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Spider Communities in Agricultural Habitats: The Effect of Habitat Interfaces on the Distribution of Species.

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ABSTRACT

Two Sites representing a change in habitat type at a community interface in an agricultural situation between managed and unmanaged areas were sampled using transects of pitfall traps crossing the interface at right angles from one habitat type to the next, during May/June, 1992.

Site 1 consisted of a lightly grazed pasture bordered on one side by a mainly coniferous plantation, with an abrupt interface between the two contrasting community types.

Site 2 consisted of a field of spring barley bordered on one side by a semi natural area of mixed deciduous woodland, with the interface consisting of a boundary approximately 2m wide between the two habitat types.

Community analysis revealed patterns of total spider abundance, species richness, and diversity across the interface.

The Site 1 interface had a negative effect on the numbers present in the pasture, but no significant effect on the numbers in the plantation. Numbers in the pasture were significantly higher than that at the interface and in the plantation. Species richness decreased progressively from the pasture to the plantation, and species diversity increased, with the interface showing intermediate values for both these factors. The transect regions displayed differences in the dominance of groups, with Tetragnathidae and Lycosidae in the pasture replaced by Linyphiidae on approaching the interface and throughout the plantation. Species were influenced in different ways by the habitat change, but most preferred one side of the interface where they occurred in highest abundance.

The Site 2 interface had a positive effect on the numbers of spiders present in the crop and in the woodland. Numbers in the interface samples were significantly higher than in the crop samples. Species richness was higher in the woodland than in the crop, and highest in the

boundary samples Species diversity was higher in the woodland than in the crop traps. The transect regions showed differences in the dominance of groups, with Linyphiidae dominant in both the crop and woodland, and Lycosidae dominant at the interface. Species showed individualistic responses to the change in habitat, with most preferring one side to the other, some were ubiquitous, and a few increased in abundance at the interface.

Similarity indices (Sφrensen and Chi-squared) were calculated to visualise the effects of local faunal exchange between habitat types at each Site, by providing a measure of similarity according to species composition. Both revealed greatest similarity between within-habitat traps than between traps from different sides of the interface. The pasture at Site 1 showed greater similarity to the interface than did the plantation. At Site 2, the interface showed a fairly high degree of similarity to both the crop and woodland.

A classification, according to spider species, was performed in order to determine whether the transect regions on either side of the interface at each Site could be characterised by the species present and their abundances. Both Sites revealed a division between the two habitat types on either side of the interface according to the community composition. This indicated that vegetation structure played an important role in determining the species composition, mediated through the effects of disturbance, as this was the most dramatic change in environmental features between the two regions either side of the interface.

In order to identify further the factors which determined the spider distribution patterns, ordination of the sites and species were performed. Canonical correspondence analysis revealed that vegetation structure was the most important factor influencing spider distribution across the interface at Site 1, and vegetation structure and % soil moisture content were important in determining the spider species distributions at Site 2. This was considered to be related to the degree of management and disturbance of the habitats.

The present study reveals a definite effect of an abrupt change in habitat type between two contrasting communities on the distribution and abundances of spider species. Comparison between Sites 1 and 2 reveal that the effects vary according to the habitat type and structure on either side of the interface, and of the boundary habitat itself. The presence of undisturbed habitats is therefore considered to significantly influence the spider fauna of cultivated land.

The use of invertebrate community analysis is considered in the context of conservation, both for the conservation of species, and for the use of data in monitoring the effects of management practices on wildlife.

CHAPTER 1

INTRODUCTION

1.1 General Introduction

Between two communities, such as grassland and woodland, there is a transitional zone marking the boundary of the two habitat types. A transitional phase between such different types of ecological community is termed an ecotone, and typically has a considerable linear extent but is narrower than the adjoining community areas themselves. The adjoining communities may show strong differences, as in grassland/woodland, where vegetation is at different developmental or successional stages. This is especially the case in habitats managed by man where a hedge or fence may represent the interface, such as in agricultural areas. The ecotonal flora and fauna may contain many organisms typical of the two adjacent communities, plus specialised organisms restricted to the ecotone itself (Terrell-Nield 1986). For this reason it is often observed that the number of species and the population densities of some species are greater here than in the two neighbouring communities. This tendency for increased variety and diversity at community junctions is termed the 'edge-effect'. Abrupt changes in environmental gradients brought about by human activities may therefore influence the distribution of species, thus altering the composition of communities (Uetz 1976).

Agriculture has resulted in the reduction of forests to scattered areas of ancient woodland, separated by grassland, crops , and other open habitats. These patches may be connected by shelterbelts and hedgerows, which are analogous to the forest edge, and thus increase diversity in the agricultural landscape. Agricultural habitats are usually considered as highly unstable, the seasonal pattern of crop growing followed by harvesting and then ploughing imposes a regime of drastic change on the fauna. Less dramatic, but equally widespread, are the effects of seasonal grazing and hay-making on grassland faunas (Duffey 1978). Land management practices often result in changes in abundance, species composition and species diversity within both the plant and animal communities (Haskins and Shaddy 1986). Therefore, there may be a dramatic change across the interface from one community type (managed) to another (unmanaged) in relation to species composition, richness and diversity of invertebrates.

In this study, two areas were chosen, each consisting of an agriculturally managed habitat adjacent to an undisturbed or semi-natural habitat type. The first a lightly grazed pasture, one edge bordered by a mixed, mainly coniferous woodland plantation. The second, an arable field containing spring barley, bordered one side by a bank of mixed oak woodland and dense ground vegetation. The invertebrate community in each area was investigated using transects crossing the interface from one habitat to the other. It was found that at both the sites, the numbers of spiders showed an interesting pattern, which differed between the two sites. It was decided, therefore to concentrate the aim of this study on the spider species distribution, numbers, species richness and diversity across the interface between the two habitat types at each of the study sites.

1.2 Factors infuencing spider communities of agricultural areas

The presence of undisturbed habitats has a significant influence on the spider fauna in cultivated land. For example, Duelli *et al.* (1990) found that semi-natural areas such as wetland or dry meadow contributed at least 60% of the spider fauna in a wheat field. Pioneer species such as *Erigone atra* and *Erigone dentipalpis* (Linyphiidae) are often found in ephemeral or disturbed habitats such as arable crops (Thornhill 1983) and intensively managed pasture. Results of studies have demonstrated the importance of vegetation structure as a habitat component (Rushton, Luff and Eyre 1989), and a study by Rushton, Topping and Eyre (1987) concluded that the management regime and site wetness are the major factors influencing spider communities on grassland sites. The importance of management has long been recognised, and practices such as grazing (Duffey 1962; Cherrett 1964) and cutting regimes have been shown to affect the structure and diversity of grassland spider communities.

