental change: a perspective from ecosystem experiments. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland. pp. 267-279.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117-143.

Clarke, K.R. & Warwick, R.M. 1994. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Natural Environmental Research Council, United Kingdom.

Dempster, J.P. 1983. The natural control of populations of butterflies and moths. *Biological Review* **58**, 461-481.

Dempster, J.P. 1989. Fragmentation, isolation and mobility of insect populations. In Collins, N.M. & Thomas, J.A. (Eds). *The Conservation of Insects and their Habitats*. Academic Press, London, pp. 143-153.

de Villiers, E.A. 1992. Control of the Litchi moth, *Agroploce peltastica* Meyr. *South African Litchi Grower's Association Yearbook* **4**, 8.

Ehrlich, P.R. & Ehrlich, A.H. 1981. *Extinction. The Causes and Consequences of the Disappearance of Species*. Random House, New York.

Gaston, K.J. 1990. Patterns in the geographical ranges of species. *Biological Review* **65**, 105-129.

Gaston, K.J. 1994. *Rarity*. Chapman & Hall, London.

Gaston, K.J. & Lawton, J.H. 1988. Patterns in the distribution and abundance of insect populations. *Nature* **331**, 709-712.

Gaston, K.J. & Lawton, J.H. 1989. Insect herbivores on bracken do not support the core-satellite hypothesis. *The American Naturalist* **134**, 761-777.

Gaston, K.J. & Lawton, J.H. 1990. Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos* **58**, 329-335.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**, 210-221.

Hanski, I. & Gyllenberg, M. 1993. Two general metapopulation models and the core-satellite species hypothesis. *The American Naturalist* **142**, 17-41.

Hanski, I., Kouki, J. & Halkka, A. 1993. Three explanations of the positive relationship between distribution and abundance of species. In Ricklefs, R.E. & Schluter, D. (Eds). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 108-116.

Hengeveld, R. & Haeck, J. 1982. The distribution of abundance. I. Measurements. *Journal of Biogeography* **9**, 303-316.

Kingsolver, J.G., Huey, R.B. & Kareiva, P.M. 1993. An agenda for population and community research on global change. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*, Sinauer Associates, Sunderland. pp. 480-486.

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Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**, 203-217.

Lewontin, R.C. 1966. On the measurement of relative variability. *Systematic Zoology* **15**, 141-142.

McArdle, B.H. 1990. When are rare species not there? *Oikos* **57**, 276-277.

McArdle, B.H., Gaston, K.J. & Lawton, J.H. 1990. Variation in the size of animal populations: patterns, problems and artefacts. *Journal of Animal Ecology* **59**, 439-454.

Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4**, 355-364.

Paine, R.T. 1969. A note on trophic complexity and community stability. *The American Naturalist* **103**, 91-93.

Power, M.E. & Mills, L.S. 1995. The keystone cops meet in Hilo. *Trends in Ecology and Evolution* **10**, 182-184.

Quinn, J.F. & Karr, J.R. 1993. Habitat fragmentation and global change. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland, pp. 451-463.

Rahel, F.J. 1990. The hierarchical nature of community persistence: a problem of scale. *The American Naturalist* **136**, 328-344.

Samways, M.J. 1994. *Insect Conservation Biology*. Chapman & Hall, London.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioural Sciences*. McGraw-Hill, New York.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* **19**, 473-511.

Usher, M.B. 1986. Wildlife conservation evaluation: attributes, criteria and values. In Usher, M.B. (Ed.). *Wildlife Conservation Evaluation*. Chapman & Hall, London, 3-44.

Walker, B.H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* **6**, 18-23.

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CHAPTER 7

An analysis of community organization: scale, the interaction continuum and community properties

A quantification of the structure and functioning of the Lepidoptera community in *Ravenelia macowaniana* Pazschke galls on *Acacia karroo* Hayne has made it possible to identify factors both within and external to the community that play a role in community organization. This quantification process determined resource parameters, temporal activity patterns, species identities, intra- and interspecific interactions, habitat quality and climate correlates with community structure, spatial community concordance and the contribution of species to community structure (Chapters 1 to 6).

As discussed (see General Introduction), it is particularly important at the start of such a study to clearly define the community. It is equally vital, however, to clearly define scales of resolution when searching for mechanisms or processes of community organization. Therefore, just as there are three spatial levels of organization to which the term community is applied (*i.e.* the individual gall, the local host-plant population, and the regional set of Lepidoptera species in the association) in the association between *R. macowaniana* galls and the Lepidoptera that inhabit them, so there is a minimum of three scales of resolution to the processes involved in community structure and functioning. These scales lie on a continuum and processes may not fall clearly into a single scale category. Nevertheless for ease of analysis this distinction is appropriate (Holt 1993). The smallest scale at which community organization processes operate in this community is within the individual habitat unit, or gall. Mesoscale processes then operate at the level of the "cluster of local communities connected by dispersal" (Ricklefs & Schluter 1993), and for the purpose of this analysis this level is taken as each locality from which galls were sampled (see Table 1.1, Chapter 1). A combination of factors operating at the habitat unit level and mesoscale contribute to local organizational processes. The regional scale of organization then refers to inter-locality comparisons between these sites, distributed in an approximately north-south gradient across South Africa (see Figure 1.2, Chapter 1). Last, the structure of natural communities are also always a reflection of geographical, evolutionary and historical processes, *e.g.* speciation, vicariance and dispersal. These operate at very large spatial and temporal scales (Holt 1993;

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Ricklefs & Schluter 1993), and are therefore beyond the scope of this study.

Although it is widely recognized that processes at all the above scales contribute to the structure and functioning of terrestrial communities, the relative importance of these vary between communities and systems (Hunter & Price 1992; Levin 1992; Ricklefs 1987; Ricklefs & Schluter 1993). As previously discussed, regional processes have traditionally been invoked as the primary determinants of the structure of herbivorous insect communities. Local processes may, however, be equally important, if not more so, for herbivore insect communities feeding on discrete plant structures (Damman 1993) (see General Introduction). These communities may be interactive or non-interactive depending on the presence or absence of strong biotic interactions between members of the local community (Cornell & Lawton 1992). Once again herbivore insect communities are commonly thought to be non-interactive (Strong *et al.* 1984).

Communities are most effectively used in monitoring environmental change once the relative roles of regional and local processes in their organization have been elucidated, and once the position of the community on the continuum from interactive to non-interactive has been established. In order to predict the types of changes in community structure that can be expected under either conditions of changing habitat quality and/or climate changes, and to select appropriate yardsticks for monitoring these changes, it is necessary to understand the extent to which each community property (*i.e.* community seasonality, larval density, species richness, evenness and composition) is affected by mechanisms operative at each spatial scale.

This chapter thus presents a synthesis of the community structuring processes operative at local (habitat unit and mesoscale) and regional scales, and a discussion of the interactive state of the Lepidoptera community in *R. macowaniana* galls. A comparison is made between this and other herbivore insect communities. The mechanisms affecting each attribute of community structure and functioning are then examined to provide appropriate measures for monitoring particular types of environmental change at different scales.