Management is considered to affect spider communities by altering the structural diversity of the habitat (Duffey 1978; Greenstone 1984), and experimental manipulation of vegetation structure has been shown to affect spider communities in scrub ecosystems. At the simplest level, agricultural grassland management reduces structural diversity by removal of the vegetation itself. Duffey (1962) illustrated this in limestone grassland, where differential grazing left pockets of high spider diversity in otherwise barren areas subjected to higher grazing pressure.

Studies have revealed that specific plant associations harbour distinct spider faunas. Comparative studies have shown that spider community composition changes with vegetational succession. Changes in family and species composition with ecological succession have been reported, as well as a general increase in species diversity through early and mid succession and a subsequent decrease in spider diversity in the climax community.

The microspatial heterogeneity hypothesis (MacArthur and MacArthur 1961), proposes that habitats which are more diverse structurally will support more species. Greenstone (1984) examined the hypothesis that vegetation structural diversity and prey availability determine diversity in scrub and meadow inhabiting web spider species assemblages along elevational gradients. It was concluded that web spider diversity was significantly correlated with vegetation tip height diversity, but not with prey availability.

It has been suggested that physiognomy of plant communities is an important determinant of spider community composition in that it influences microhabitats and microclimate conditions available to spiders, as revealed in a study of community composition of cursorial spiders along a successional gradient (Bultman, Uetz and Brady 1982). Therefore, changes in plant structure across an interface from one community to another should result in compositional changes in resident spider faunas.

Techniques of ordination and classification have been extensively used to simplify invertebrate community data so that trends in the species composition can be more readily described. Classification and ordination analyses are useful in preliminary examinations in community ecology in that they can be used to create simple models describing the factors determining community structure. Rushton and Eyre (1992) ordinated spider species from a range of grassland sites sampled with pitfall traps, using detrended correspondence analysis (DECORANA) and classified using two-way indicator species analysis (TWINSPAN). Discriminant analysis indicated that the management regime was the most important distinguishing variable between habitat types. Vegetation height, soil moisture and site altitude were also significant discriminators. Rushton and Eyre (1989) sampled spider communities on intensively managed agricultural grasslands using pitfall traps, and investigated the factors affecting the distribution of the communities using TWINSPAN, canonical correspondence analysis (CANOCO) and discriminant analysis. The major factors affecting the communities were altitude and pasture utilisation strategy. Results suggested that the spider communities of intensively managed pastures may reflect the surrounding land use patterns and indicate that spider community data may be of use in assessing the environmental impact of large scale changes in land use such as those brought about by agricultural policy.

Gibson, Hambler and Brown (1992) studied changes in spider assemblages in relation to succession and grazing management. They concluded that most features of the assemblages could be explained by the effects of grazing on plant architecture. Species were characteristic of certain habitats. For example, species characteristic of heavily grazed areas were mainly widespread and common Linyphiidae, reported as characteristic of arable land or other disturbed habitats with poorly developed plant architecture (Rushton, Topping and Eyre 1987). Nyffeler, and Benz (1988a) found that Linyphiidae (*Erigone* spp. and *Oedothorax* spp.) dominated the spider faunas on the ground surface of winter wheat fields and hay meadows, and explained this by the fact that these agroecosystems never get beyond the initial stage of an ecological succession because of the periodical destruction of the field layer by mowing or ploughing, and that in such situations the ground surface is colonised by these so-called pioneer species. These species can disperse by aerial 'ballooning', even as adults. Several are multivoltine (e.g. *Bathyphantes gracilis* and the *Oedothorax* and *Erigone* spp). In addition, species such as *Oedothorax fuscus* and the *Erigone* spp are thermophiles which benefit from the microclimate of short turf (deKeer *et al.* 1989).

As architectural diversity increases through succession or with relaxation of grazing pressure, a variety of other species colonise. Larger, web-building species were found to be the most sensitive to grazing pressure (Gibson, Hambler and Brown 1992). Dispersal and initial colonisation may be relatively quick for spiders, as even the larger web-spinners are capable of aerial dispersal as immatures. The response to structure is dominant and occurs rapidly. Uetz (1979) observed significant positive correlations between spider diversity and litter depth. The deeper the litter layer and the more rigid the plant structures present, the more species accumulate. Those species which need the microclimate or bare ground structure of heavily grazed turf are therefore excluded from later successional and lightly or ungrazed areas.

The effect of management on the presence and relative abundances of spider species may not be solely due to the effect on the vegetation structure. Chemical pesticides and fertiliser treatments may also differentially affect species. In this study, fertiliser was used at Site 2. Kajak (1978) investigated the influence of NPK (nitrogen, phosphorus, potassium) treatment on density, biomass and locomotory activity of spiders. The spider community responds to fertiliser treatment by changes in numerical dominance of species. Larger species (Lycosidae) are replaced by smaller ones (Linyphiidae), and as a result the mean spider biomass and locomotory activity of spiders was reduced on fertilised plots. There were no changes observed in the species diversity of spiders. Values of Simpson's species diversity index were very similar in the fertilised and unfertilised plots. The study found that the concentration of N and P was higher in the bodies of spiders collected in fertilised plots, and was more pronounced in the bodies of larger spiders than in smaller ones. Siepel *et al.* (1989) consider three management measures: fertilisation, mowing, and grazing and describe their effects on community diversity and composition, and on the species abundance of invertebrates. They conclude that low fertilisation levels result in the highest numbers of individuals. Grazing results in lowered diversity and a decrease in numbers on species as compared with no management and with mowing. Mowing results in higher numbers of individuals compared with no management and with grazing in grasslands.