Community structure at the habitat unit level

Larval survival, density, body mass and community functioning in individual galls are influenced by direct and interactive effects between resource conditions, intraspecific and interspecific competition, and, to a limited extent, parasitism.

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The seasonality of resource availability is the primary driving force behind the temporal organization of the Lepidoptera community in *R. macowaniana* galls and the galls are characteristically ephemeral and temporally discrete in nature. Within-season community structure is primarily determined by the stage of gall development and the resource condition (quality and quantity) of individual galls. Because *R. macowaniana* galls are an ephemeral resource, the gall development process is one of the major determinants of the presence and abundance of species and individuals in galls. Resource conditions are often important factors structuring natural communities and host plant phenology plays an important role in the population dynamics of herbivorous insects (Connor *et al.* 1994; Hunter 1990; Tilman 1982). Seasonal changes in gall tissue quality in this community facilitate structural changes in the community between mid-summer (January and February) and late-summer communities (March) as well as between summer and winter communities (see Chapter 5). In addition, gall mass is not only a reflection of the size of the galls, but also of gall tissue quality. As the gall ages, or is increasingly consumed by Lepidoptera larvae, the rate of gall dehydration increases and the mass of the gall decreases. The significantly positive relationship found between gall mass and larval density therefore suggests that community structure at this level is largely influenced by resource condition.

Intraspecific and interspecific aggregation and positive species associations and abundance covariations were found in the galls. Limits to larval density and body mass compensation effects were also detected. Resource limitation within individual galls thus affects adult fecundity and the contribution of species to community structure the following season (Chapter 3). In contrast, the level of parasitism was very low and has only a limited effect on population abundances in the community. These mechanisms of community structure and function are unusual in comparison to many other studies of herbivore insect communities. Herbivore insects have seldom been shown to closely track the availability of host-plant resources and have commonly been demonstrated as maintained at low population levels by parasitoids and predators (Claridge 1987). However, these patterns are not unusual in comparison to studies of other insect communities feeding on discrete, ephemeral and patchily distributed resources (Atkinson & Shorrocks 1984; Doube 1987; Hanski 1981, 1983; Kneidal 1985). Elton (1949) termed discrete, ephemeral community units "centres of action" and it has since been shown that these "centres of action" are often patchily distributed and characterized by strongly aggregated distributions of individuals (Shorrocks & Rosewell

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1987), as was found for *R. macowaniana* galls and the Lepidoptera community. This patchiness and high intraspecific aggregation is thought to account for the high species richness of communities utilizing such resources. Although significant interspecific aggregation also occurred in *R. macowaniana* galls, patchy gall distribution and intraspecific aggregation may account for the high species richness of the Lepidoptera community. An alternative mechanism promoting species coexistence on patchy, ephemeral resources is resource partitioning (Shorrocks & Rosewell 1987). No spatial or temporal resource partitioning was however found in the community occupying *R. macowaniana* galls (Chapter 3). Resource mediated factors, *i.e.* gall availability, distribution and quality, as well as competition are, thus, the dominant organizational mechanisms within habitat units.

Mesoscale community structure

The structural mechanisms at this level (within localities) of organization of insect communities are likely to include a combination of the choice of oviposition site by adult moths, local resource distribution and abundance, intra- and interseasonal variation in gall seasonality and development, as well as unique features of local habitat quality.

According to optimal foraging theory herbivore insects select oviposition sites that will provide the highest quality resources to the developing larvae after hatching, although patterns of oviposition site choice are also influenced by the spatial and temporal availability of host plants or plant structures (Koricheva & Haukioja 1994; Pyke *et al.* 1977; Williams 1983). The high percentage occupancy of *R. macowaniana* galls and the high spatial concordance in community structure suggests that the adult moths actively select galls as preferential oviposition sites (possibly as a result of their high nitrogen and moisture content) or at least recognize them as such. The positive intra and interspecific aggregation of species in galls provides further support for efficient gall location by the adult moths. However, as discussed above, the patchy distribution of *R. macowaniana* galls appears to facilitate the coexistence of more species at the mesoscale than are accommodated in single galls (Shorrocks & Rosewell 1987). Similarly, spatial models of species interactions analyzed by McLaughlin & Roughgarden (1993) show that regional and local species diversity is strongly influenced by the interaction between environmental variability (patchiness) and species dispersal characteristics. The species diversity of communities is highest when dispersal rates are moderate in patchy environments (McLaughlin & Roughgarden 1993). The dispersal rates

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of the Lepidoptera species in this community are moderate, because although the larvae are sedentary within galls the adults are capable of rapid dispersal. Rapid or slow dispersal rates under patchy environments result in far lower local diversity (McLaughlin & Roughgarden 1993).

The onset of galling and the duration of the gall development period is determined by tree water status, tree age, and the present season's rainfall pattern. As discussed in Chapter 1, this is highly variable. Community development may proceed only once gall development has begun, and may occur as early as November in some localities and only by late January in others. The duration of community activity may also be as short as two months or extend over a period of four months, once again dependent on rainfall conditions and tree water status.

Local habitat quality also plays a role in determining community structure and functioning at this level and the larval density, species richness, species composition and the evenness of the relative abundance distribution of the Lepidoptera community is affected by habitat patch size and isolation, the level of physical disturbance in the patch and the proximity of agroecosystems (see Chapters 4 and 5). Other studies of the impact of habitat quality on terrestrial insect communities show similar results (*e.g.* Brown 1993; Dempster 1991).

Once again, therefore, resource abundance and seasonality as a result of local variation in rainfall patterns have a marked effect on community structure and functioning, as do features of local habitat quality. Although only supported by speculation in this study, the location of galls by adult moths and choice of oviposition site must also play an important role in local community organization.

Regional determinants of community structure and functioning

Because the distribution of the association between *R. macowaniana* galls and the Lepidoptera community is widespread, the community functions within a range of climatic conditions. Regional differences in community structure were shown to be correlated with total annual rainfall and annual rainfall variability. Regional climate differences were also responsible for differences in the seasonality of community activity (Chapter 5). The structure of insect and other communities has frequently been shown to be strongly correlated with climate gradients across continents and subregions (*e.g.* Currie 1991; Dennis & Shreeve

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1991). On a regional level, therefore, climate has an influence on the structure and functioning of the Lepidoptera community.

The relative contribution of local and regional processes

From the above discussion it is clear that both local (biotic and abiotic, bottom-up and top-down) and regional processes are involved in determining the structure and functioning of the Lepidoptera community in *R. macowaniana* galls (Fig. 7.1). Of these processes, failed gall development, although sporadic, has the most severe effect on Lepidoptera community structure (local community extinction), and is a phenomenon associated with local weather cycles of drought and good rainfall seasons (Chapter 1). These cycles and their frequency and severity are, however, a consequence of global climate conditions and thus can be considered a regional, rather than a local process. It could, however, be argued that during periods of normal gall development local processes have greater potential to induce changes in community structure, overriding regional process effects. Local habitat disturbances are generally irreversible, short-term, intraseasonal occurrences that have severe effects on local community structure (reducing species richness, larval density and evenness of relative abundance distributions). In contrast, the effects of regional climate change are far slower, although they may be as severe.

The position of the community on the non-interactive - interactive continuum

Because both local and regional processes were found to influence the structure and functioning of the Lepidoptera community, how does this community compare to other herbivore insect communities that have mostly been categorized as non-interactive?

Two models for non-interactive communities are provided by Strong *et al.* (1984). In the first model, community structure results from colonists having a limited ability to invade a habitat and the community therefore remains unsaturated and non-interactive. In the second, the species richness of the local community is dependent on extrinsic recolonization as a result of density-independent fluctuations in the abiotic environment. The latter is considered to be characteristic of many insect communities on their host plants (Abbott *et al.* 1992; Cornell 1993; Strong *et al.* 1984). In contrast, the Lepidoptera community in *R. macowaniana* galls was shown to be interactive in at least two localities (Chapter 5). However, the presence of interactions between larvae was partly dependent on the density

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of individuals in the gall, and although this density was reached in a large number of galls at Aston Bay and Sundays River Valley (the localities used for the analysis in Chapter 5), there were instances where larval densities were below this threshold (Chapter 5). Nevertheless, even where the latter was true, priority effects could still occur whereby later occupants will encounter lower quality plant tissue as a result of previous feeding by other individuals (Chapter 5). The type and level of competition between species in the galls was, therefore, not classical, strong and direct competition that results in competitive exclusion and negative species associations and abundance covariations (Arthur 1987; Wootton 1994). Therefore, although the community is interactive, it is not consistently so and the interactions are indirect, resource-mediated and may be weak.

Alternatively, strong biotic interactions between residents in a community produce strongly interactive communities. Communities saturated with species are interactive, although species saturation is not a necessary condition for a community to be interactive (Cornell 1993). Characteristics of saturated communities include density compensation as a result of species interactions, niche shifting, a high ratio of core to satellite species (Hanski 1982), and an absence of empty niches (Cornell 1993). The Lepidoptera community in *R. macowaniana* galls satisfies some of these criteria. Competitive interactions occur and the ratio of core to satellite species is high (seven common and concordant versus four rare and non-concordant species (see Chapter 6 and Hanski 1982)). Empty niches are absent in this community, and the gall resource is extensively utilized with over 90% occupancy, although it's patchy distribution may permit colonization of the community by additional species without resulting in the loss of resident species. No niche shifting by species was evident.

If a community is non-saturated on the other hand, the number of species in the community would either be in a state of stochastic equilibrium, or limited as a result of 'pool-exhaustion' (Cornell 1993). The species richness of this community is, however, certainly not set by a stochastic equilibrium because the species turnover rate is not high, nor is there a high ratio of satellite to core species in the community. The community meets some of the conditions for a non-saturated community as a result of 'pool exhaustion', *i.e.* the species turnover is low, no niche-shifting is evident, and competition occurs (Cornell 1993). The last condition for local 'pool-exhaustion' is however also the presence of 'obvious empty niches' (Cornell 1993) and once again no empty niches are evident in this community.

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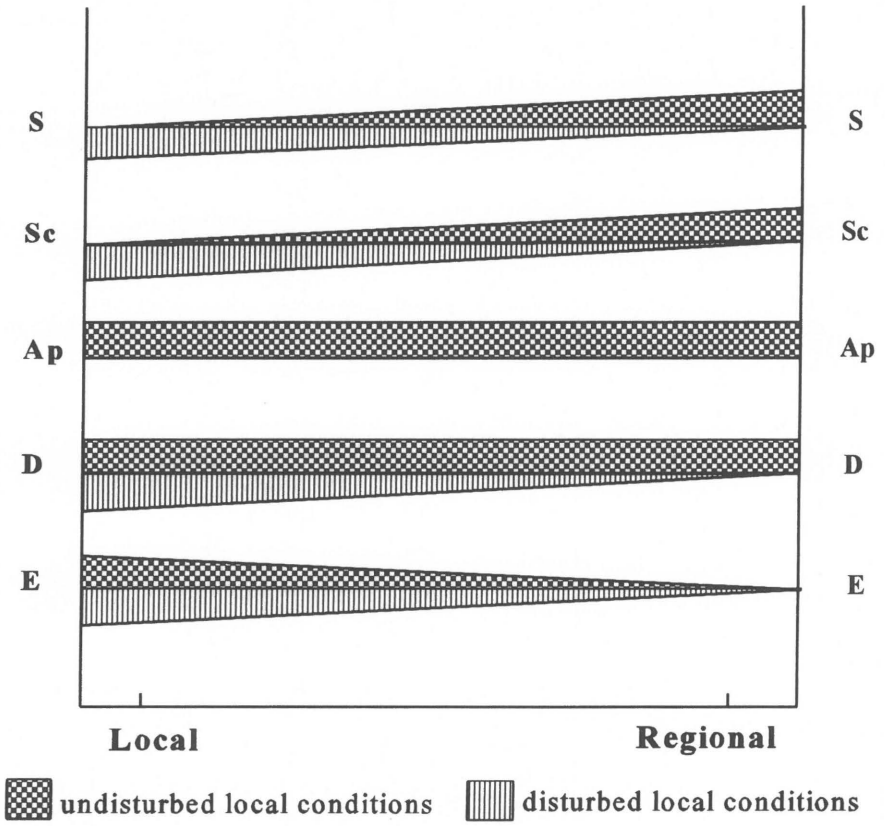

Fig. 7.1. The relative contribution of local and regional processes, and disturbed and undisturbed habitat conditions, to the value of each component (property) of community structure; S, species richness; Sc, species composition; Ap, activity period of community; D, larval density; E, evenness of relative abundance distribution (listed from greatest regional to greatest local process contribution); height of bars on y axes reflect the relative contribution of local and regional processes to the value of each community property.

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Some evidence therefore exists in favour of both non-interactive, and interactive-saturated models. There are two broad classes of interactive models, *i.e.* niche-heterogeneity and spatio-temporal heterogeneity models (Cornell 1993). The Lepidoptera community does not fit into the class of niche-heterogeneity models as no observable niche partitioning occurs between community members (MacArthur 1972; Tilman 1985). One of the spatio-temporal models, however, appears to apply best to this Lepidoptera community, *i.e.* the aggregation model by Shorrocks & Rosewell (1986). In this model the aggregated utilization of fragmented habitats reduces the overall intensity of competition (as was the case in the Lepidoptera community) and a ceiling to local species richness is predicted (Cornell 1993; Shorrocks & Rosewell 1986). In addition, niche space need not be partitioned for coexistence to occur. The other spatio-temporal models predict temporal changes in species composition and relative abundances (Hubbell & Foster 1986; Sale 1977), habitats characterized by periodic disturbances coupled with slow population growth rates (Huston 1979), and spatial variation in the risk of attack by specialist predators (Armstrong 1989) (Cornell 1993). None of these correspond with the findings on the structure and functioning of the Lepidoptera community in *R. macowaniana* galls. Shorrocks and Rosewell's (1986) model therefore seems most appropriate.