1.2 Aims of present study

Numerous studies have been carried out to determine factors which influence the spider community of particular habitats, and the effects of varying degrees of agricultural management on the species composition, abundance and diversity. This study aims to determine the factors which influence the ground surface spider community along a transect where there exists an abrupt change in habitat type brought about by agricultural practices. It is therefore not a comparison of discrete regions such as separate grassland areas which are subject to different management and or grazing pressures, but rather the investigation of differences in community structure in two close, adjoining areas which have dramatic differences in vegetation type and structure with one managed and the other undisturbed. The closeness of the two habitat types would suggest a degree of overlap between the communities according to the species composition, with the interface comprising species from both habitats. Peck and Whitcomb (1978) compared ground surface populations of cursorial spiders from a pine-oak forest and a proximate pasture in south central USA as measured by continuous pitfall trapping over two years. Only 23 out of 57 species were collected in both habitats, and only 11 occurred in sufficient numbers to be indicative. Males were less likely to be restricted to one habitat than females, and species displacement occurred throughout the year. They conclude that although certain spiders are to be found in certain habitats and geographical ranges, it seems evident also that their temporal range and microhabitat requirements are at least as significant in their distribution as the geographical data that are usually cited for the various species. Duelli *et al* (1990) investigated the population movements of arthoropods between natural and cultivated areas. The 'edge permeability' between habitat patches in a mosaic landscape of mixed intense agriculture and semi-natural areas was investigated with directional trap devices along field borders and in a 300m long transect through crop fields, pasture, wetland and a dry meadow. Almost all arthropod species identified were found to undergo population exchanges over the field borders, and abundances of species depended on habitat quality. They found that the distribution patterns of Staphylinidae and Araneae often showed gradual changes between the preferred habitat and the neighbouring areas. The present study aims to demonstrate the effects of one habitat type on the other according to presence of spider species, their abundance and diversity, and to relate this to environmental parameters, e.g. vegetation structure and soil moisture content, of the transect positions on either side of the interface. In this way, the effect of an abrupt change in habitat type between two contrasting communities on the spider population dynamics can be analysed.

CHAPTER 2

METHODS

2.1 Study Areas

Two study areas were chosen to investigate the effects of community boundaries/interfaces on spiders. Both sites represented abrupt changes in environmental gradients brought about by human activities, and were investigated to see how this influenced the distribution of spider families and species, and how the resulting community composition was altered.

2.1.1 Site 1. Pasture interface with woodland plantation (Plate 1)

The pasture was poor in herb species other than grasses, and during the study was subject to some light grazing. Following the fieldwork period, grazing was removed and development into a hay meadow occurred. The pasture-woodland interface consisted of a post and barbed wire fence where vegetation grew taller and more dense than in either bordering habitat, and to a width of approximately 0.5 metres.

The 23 year old plantation was a mixed forest of Norway spruce, Scots pine, and western hemlock, with occasional beech and silver birch. Two rows of beech occurred immediately inside the border fence on the plantation side. The forest floor consisted predominantly of bare ground covered with a layer of leaf litter and other dead plant material. The trees were sufficiently widely spaced for a patchy covering of grasses to develop in the more open areas, and this increased through the study period.

2.1.2 Site 2. Arable field interface with natural mixed woodland (Plate 2)

The 20 ha cereal field contained Spring Barley. No insecticide or herbicide were used, and fertiliser was applied as Nitram (containing nitrate) at a rate of 180 Kg/ha on 6 March 1992, and as Nitram at a rate of 240 Kg/ha and 25-O-16 (containing 25% nitrate, 0% phosphorus and 16% potassium) at a rate of 494 Kg/ha on 10 April 1992. During the period of study, the crop height increased from an average of 0.75m to 1.2m. The crop-woodland interface consisted of a post and barbed wire fence surrounded by dense, tall vegetation, mainly grasses, cleavers, nettles and brambles, to a width of approximately 1.5m beyond the fence into the field. A narrow track of bare ground (0.5m) was situated between the crop and the boundary vegetation.

Plate 1 View of Site 1 showing the pasture interface with the plantation.

Plate 2 View of Site 2 showing the barley field interface with the woodland.

The mixed woodland was situated on a bank which rose at an angle of approximately 30^{0} from horizontal and extended along one edge of the field, and to a maximum width of 20m beyond which was a heavily grazed cattle pasture. The trees consisted of widely spaced oak, hawthorn, ash, hazel and elder, with a dense undergrowth of shrubs, herbs and grasses.

2.2 Field Survey Methods

The sampling method chosen was a line transect, along which samples or habitat data were taken at regular intervals, starting in one community and ending in the other. Methods described were carried out at both of the sites.

2.2.1 Invertebrate sampling

Invertebrate community sampling was by pitfall trapping. The pitfall traps were plastic vending cups, 90mm deep and 65mm in diameter. These were set in the ground, each with the rim level with the soil surface. A transect consisted of 15 pitfalls situated along a line of 28m, crossing from one habitat to the next at a 90^{0} angle. Pitfalls were placed at 2m intervals and arranged such that seven were located on either side of the boundary and one on the interface itself. Three parallel transect replicates were made, situated at 4m intervals. Each pitfall was filled to a depth of 2cm with 2% formalin and teepol (detergent solution) to wet, kill and preserve the specimens caught until collection. The traps were emptied weekly for a period of 3 weeks for each site. On each collection date, all the invertebrates from each trap were emptied into separate specimen tubes labelled with the date, transect number and trap position. Each trap was then reset and refilled with formalin.

Pitfall traps are commonly used by arachnologists (Curtis 1980), although the validity of their use is questionable. It is generally appreciated that the capture rate in pitfalls depends both on population density and on activity. Trap efficiency is also important and may vary between species and habitats. There is therefore a degree of uncertainty as to whether the species abundance pattern in pitfall samples reflects the pattern in the community being sampled. However, other sampling methods also have drawbacks. For further discussion of trapping methods, and the problems associated with pitfall trapping, see discussion in Chapter 5. Pitfall trapping was chosen for this study due to the advantage over other methods that high numbers of individuals and species can be recorded, sampling is continuous, and it gives a good indication of what species are present, and relative numbers of any particular species in different areas.

2.2.1 Laboratory sorting and identification

The invertebrates collected were sorted into families, and the numbers occurring in each pitfall recorded separately. The Araneae were separated out and preserved in 70% alcohol in glass tubes labelled with the date, transect number and trap position. Each spider was examined in alcohol in a shallow dish containing a layer of fine sand. This was placed under a stereoscopic microscope with variable magnification, illuminated with two high intensity light sources. Spiders were identified using Roberts (1985, 1987). Determination of sex (male, female or immature) is the first step of identification to species. The main characteristics for distinguishing male, female and immature spiders are as follows:

In mature males, the final segment of the pedipalps (the leg-like mouth parts at the front of the body) are modified to carry a copulatory organ of varying complexity. Immature and female spiders have a simple pedipalp without a modified final segment. Most adult females are distinguished form immatures by having a sclerotised plate or process (called the epigyne) in the centre of the lower abdomen immediately infront of the epigastric fold. The epigyne is at the entrance to the female reproductive organs and receives the male palp during copulation. Its structure varies in complexity between species.