These processes of community organization in the Lepidoptera community are very different from the dominant organizational processes in bracken communities (and numerous other herbivore insect communities, see *e.g.* Abbott *et al.* 1992; Bultman & Faeth 1985; Cornell 1993; Strong 1982). The latter are characterized by obvious vacant niches, an absence of species interactions, stochastic colonization over time and no detected ceiling to species richness (Lawton *et al.* 1993). The Lepidoptera community in *R. macowaniana* galls, therefore, has more in common with communities associated with other ephemeral, patchily distributed resources, *i.e.* rich diversity of coexisting species, high levels of intraspecific aggregation, competition and frequent absence of resource partitioning (Atkinson & Shorrocks 1984; Doube 1987; Hanski 1981, 1983; Kneidal 1985, Shorrocks & Rosewell 1987) than with herbivore insect communities in general. However, this perception may partly be a function of the fact that past conclusions on the paucity of competition in herbivore insects were based largely on studies of folivore guilds, the inference of the presence or absence of interspecific competition from insect distributional data (Connor & Bowers 1987), and the search for strong, consistently symmetrical and direct competition

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between species (Denno *et al.* 1995; Faeth 1987). In contrast, interactions have recently been found to be most frequently detected between species feeding on discrete resources (seeds, fruits and stems) and most interspecific competitive interactions have been shown to be mostly asymmetrical and indirect (Damman 1993; Denno *et al.* 1995). Interspecific interactions can also not be directly inferred from insect distributional data (Denno *et al.* 1995).

Processes affecting the properties of community structure

Now that the major organizational processes and their scales of functioning have been established for the Lepidoptera community in *R. macowaniana* galls, the processes affecting individual community properties can be examined. Each property of the community may be most sensitive to particular aspects of environmental change and therefore identifying the most important mechanisms behind individual community properties provides 'key measures' to be used in specified monitoring programmes. The properties quantified were the time and duration of community activity, the density of individual Lepidoptera larvae in the galls, the species richness and evenness of the relative abundance distributions of species in the community at each locality, and the identity of the species (species composition) in the community.

i. Activity period

The timing and duration of Lepidoptera larval activity in *R. macowaniana* galls is determined primarily by the seasonality of gall development (see Chapter 1). The activity of the community that inhabits live galls is, thus, restricted both to particular months each year (commonly January to March) and to the absolute duration of live-gall availability. Both the timing and duration of local gall development are dependent on local rainfall conditions and, therefore, vary from season to season. Regional climate conditions, however, also affect the timing and duration of local larval activity. At coastal localities, with higher annual rainfall and comparatively aseasonal rainfall patterns, the gall development period begins earlier and is of longer duration than gall development at lower rainfall, seasonal localities. In addition, a unique winter, dead-gall inhabiting Lepidoptera community is active under more aseasonal climate conditions. Local weather patterns have the potential to decrease the duration of larval activity in the galls by the late onset of summer rains and lower than average rainfall.

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This was particularly evident at Parys during the 1994 season where live galls, and larvae, were present only between January and late February under conditions of late and below average rainfall. In contrast, regional climate conditions determine the potential maximum duration of larval activity, as well as the presence of a winter-gall inhabiting Lepidoptera community. Therefore, local interseasonal variation in weather conditions, as well as regional climate conditions are particularly important determinants of the structure and functioning of the community (Fig. 7.1). The seasonality of the activity period in galls, thus, provides a sensitive gauge for monitoring the impact of climate change.

ii. Larval density

The number of individual Lepidoptera larvae in galls was positively correlated with gall mass (Chapter 5) and, because gall mass is affected by tree water status (Chapter 1), local variation in rainfall and regional climate patterns indirectly affect larval density. The upper limit to larval density in the galls was, however, determined by resource mediated competition between members of the community (Chapter 3). Local habitat disturbance that causes a reduction in resource availability, *e.g.* fire, may, however, result in above average larval densities with concomitant strong, asymmetrical interspecific competition (Chapter 4). Parasitism and predation do not have a significant effect on larval densities (Chapter 1), but below average larval densities may occur as a result of small habitat patch size (*i.e.* the area supporting the *A. karroo* population) and a high degree of patch isolation (Chapter 4). Once again, therefore, both local (including biotic interactions and natural weather events) and regional processes (climatic conditions) influence the larval density component of community structure, although local disturbance conditions can have a marked impact on this property of community structure (Fig. 7.1).

iii. Species richness

The upper limit to the species richness of local gall-inhabiting communities is determined by regional climate variables (Chapter 5), whereas the species richness of a particular locality may be reduced by local habitat disturbance (Chapter 4) (Fig. 7.1). High annual precipitation and a low coefficient of variation in the annual precipitation pattern was associated with high species richness at Aston Bay, Sundays River Valley and Richards Bay, whereas low total precipitation at Bloemfontein was associated with low species richness

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(Chapter 5). In addition, at Moreleta Nature Reserve, a species richness lower than the local species richness was associated with habitat disturbance in the form of fire (Chapter 4). Species richness is, thus, largely determined by regional processes, but may be modified under disturbed local habitat conditions (Fig. 7.1).

v. Species composition

The presence or absence of particular species at each locality was determined primarily by regional climate differences and secondly by local habitat quality conditions (Fig. 7.1). A number of unique species were present at coastal localities, including species inhabiting dead-galls during winter (Chapter 5). The local impact of an adjacent agroecosystem not only resulted in the invasion of an additional pest species, but the two pest species in the community at this locality were present in above average abundances (Chapter 6). Similarly to species richness, this property of community structure is primarily determined by regional processes, but may be modified by local habitat quality.

v. Evenness of relative abundance distribution

Evenness was a useful index of local habitat quality conditions (Chapter 4), whereas it showed no trends in the analysis of community differences between localities with different climate regimes (Chapter 5). Similarly, the relative abundance distributions of the nine localities sampled across South Africa show no distinction between coastal and inland localities (Fig. 7.2a), as were identified using multivariate ordination techniques (Chapter 5). Fig. 7.2b. shows the log relative abundance distributions of the four localities, with different disturbance regimes, sampled within the Pretoria area (see Chapter 4). The distribution of the urban nature reserve (Moreleta) and the industrial site (Proclamation Hill) are less even and have a sharper decline (*i.e.* greater species dominance, Magurran 1988) than the two rural sites (Hartebeespoort and Pienaarspoort) (Fig. 7.2b). Relative abundance distributions appear to be more useful at a local comparative level than on a regional scale, and evenness values and relative abundance distributions appear to be determined largely by local habitat quality conditions (Fig 7.1).

In summary, properties of the moth community in *R. macowaniana* galls that should be monitored closely in order to detect changes in climate, include increases or decreases in maximum local species richness, and the loss of, or gain to, the community of dead-gall

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inhabiting Lepidoptera species. Medium to long-term shifts in the duration of the gall development and larval activity periods will also be indicative of regional climate change.