Identification to species is based on the structure and shape of the male palp and female epigyne of adult spiders. Each spider caught was identified to species level, or recorded as immature when the palp or epigyne were not sufficiently developed to enable accurate identification. Immatures and sub adults were identified to family. A male and female specimen of each species were preserved in 70% alcohol in a labelled glass tube for reference. Numbers of each species caught in each trap position were combined for the 3 transects of each separate date. Results for each date were also combined to give total numbers caught at each transect position for each site.

2.2.2 Vegetation species composition

A survey was carried out to record the species present in each site area, i.e. pasture, boundary and plantation for Site 1, and barley crop, boundary and mixed woodland for Site 2. A list of species for each area was compiled, presented in Appendix 1.

2.2.3 Vegetation structure

This involved the quantitative description of vegetation physiognomy using vertical quadrats, after the method of Curtis and Bignal (1985). The description of vegetation physiognomy in quantitative terms can provide useful information about the influences of plant growth form on other ecosystem components, including the invertebrate community.

A quadrat, 0.25m by 0.25m and divided into 25, 5cm^2 subdivisions, was held vertically and the vegetation observed by looking horizontally through the quadrat. Three variables were recorded: the frequency of structures which were inclined more towards a vertical orientation, the frequency of structures which were more horizontally directed, and the overall density of vegetation expressed as percentage cover. This was repeated at successive heights above the substratum to describe a vertical profile through the vegetation in terms of density and disposition of plant forms.

The frequency of plant structures was recorded in terms of:

(i) the number of squares which contained vertical structures (e.g. stems), i.e. orientated at 45-90° from the horizontal plane;

(ii) the number of squares which contained horizontal structures, i.e. inclined at 0-45°.

(iii) the percentage cover of plant structures within the quadrat, as an expression of overall density.

This vertical quadrat method was carried out at each transect position adjacent to where each trap was placed, and mean values for each transect position calculated.

2.2.4 Soil moisture content

Three soil samples were taken from each pitfall position of a transect using a 25mm diameter corer. Plant debris was removed, and the top 5cm mixed. Approximately 10g of each sample was weighed and dried at 105°C in an air-circulation oven over 12 hours. To calculate the moisture content, the loss in weight on drying was divided by the initial sample weight and multiplied by 100 to give the percentage moisture content. A mean value for each site was calculated.

2.3 Community Analysis

Methods described were carried out at both sites.

2.3.1 Species abundance relationships

Species abundance models provide a basis for the examination of species diversity, Fisher *et al.* (1943). A species abundance distribution utilises all the information gathered in a community and is the most complete mathematical description of the data (Magurran 1988). No community consists of species of equal abundance, but there exists a relatively small number of abundant species compared with a large proportion of more rare species. A variety of species abundance distributions have been proposed to describe observed patterns. The four main models are the geometric series, the logarithmic series, the log normal distribution, and Macarthur's broken stick model. When plotted on a rank/abundance graph, the four models can be seen to represent a progression ranging from the geometric series where a few species are dominant with the remainder fairly uncommon, through the log series and log normal distributions where species of intermediate abundance become more common, and ending in conditions represented by the broken stick model in which species are as equally abundant as is ever observed in the real world. The geometric and log series models are closely related. Here the class containing one individual is always the largest and is most applicable in situations where one or a few factors dominate the ecology of a community.

Rank/abundance plots were used in this study, as one of many methods which can be used to present species abundance data, to see which model provided the best fit to the observed species abundances and to reveal patterns of dominance and eveness of species within the communities.

2.3.2 Diversity measurement

Diversity takes into account 2 factors: species richness and eveness (equitability, i.e. how equally abundant the species are). Species richness provides a useful measure of diversity, and was calculated for each transect position total. If, however, a sample rather than a complete catalogue of species in the community is obtained, it becomes necessary to distinguish between numerical species richness, which is defined as the number of species per specified number of individuals, and species density, which is the number of species per specified collection area.

The diversity of a community may be described by referring to the model which provides the closest fit to the observed pattern of species abundances. In this study, a logarithmic series was obtained from abundance data. A non-parametric index, Simpson's diversity (Simpson 1949),which makes no assumptions about the underlying species-abundance distribution (Southwood 1978) was also calculated. The Shannon-Weiner index of diversity is often used in community analysis, and assumes that the individuals are randomly sampled from an 'indefinitely large' population, and that all species are represented in the sample. A source of error is the failure to include all species from the community in the sample, and this error increases as the proportion represented in the sample declines. Results from this study suggest that the entire community was not sampled, as demonstrated when the number of species was plotted against the number of samples for Site 1 (Fig 3.6), and that the community was represented to a different extent either side of the boundary. The Shannon-Weiner index was therefore not considered to be suitable for this study. The Brillouin index is used when the randomness of a sample cannot be guaranteed, for example pitfall traps may differentially trap different species (see discussion). However, it is also used when the community has been completely censused with every individual accounted for, i.e. it describes a known collection (Magurran 1988), and depends on sample size. As the entire community was not sampled, and sample sizes in different regions of the transect varied, this index was considered unsuitable. Simpson's index (1949) gives the probability of any 2 individuals drawn at random from an infinitely large community belonging to different species. This is a dominance measure, and is weighted towards the abundances of the commonest species while being less sensitive to species richness. Other studies (e.g. Giavelli, Rossi and Satore 1986) have concluded that for an absolute estimate of the species diversity in a given community, Simpson's index appears to be the most reliable. To compare the species diversity of more than one ecological region, the index needs to be independent of possible differences in sample size for the ecological situations to be compared, and if a bias exists it should be as far as possible independent of sample size and in the same direction for the situations compared. Simpsons index satisfies these conditions (Giavelli, Rossi and Satore

1986). It was therefore considered to be the most suitable for the present study, and was calculated for each transect position and for the communities as a whole either side of the interface.

2.3.3 Distributions of spider families and species

At each transect position, the abundances of spider families and common species (10 or more individuals caught in total) were calculated and presented graphically to demonstrate the differences between transect positions crossing the interface from one habitat type to the other at each site.