Properties that may be used to monitor closely local deterioration in habitat quality are decreases in the evenness of species relative abundance distributions, marked increases or decreases in larval density and medium to long term loss of species from the community.

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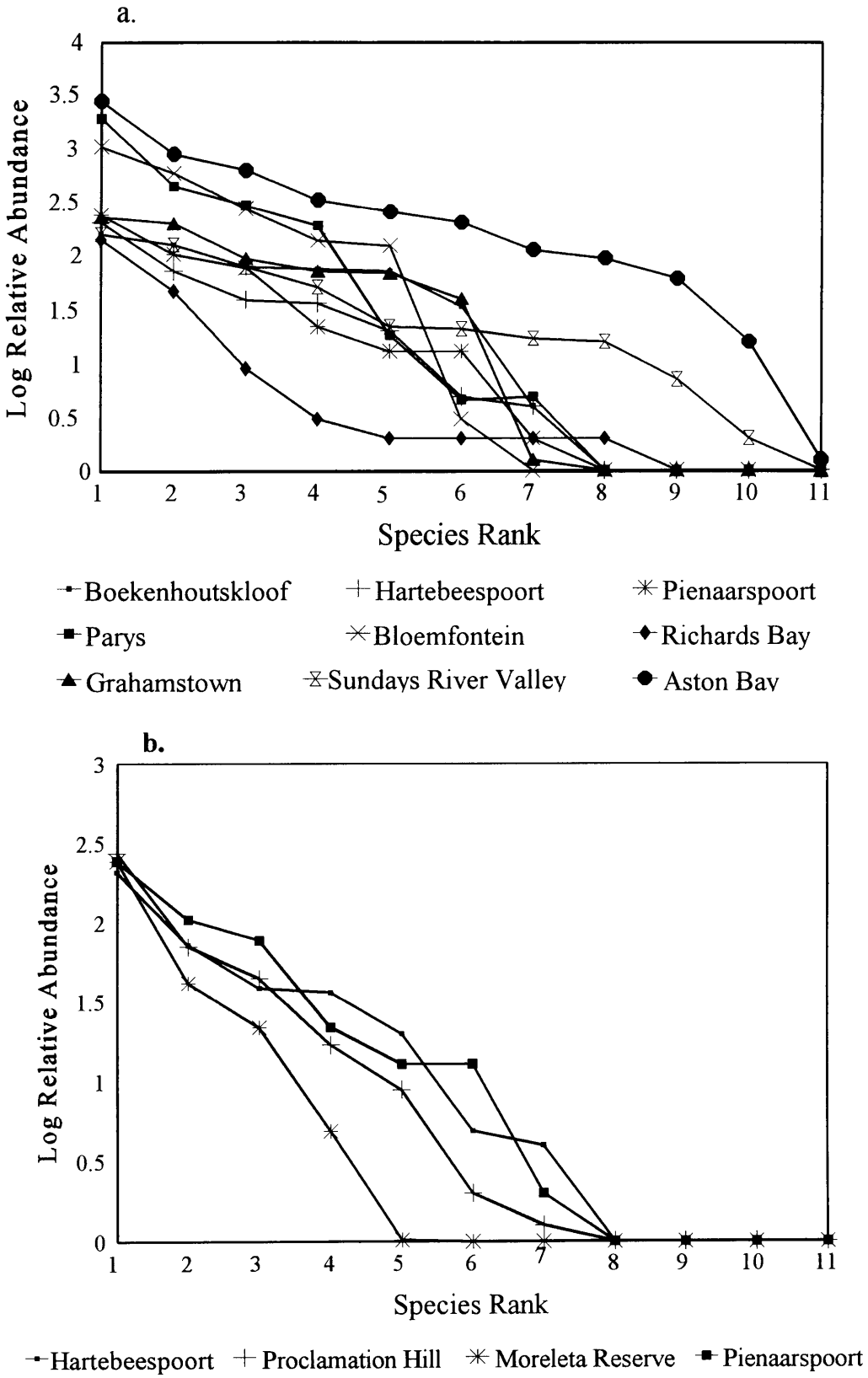

Fig. 7.2 a and b. Rank abundance plots of log relative abundance of species in the Lepidoptera community from a. all nine localities and b. localities used in the habitat disturbance study.

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REFERENCES

Abbott, I., Burbridge, T., Williams, M. & Van Heurk, P. 1992. Arthropod fauna of jarrah (*Eucalyptus marginata*) foliage in mediterranean forest of Western Australia: spatial and temporal variation in abundance, biomass, guild structure and species composition. *Australian Journal of Ecology* **17**, 263-274.

Armstrong, R.A. 1989. Competition, seed predation, and species coexistence. *Journal of Theoretical Biology* **141**, 191-194.

Arthur, W. 1987. *The Niche in Competition and Evolution*. John Wiley & Sons, New York.

Atkinson, W.D. & Shorrocks, B. 1984. Aggregation of larval Diptera over discrete and ephemeral breeding sites: the implications for coexistence. *The American Naturalist* **124**, 336-351.

Brown, M.W. 1993. Resilience of the natural arthropod community on apple to external disturbance. *Ecological Entomology* **18**, 169-183.

Bultman, T.L. & Faeth, S.H. 1985. Patterns of intra and interspecific association in leaf-mining insects on three oak species. *Ecological Entomology* **10**, 121-129.

Claridge, M.F. 1987. Insect assemblages - diversity, organization, and evolution. In Gee, J.H.R. & Giller, P.S. *Organization of Communities Past and Present*. Blackwell Scientific, Oxford, pp. 141-162.

Connor, E.F., Adams-Manson, R.H., Carr, T.G. & Beck, M.N. 1994. The effects of host plant phenology on the demography and population dynamics of the leaf-mining moth, *Cameraria hamadryadella* (Lepidoptera: Gracillariidae). *Ecological Entomology* **19**, 111-120.

Connor, E.F. & Bowers, M.A. 1987. The spatial consequences of interspecific competition. *Annales Zoologici Fennici* **24**, 213-226.

Cornell, H.V. 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. In Ricklefs, R.E. & Schluter, D. (Eds). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 243-252.

Cornell, H.V. & Lawton, J.H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**, 1-12.

Currie, D.J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist* **137**, 27-49.

Damman, H. 1993. Patterns of interaction among herbivore species. In Stamp, N.E. & Casey, T.M. (Eds). *Caterpillars Ecological and Evolutionary Constraints on Foraging*. Chapman & Hall, New York, pp. 132-169.

Dempster, J.P. 1991. Fragmentation, isolation and mobility of insect populations. In Collins, N.M. & Thomas, J.A. (Eds). *The Conservation of Insects and their Habitats*. Academic Press, London, pp. 143-153.

Dennis, R.L.H. & Shreeve, T.G. 1991. Climate change and the British butterfly fauna: opportunities and constraints. *Biological Conservation* **55**, 1-16.

Denno, R.F., McClure, M.S. & Ott, J.R. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology* **40**, 297-331.

Doube, B.M. 1987. Spatial and temporal organization in communities associated with dung pads and carcasses. In Gee, J.H.R. & Giller, P.S. (Eds). *Organization of*

Digitised by the Department of Library Services in support of open access to information, University of Pretoria, 2021

Communities Past and Present. Blackwell Scientific, Oxford, pp. 255-280.

Elton, C. 1949. Population interspersion: an essay on animal community patterns. *Journal of Animal Ecology* **37**, 1-23.

Faeth, S.H. 1987. Community structure and folivorous insect outbreaks: the role of vertical and horizontal interactions. In Barbosa, P. & Schulz, J.C. (Eds). *Insect Outbreaks*. Academic Press, New York, pp. 135-171.

Hanski, I. 1981. Coexistence of competitors in patchy environments with and without predation. *Oikos* **38**, 210-221.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**, 210-221.

Hanski, I. 1983. Coexistence of competitors in patchy environments. *Ecology* **64**, 493-500.

Holt, R.D. 1993. Ecology at the mesoscale: the influences of regional processes on local communities. In Ricklefs, R.E. & Schluter, D. (Eds). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 77-88.

Hubbell, S.P. & Foster, R.B. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. In Diamond, J. & Case, T.J. *Community Ecology*. Harper & Row, New York, pp. 314-329.

Hunter, M.D. 1990. Differential susceptibility to variable plant phenology and its role in competition between two insect herbivores on oak. *Ecological Entomology* **12**, 373-382.

Hunter, M.D. & Price, P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**, 724-732.

Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* **113**, 81-101.

Kneidal, K.A. 1985. Patchiness, aggregation, and the coexistence of competitors for ephemeral resources. *Ecological Entomology* **10**, 441-448.

Koricheva, J. & Haukioja, E. 1994. The relationship between abundance and performance of *Eriocrania* miners in the field: effects of the scale and larval traits studied. *Journal of Animal Ecology* **63**, 714-726.

Lawton, J.H., Lewinsohn, T.M. & Compton, S.G. 1993. Patterns of diversity for the insect herbivores on bracken. In Ricklefs, R.E. & Schluter, D. (Eds). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 178-184.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**, 1943-1967.

MacArthur, R.H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Harper & Row, New York.

Magurran, A.E. 1988. *Ecological Diversity and its Measurement*. Croom Helm, London.

McLaughlin, J.F. & Roughgarden, J. 1993. Species interactions in space. In Ricklefs, R.E. & Schluter, D. (Eds). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 89-98.

Pyke, G.H., Pulliam, H.R. & Chanov, E.L. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* **52**, 137-154.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**, 167-171.

Ricklefs, R.E. & Schluter, D. 1993. Species diversity: regional and historical influences. In

Digitised by the Department of Library Services in support of open access to information, University of Pretoria, 2021

Ricklefs, R.E. & Schluter, D. (Eds). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 350-364.

Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. *The American Naturalist* **111**, 337-359.

Shorrocks, B. & Rosewell, J. 1986. Guild size in drosophilids: a simulation model. *Journal of Animal Ecology* **55**, 527-541.

Shorrocks, B. & Rosewell, J. 1987. Spatial patchiness and community structure: coexistence and guild size of drosophilids on ephemeral resources. In Gee, J.H.R. & Giller, P.S. (Eds). *Organization of Communities Past and Present*. Blackwell Scientific, Oxford, pp. 29-52.

Strong, D.R. 1982. Harmonious coexistence of hispine beetles on *Heliconia* in experimental and natural communities. *Ecology* **63**, 1039-1049.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific, Oxford.

Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton.

Tilman, D. 1985. The resource ratio hypothesis of succession. *The American Naturalist* **125**, 827-852.

Williams, K.S. 1983. The coevolution of *Euphydryas chalcedona* butterflies and their larval host plants. III. Oviposition behaviour and host plant quality. *Oecologia* **56**, 336-340.

Wootton, J.T. 1994. The nature of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**, 443-466.

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CHAPTER 8

Prospects for environmental monitoring: an evaluation of the bioindicator potential of the gall-inhabiting moth community

The criteria that determine which species constitute good biological indicators and, in particular, good insect indicators have been discussed by numerous authors (Brown 1991; Holloway 1980; Holloway & Stork 1991; Kremen 1992; Kremen *et al.* 1993; Lenhard & Witter 1977; Noss 1990; Pearson & Cassola 1992; Spellerberg 1991) and there is mostly agreement on these. There have also been numerous exposes on the need for, and requirements of, ecological monitoring programmes (Kremen *et al.* 1994, Lubchenco *et al.* 1991, Kingsolver 1993).

The characteristics of a good bioindicator, or monitoring programme, are nevertheless largely dependent on the environmental issue being addressed, as well as on the spatial scale at which the latter operates. For example, the features of an indicator of the impact of local industrialization are likely to be different to those features of an indicator of regional changes in climate conditions. A bioindicator, however, is always a species, or community, indicating the condition of the environment (Spellerberg 1991) and all species are, therefore, potential indictors. The presence or absence, size, fecundity and population abundances of species will always be a reflection of the state of their immediate environment (Lenhard & Witter 1977). However, not all organisms respond rapidly and conspicuously to changes in the environment, and it is those species that do that provide the most useful signals of the impact of anthropogenically induced, or other, environmental change.

In addition, assemblages of species provide "finer gauges of biotic responses" (Kremen 1992) than do individual species. Assemblages, or communities, can also be used for monitoring at two biological levels (Kremen 1992). Monitoring the entire community can be used to track the response of that community to a specified environmental change (Kremen 1992), whereas monitoring individual species populations within the community can be used to select the most sensitive species to be used in more intensive monitoring (Kremen 1992; McGeoch 1994). Monitoring species groups, rather than individual species populations, therefore encompasses a degree of ecological complexity that provides a compromise between cost, in terms of person-hours and funding, and information content (McGeoch 1994). It also

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facilitates the identification of pivotal and indicator species, and it is these species that can provide mechanistic ecophysiological information regarding the impact of environmental change on organisms (McGeoch 1994). Interactions between species, which can best be identified at the most inclusive, *i.e.* community, level, are considered to be the elements of biotic systems most sensitive to environmental change (Carpenter *et al.* 1993). In addition, some of the longest-term ecosystem studies, those on the effects of chemical stressors on lakes, have shown that many of the most sensitive indicators of ecosystem change were community variables such as species diversity, food chain length, distribution of life history strategies, and sizes and life spans of organisms (Carpenter *et al.* 1993). Using invertebrate communities as monitoring tools is thus a bet-hedging approach which offers the fastest and safest route to the detection of change in ecosystems.

The goal of a monitoring programme is, therefore, to evaluate changes in the composition, structure and functioning of ecosystems over time in response to anthropogenic changes (Kremen *et al.* 1993). The role of indicators in monitoring programmes is twofold: as indicators of changes in the state of the environment, and as indicators of the impact of these environmental changes on biotic systems. The former role is often better achieved by direct measurement of the changing environmental variable itself, *e.g.* air pollution levels or changes in atmospheric carbon dioxide levels (Kremen 1992; Noss 1990). Understanding the responses of particular terrestrial communities to environmental changes, however, makes an important contribution to understanding ecosystem functioning as a whole, and will be crucial to the future conservation of biotic diversity and maintenance of ecosystem functioning.