2.3.4 Similarity measurements

Similarity coefficient:

Analysis was carried out by calculating how similar the different transect regions were in terms of species presence and absence. Each transect region was compared with each other region , with 4 possibilities for each species: present in both regions; present in one region but absent from the other; the reverse of this; absent from both regions but present somewhere else along the transect. For each position, the number of species falling into each of the categories is calculated. From this, the Sørensen quotient of similarity (I) was calculated for each site pair. In the case of a transect line which passes from one vegetation community to another, a change in spider species similarity pattern is shown by decreasing values in I with increasing separation of regions. For communities to be clearly delineated, the "cross similarity" between sites in one community type and another should be low. A dendrogram was constructed by nearest-neighbour clustering of transect regions based on the quotient of similarity to give a graphical representation of these results.

Chi-squared similarity:

The corrected chi-squared makes few assumptions about the distribution of the data, since it is a non-parametric analysis, and has the advantage that a probability can be attached to each pair of comparisons. Chi-squared analysis was calculated using the data from the 4 categories described above (after method described by Terrell-Neild 1986). A dendrogram was constructed as above to show clustering of transect regions showing closest affinity according to species composition as calculated.

2.4 Multivariate Community Analysis

2.4.1 Classification

Classification places the sample units into groups according to their affinities so that the relationships between the groups are revealed. The similarities between all pairs of observations (each pair corresponding to the species and its abundance for each transect region sampled) are calculated, resulting in a dichotomy in which the pairs which have the highest similarities are grouped together. The aim of this procedure was to (a) classify samples: group the transect regions according to the presence and abundance of the main spider species, so that similarities of the clustered regions became evident, and (b) classify species: group the species to show the community composition at the different regions.

For this study, Two Way Indicator Species Analysis (TWINSPAN) was used (Hill 1979). This is a FORTRAN program which first constructs a classification of the samples, and then uses this classification to obtain a classification of the species according to their ecological preferences. The 2 classifications are then used together to obtain an ordered 2-way table that expresses the species' synecological relations as succinctly as possible (Hill 1979). In the first instance TWINSPAN identifies the direction of variation by ordinating the samples (primary ordination). It then divides the ordination to give a crude dichotomy and identifies differential species that are preferential to either side of the division. A differential species is one with clear ecological preferences, so that its presence can be used to identify particular environmental conditions. The differential species then form a basis for a 'refined' ordination which is further divided at the most appropriate point. Indicator species are derived form the 'refined' ordination, based on ordination of the most strongly differential species (Hill 1979). Dendrograms were constructed based on the sample and species classifications produced by TWINSPAN, with indicator species identified at each stage.

2.4.2 Ordination

To recognise the factors determining the distribution of the spider community, an ordination of the sites and species was made using Canonical Correspondence Analysis, CANOCO (Ter Braak 1988). This is a FORTRAN program which relates the composition of species communities to their environment. Canonical ordination is a combination of ordination and multiple regression, where the regression model is inserted into the ordination model. As a result, the ordination axes appear in order of variance explained by linear combinations of environmental variables. The ordination technique of correspondence analysis is an iterative ordination algorithm: from initial arbitrary samples scores, species scores are derived, from which new samples scores are derived, species scores are obtained, and so on. Canonical ordination techniques can be obtained by carrying out multiple regressions within the iterative algorithm: each time new sample scores are derived, they are regressed on the environmental variables.

The resulting species scores are parameters of response curves of species with respect to the ordination axes. CANOCO is therefore used to ordinate species data. typically data on abundances or incidences of a set of species or samples. The variation in the species data is to be explained via the ordination axes by environmental variables and covariables (Ter Braak 1988). In this study, the common spider species found at a site were ordinated, and related to the environmental variables: soil moisture content, vegetation structure, and habitat type (scores being designated to each transect position according to habitat type/agricultural management).

CHAPTER 3

SITE 1 RESULTS

A table showing the total numbers in each invertebrate group collected is shown in Appendix 2.

A species list for the spiders identified from Site 1, using correct nomenclature, is shown in Appendix 3. Subsequent references to species in the text will use the abbreviated form. Appendix 4 shows the total numbers of each of these species. Table 3.1 shows the numbers of the 18 most common species (where 10 or more individuals were recorded). Including rare species, a total of 2045 spiders was collected, and included 52 species and 7 families. The pasture samples contained the most individuals (1860), representing 36 species and 6 families. Those from the plantation contained 139 individuals representing 34 species and 5 families. Samples from the boundary contained 46 individuals representing 13 species and 3 families. The sample size of the boundary was 1/7 that of either pasture or plantation and therefore cannot be compared directly. For the same sample area, the number of individuals trapped in the boundary is expected to be 7x46=332, a value intermediate between the pasture and plantation numbers. A total of 18 species were found in the pasture only, 16 in the plantation only, and 18 species were found in both habitats. No species were restricted to the interface only.

3.1 Community Analysis

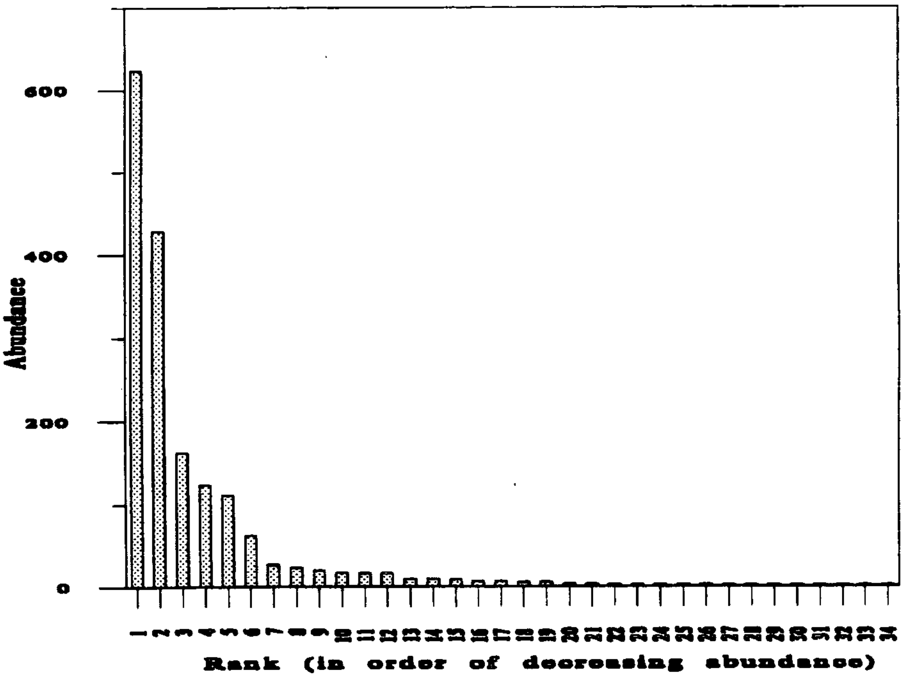
3.1.1 Species abundance relationships

Rank abundance plots showing the patterns of species abundances for the community on each side of the interface were constructed and found to follow a log series distribution (Figs 3.1a and 3.1b). This is shown by the high numbers of rare species, intermediate numbers of more common species, and low numbers of common species. When the pasture and plantation plots are compared, the plantation shows lower dominance, due to lower abundance of the most common species, and higher eveness, due to a smaller range in abundance between species. This is expected to result in a higher diversity for this habitat. From Fig 3.1 it can be seen that the pasture shows a steeper gradient than the plantation, suggesting a smaller

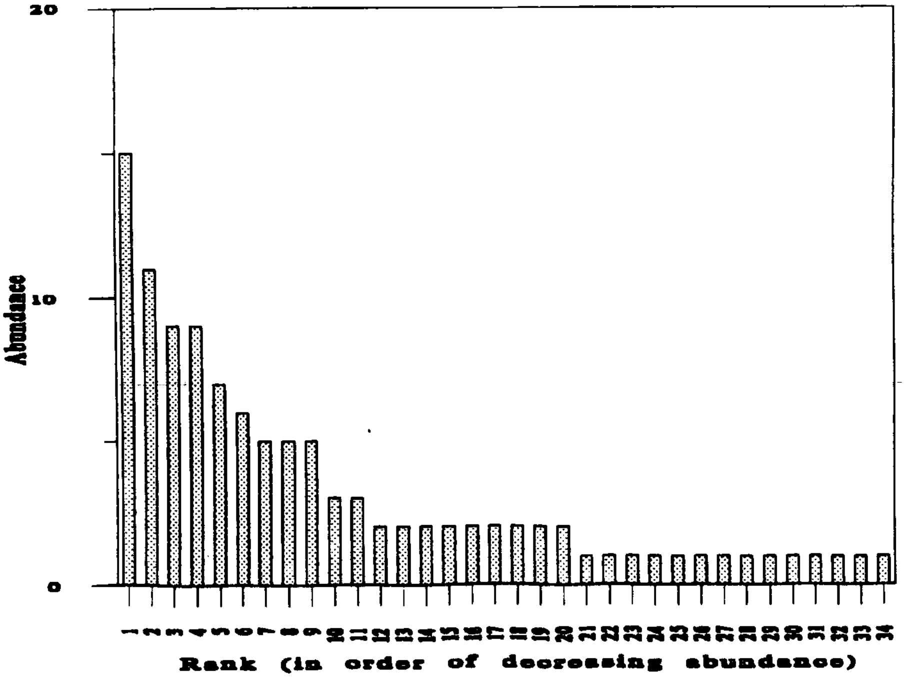
						Trap										
Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	Tot
Thomisidae																
Xyticus. cristatus	12	1	1	1	7	1	0	0	0	0	0	0	0	0	0	23
Lycosidae																
Pardosa pullata	139	79	58	82	44	17	9	1	2	2	1	0	0	0	0	434
Pardosa amentata	1	3	2	0	4	2	5	0	0	0	2	0	0	0	0	19
A.lopecosa pulverulenta	3	7	0	3	1	0	2	0	0	0	0	0	0	1	0	17
Trochosa terricola	4	4	1	3	3	4	8	1	0	1	0	0	0	0	0	29
Tetragnathidae																
Pachygnatha degeeri	138	104	118	104	75	59	25	6	1	0	0	0	1	0	0	631
Linyphiidae																
Oedothorax fuscus	1	0	2	7	3	2	1	0	1	0	0	0	0	0	0	17
Oedothorax retusus	27	25	27	31	41	9	3	1	0	0	0	0	0	0	0	164
Tiso vagans	4	1	2	1	1	0	0	0	0	1	0	0	0	0	0	10
Saignya frontata	0	0	0	1	4	0	4	0	5	0	0	0	0	0	0	14
Erigone dentipalpis	4	7	3	9	29	45	15	0	0	1	0	0	0	1	0	114
Erigone atra	3	1	1	5	22	17	13	0	1	0	0	0	0	0	1	64
A.gyneta decora	8	3	5	11	44	33	20	2	2	0	0	0	0	0	0	128
Microneta viaria	0	1	1	0	0	0	1	0	0	2	4	0	1	3	1	14
Centromerita bicolor	0	3	1	0	1	14	1	0	0	0	0	0	0	0	0	20
Lepthyphantes tenuis	0	1	1	0	1	1	0	6	4	2	4	1	1	2	1	25
Lepthyphantes cristatus	0	0	0	0	0	1	1	8	2	2	1	0	2	2	0	19
Linyphia hortensis	0	0	0	0	0	0	0	1	1	1	0	1	2	2	2	10

Table 3.1 Totals of common spider species (10 or more individuals collected over the 3 week trapping period), Site 1 pasture/plantation transect, where A to G represent the pasture, H the interface, and I to O the plantation transect regions.

number of species with intermediate abundance when compared with the total community numbers. This is indicative of a geometric distribution of species abundance.



a



b

Fig 3.1 Rank abundance plots of numbers of specimens of each species, Site 1. a=pasture, b=plantation.

Because the ratio of the abundance of each species to the abundance of its predecessor is constant through the ranked list of species, a geometric series will appear as a straight line if plotted on a log abundance/species rank graph. Figs 3.2a and 3.2b show the log abundance/species rank plots for the pasture and plantation respectively. Both graphs deviate from the geometric distribution, the plantation to a greater extent than the pasture, suggesting that the pasture has an abundance distribution intermediate between a geometric and a log series. The geometric series represents a situation where a few species are dominant and the rest rare, and is typical of disturbed habitats (Magurran 1988). The fact that some grazing took place in the pasture may have resulted in this community being intermediate between the geometric and log series distributions.

3.1.2 Diversity

Fig 3.3 shows the total number of spiders trapped at each transect point for the three weeks combined. It shows a pattern of declining numbers from the pasture through the boundary to the plantation. Chi-squared analysis was carried out on the totals for each position to determine the differences between successive traps. Results show a significant reduction in total numbers from 6m into the pasture to the interface. This suggests that the interface has a negative influence on the number of spiders in the community in the pasture to a distance of 6m (see Fig 3.3 for details). Table 3.2 shows the number of spiders, species richness, the values of the Simpson diversity index for each transect position.