The aim of this study was, therefore, to determine the response of the Lepidoptera community in *Ravenelia macowaniana* Pazschke galls to habitat quality, in the form of patch isolation, air pollution and physical disturbance, as well as to a range of climate regimes. Based on the results of the previous seven chapters, this chapter now provides an evaluation of the suitability and efficacy of the Lepidoptera community as a bioindicator and its potential use in an environmental monitoring programme.

Qualities of suitable and effective arthropod indicator communities

Suitable and effective indicators must fulfil criteria in two broad categories, *i.e.* biological efficacy (including taxonomic, distributional, reliability, representation and

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sensitivity criteria) and economic suitability (including financial cost and time efficiency) (Holloway & Stork 1991). These criteria, used in the evaluation of the Lepidoptera community in *R. macowaniana* galls to follow, were extracted from the following sources: Brown 1991; Holloway 1980; Holloway & Stork 1991; Kremen 1992; Kremen *et al.* 1993; Lenhard & Witter 1977; Noss 1990; Pearson & Cassola 1992; Spellerberg 1991.

Evaluation of the bioindicator potential of the Lepidoptera community

i. Biological suitability

Information on the life-history characteristics of species and parameters of a bioindicator community should be easily accessed, quantified, and analyzed to facilitate the rapid collection of large and reliable data sets that can then be interpreted in relation to the environmental changes being monitored.

Sampling and quantification of species abundances in this Lepidoptera community are based entirely on the larval stages of the species resident in *Ravenelia macowaniana* galls. The advantages associated with sampling this life history stage is that the larvae are sedentary with no, to limited, dispersal between oviposition and pupation. In addition each gall represents a discrete habitat unit and habitat variables and population densities are readily quantified. Population estimates are, therefore, not subject to the sampling biases associated with more vagile organisms (Levin 1992).

Restricting sampling to the larval stages, however, means that sampling can only be carried out in three to four months of each year. In addition, no information is gathered on the biology and behaviour of the adult moths. This information is, however, not necessary to complete yearly surveys of population abundances, because adult fecundity and mortality will be reflected in the larval abundances the following season. Kremen (1992) also showed that little specific life history information of species in assemblages is required to enable their use in monitoring.

ii. Taxonomic feasibility

It is vital that the taxonomy of species in indicator communities is sound and stable and that species can be identified by technical and field staff after short training and with the assistance of illustrated manuals. The larval key that was compiled for the species in this community (Chapter 2) can readily be modified for use by the layperson in the form of an

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illustrated manual. Although a compound microscope is required to examine setal structures, the most widespread and abundant species in the community are particularly simple to separate and identify. These five species were also identified as the most typical and discriminant species in the community and, therefore, as potential pivotal species and the best indicator species (Chapter 6). Larval taxonomy is based on the taxonomy of the adult moths, which in eight of the 22 species is uncertain (see Chapter 2). Although the taxonomy of these species is uncertain, terrestrial arthropod species can yet be successfully used for monitoring if they can be accurately identified as morphospecies (Kremen *et al.* 1993). It is, indeed, possible to separate and identify all the species in the Lepidoptera community as distinct morphospecies and the state of the taxonomy of the eight species does, therefore, not prohibit accurate quantification of species abundances and community structure.

iii. Local and geographic distribution

The wider the geographic range and the more diverse the habitat types occupied by an indicator taxon, the broader the range of experimental design and comparison that can be made, and the greater the utility of the taxon as a bioindicator (Pearson & Cassola 1992).

Acacia karroo Hayne, the host of the Lepidoptera-supporting rust-fungus galls, is widespread and often ubiquitous in South Africa and community structure can, thus, be compared between regions with a range of climatic regimes, as was done in this study (Chapter 5). In addition, as a result of the pioneering trait of *A. karroo* it occurs in both naturally and anthropogenically disturbed habitats, as well as in comparatively undisturbed areas. Galls are also present in each of the latter habitat categories and this facilitates the comparison of Lepidoptera community structure between a range of habitat quality conditions (Chapter 4).

Despite the regionally wide distribution of *R. macowaniana* galls, the local distribution of galls on *A. karroo* is patchy and large areas of trees often remain uninfested. However, once a gall-containing patch has been located, these patches tend to house galls yearly. In addition to gall abundance, the Lepidoptera community was present in live galls from every tree sampled across South Africa during the study and the community is, therefore, reliably present.

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iv. Reliability

The spatial and temporal distribution of a bioindicator should be predictable to ensure long-term continuity in a monitoring programme.

Although the same patches of *Acacia karroo* tend to support galls on a yearly basis, it was discovered that local gall development may fail entirely over one or more seasons after prolonged periods of below average rainfall. However, during the four years of this study when gall development failed in a particular locality, adjacent localities experienced normal gall development and sampling did, therefore, not have to be interrupted entirely. In addition, although it is conceivably possible that gall development may not occur at a particular locality for an indefinite period during drought conditions, gall development resumed during this study after only two seasons of absence. Although the phenomenon of gall developmental failure reduces the suitability of the community for monitoring, it does provide interesting opportunities to monitor the effect of habitat fragmentation on recolonization after local community extinction as a result of failed gall development.

v. Representation

The utility of a bioindicator is greatly enhanced if the trends it indicates are a reflection of trends in related and unrelated taxa within the ecosystem (Pearson & Cassola 1992). The larval community in *R. macowaniana* galls is phytophagous and associated exclusively with a specialized parasitic relationship between *Acacia karroo* and the rust fungus. The community is, therefore, representative of the state of lower trophic levels. In addition, because a number of the Lepidoptera species in the community are known to be oligophagous to polyphagous, the gall-inhabiting community also represents a defined subsample of the broader Lepidoptera community.

The invasion of pest species into natural ecosystems as a result of the conversion of land to agricultural production was clearly demonstrated in this community (Chapter 5). *Cryptophlebia peltastica* and *Lobesia stericta* were dominant in the community adjacent to an agroecosystem and *R. macowaniana* galls are potentially host to any boring Lepidoptera pest species in South Africa and, thus, an interesting case-study of the impact of agricultural land expansion.

The relationship between the patterns observed in this Lepidoptera community and other taxa has yet to be tested and no conclusions can presently be drawn concerning its

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degree of representation of the broader plant or invertebrate community, except that the species are not host-specific and could be indicative of the habitat at large.

vi. Sensitivity

A bioindicator must be sensitive to spatial and temporal patterns in the environment and readily and predictably reflect these changes. It should also be possible to differentiate between the natural cycles of the indicator taxon and those changes induced by anthropogenic stress.