Species richness: the number of species caught at each transect position is shown in Fig 3.4. The species richness shows a general decline from the pasture through to the plantation, with the boundary species richness being intermediate between that of the pasture and the plantation.

Species diversity: Fig 3.5 shows the change in diversity along the transect. A peak is reached at the position 2m from the interface. At the interface, there is a slight decline in species diversity,. At the first position (I) 2m into the plantation, diversity increases and peaks before declining and rising once more beyond 8m into this habitat. The diversity for trap L appears to be unusual. It is probable that this is an artefact of the smaller number of individuals in samples collected from the plantation (Fig 3.3). This was especially the

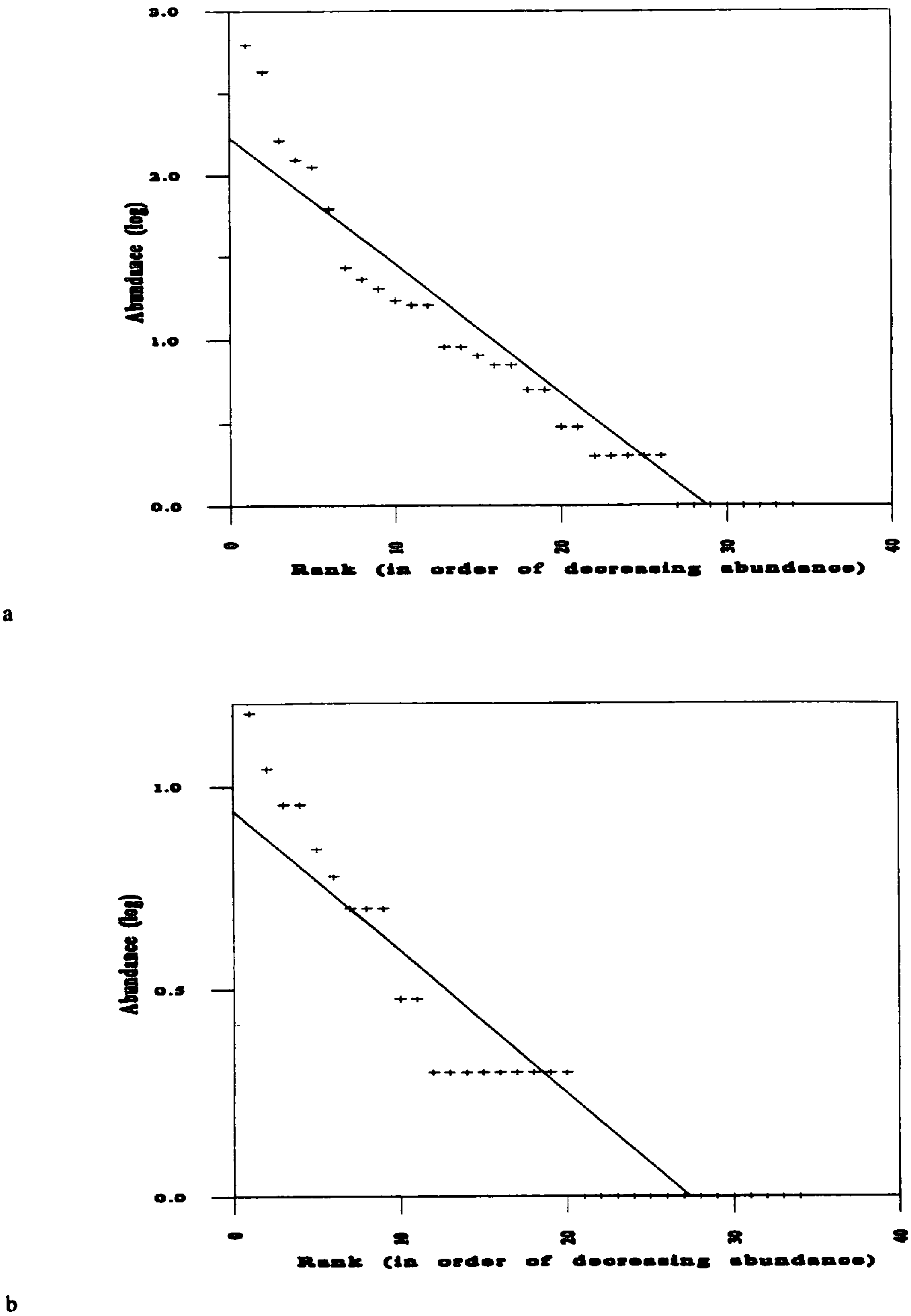


Fig 3.2 Log abundance distribution of ranked species for Site 1. a=pasture, b=plantation.

case at L where no spiders were caught in any of the transects for the first week of trapping. This was not expected as site L did not appear different in any way to its nearest woodland sites K and M. I would therefore suggest that the diversity in the plantation typically levels off and remains nearly constant.

Trap	N	S	Diversity
A	353	17	1.15
B	246	20	1.22
C	231	18	1.08
D	265	18	1.32
E	287	21	1.88
F	210	17	1.77
G	119	22	2.16
H	32	13	1.91
I	26	15	2.33
J	18	13	2.45
K	20	11	2.08
L	5	5	1.61
M	12	10	2.20
N	19	12	2.33
O	10	8	1.97
Tot	1853	52	1.66

Table 3.2 Number of spiders (N), species richness (S) and diversity (Simpson) for transect position totals (immatures not included), Site 1 pasture/plantation transect, where A to G represent the pasture, H the interface, and I to O the plantation transect regions.