The Lepidoptera community in *Ravenelia macowaniana* galls is sensitive to habitat quality and climatic conditions. In addition, a number of the common species, *Cydia (Cydia) victrix*, *Ascalenia pulverata*, *Characoma submediana* and *Anarsia gravata*, were identified as key indicator species and potential pivotal species. The level of dissimilarity between communities from different localities was not particularly high (mostly below 30 %, see Fig. 5.4., Chapter 5) and it may be argued that the discriminant ability of the community is, therefore, not very great. However, species with broad distribution ranges are necessarily less sensitive to climatic variables and this low level of dissimilarity may, therefore, be expected. The community structural differences within the 30 % dissimilarity were, nonetheless, distinct.

vii. Cost efficiency

It is essential that any monitoring programme require minimum time expenditure and be financially viable, particularly if it is to be executed on a long-term basis. Financial, personnel and time constraints will determine both the likelihood of the adoption of such a programme, as well as its long-term continuation. This is particularly important in a developing country with limited resources, such as South Africa, where any conservation programme must be justifiable not only in terms of benefit to the short- and long-term sustainability of natural resources, but must justify present expenditure in relation to more urgent demands for housing, education and social security (Costanza & Daly 1992).

The procedures involved in gall sampling, larval extraction, identification and data analysis of the Lepidoptera community are straightforward and inexpensive. The sampling of galls from a single locality takes between one to three hours, excluding the required travelling time. The greatest financial cost is transport, because little capital or other

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equipment is required. The laboratory equipment that is required includes glass vials, forceps, preservative (Chapter 1), and a dissection and compound microscope.

Once the galls have been sampled, it is possible to extract the larvae, either in the field or in the laboratory, with the aid of a dissection microscope. This process is slightly more time consuming as it must preferably be completed within 48 hours of gall sampling. Two working days (eight hours per day) are generally required for a single person to complete the larval extraction process for a sample of 100 galls. The identification of the larvae can be completed thereafter, when convenient, because the larvae are preserved indefinitely in the prescribed preservative. The process of larval identification for a sample of 100 galls takes a trained person approximately 3 working days. The greatest time constraint is, therefore, to complete the sampling of all localities across the geographic range, a number of times each, during a single three month gall-development period. However, galls can be sampled by independent field workers, kept refrigerated and transported within three days to the central research station.

In total, an estimated 10 persons would be required to spend approximately 20 working days per year (January to March) to complete the season's monitoring. This includes only gall sampling and larval extraction procedures. A further two months are required for a single person to complete the larval identification process and an additional month to complete the data analysis. Considering the geographic range covered and the quantity and information content of the data obtained from the monitoring procedure outlined above, the cost of such an exercise, in terms of person-hours and funding, is not excessive.

CONCLUSION

Although a baseline has been established to use the Lepidoptera community in a regional monitoring programme in South Africa, the predictive ability of this bioindicator can only be improved with long-term monitoring, including additional localities, throughout the region. Understanding the functioning of a single terrestrial biotic system, such as the moth community that inhabits *R. macowaniana* galls on *A. karroo*, provides insight into the possible effects of environmental change on other terrestrial biotic communities. These include a decrease in species population sizes and richness as a result of habitat disturbance, the effect of agroecosystems on natural communities and the loss of species with a decrease in rainfall and climatic equitability. Understanding the system at this level also highlights

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pertinent areas for future research that will most rapidly provide answers on the resilience and sustainability of the system and on interpreting monitored trends, *e.g.* the inclusion of additional coastal localities in monitoring. In addition, by integrating information on other representative biotic communities (*e.g.* plant and soil communities), models on the impact of environmental change on entire terrestrial ecosystems can be constructed. Although the Lepidoptera community in *R. macowaniana* galls fulfills the necessary economic criteria and the majority of the biological criteria (*i.e.* biological, taxonomic, distribution and sensitivity criteria) it only partially fulfills others (representation and reliability). No single indicator will possess all the criteria necessary to be both representative of, and sensitive to, changes within an ecosystem (Noss 1990). A set of complimentary indicator taxa, representing different trophic levels and taxonomic and functional groups, will, therefore, provide the most comprehensive and sensitive monitor of ecosystem changes (Kremen *et al.* 1993; Noss 1990).

The information acquired on the structure and functioning of the Lepidoptera community, across habitat quality and climate gradients, has shown the community to be a sensitive and practicable bioindicator and has provided the baseline information necessary to establish a regional environmental monitoring network (see Dennis & Shreeve 1991). The precision with which predictions of future impacts of development and climate change on the this biotic system can only be improved with continued monitoring, and by expanding monitoring to represent previously unsampled regions. Therefore, although a baseline for such a monitoring programme has been established with this moth community, the full value of this, like any other, monitoring programme lies in a long-term, regional scale, multi-taxon programme (Kingsolver *et al.* 1993).

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REFERENCES

Brown, K.S. 1991. Conservation of neotropical environments: insects as indicators. In Collins, N.M. & Thomas, J.A. (Eds). *The Conservation of Insects and their Habitats*. Academic Press, London, pp. 349-404.

Carpenter, S.R., Frost, T.M., Kitchell, J.F. & Kratz, T.K. 1993. Species dynamics and global environmental change: a perspective from ecosystem experiments. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland. pp. 267-279.

Costanza, R. & Daly, H.E. 1992. Natural capital and sustainable development. *Conservation Biology* **6**, 37-46.

Dennis, R. L. H. & Shreeve, T. G. 1991. Climate change and the British butterfly fauna: opportunities and constraints. *Biological Conservation* **55**, 1-16.

Holloway, J.D. 1980. Insect surveys - an approach to environmental monitoring. *Atti XII Congr. Naz. Ital. Entomol., Roma*, 239-261.

Holloway, J.D. & Stork, N.E. 1991. The dimensions of biodiversity: the use of invertebrates as indicators of human impact. In Hawksworth, D.L. (Ed.). *The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture*. CAB International, London, pp. 37-61.

Kingsolver, J.G., Huey, R.B. & Kareiva, P.M. 1993. An agenda for population and community research on global change. In Kareiva, P.M., Kingsolver, J.G. & Huey, R.B. (Eds). *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland, pp. 480-486.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**, 203-217.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F. & Sanjayan, M.A. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**, 796-808.

Kremen, C., Merenlander, A.M. & Murphy, D.D. 1994. Ecological monitoring: a vital need for integrated conservation and development programs in the tropics. *Conservation Biology* **8**, 388-397.

Lenhard, S.C. & Witter, J.A. 1977. Insects as biological indicators of environmental change. *Bulletin of the Entomological Society of America* **23**, 191-192.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**, 1943-1967.

Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J. & Risser, P.G. 1991. The sustainable biosphere initiative: an ecological research agenda. *Ecology* **72**, 371-412.

McGeoch, M.A. 1994. The use of invertebrate assemblages for environmental monitoring: *status quo* in South Africa and future directions. *Abstracts Volume: Zoological Society of Southern Africa Symposium, Pietermaritzburg July 1994*, p. 93.

Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4**, 355-364.

Pearson, D.L. & Cassola, F. 1992. World-wide species richness patterns of Tiger Beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology* **6**, 376-391.

Spellerberg, I.F. 1991. *Monitoring ecological change*. Cambridge University Press, Cambridge.

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