To determine if the total spider community had been sampled, plots were made for the pasture and plantation separately, of sample number against number of species (Fig 3.6). Theoretically, the number of

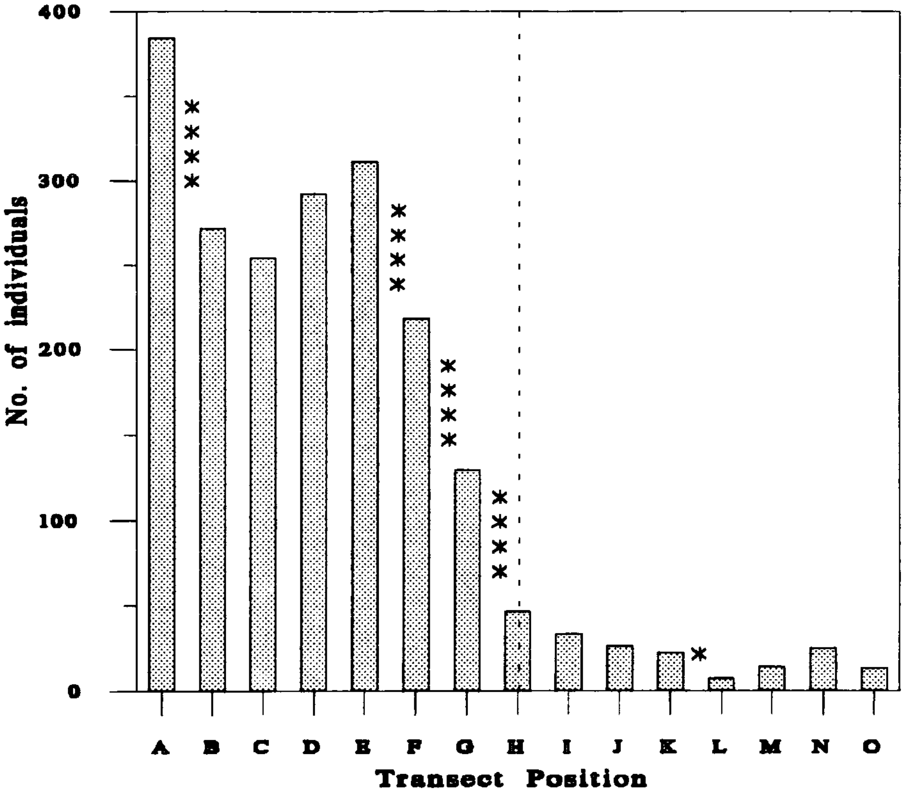


Fig 3.3 Total number of spiders recorded for each transect position over the three week trapping period for Site 1, where A to G represent the pasture, H the interface, and I to O the plantation transect regions. Significant differences between successive traps as calculated by chi-squared analysis are shown, where the significance levels are: **** (P=0.005), *** (P=0.001), ** (P=0.05), * (P=0.01) with 1 df.

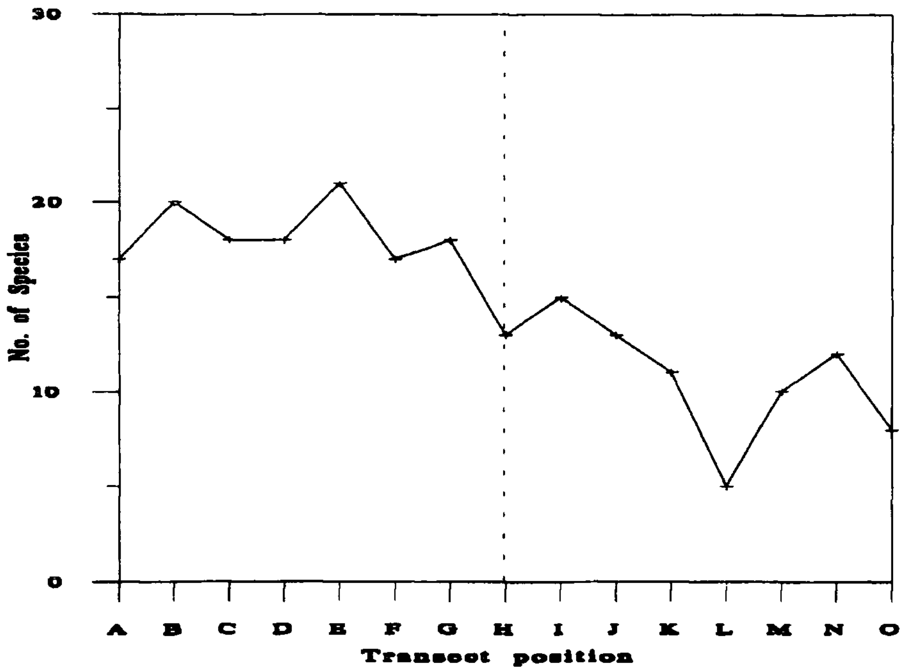


Fig 3.4 Species richness at each transect position, Site 1, where A to G represent the pasture, H the interface, and I to O the plantation transect regions.

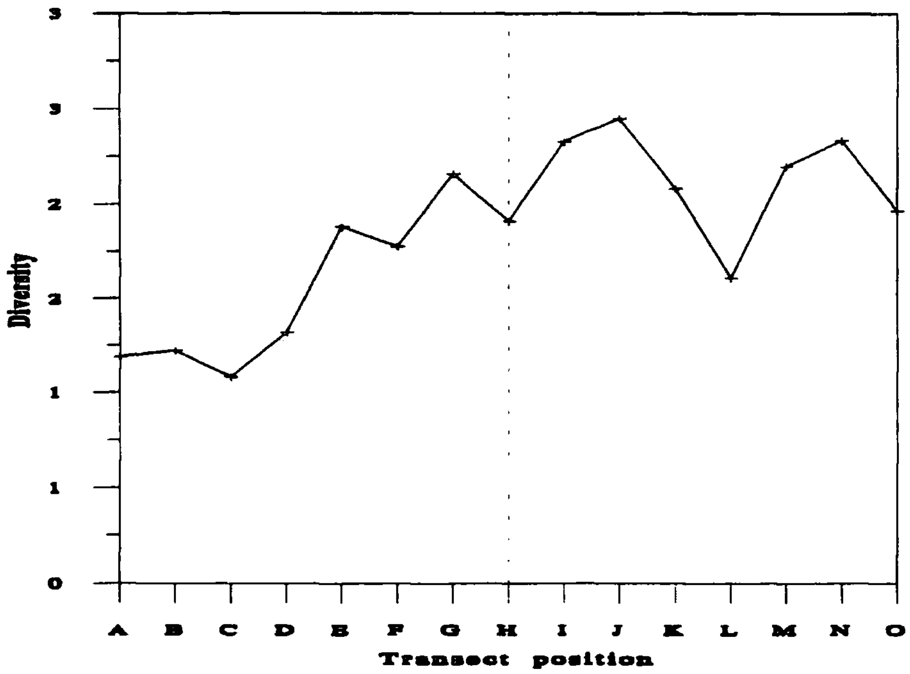


Fig 3.5 Change in diversity as measured by Simpson's index for Site 1, where A to G represent the pasture, H the interface, and I to O the plantation transect regions.

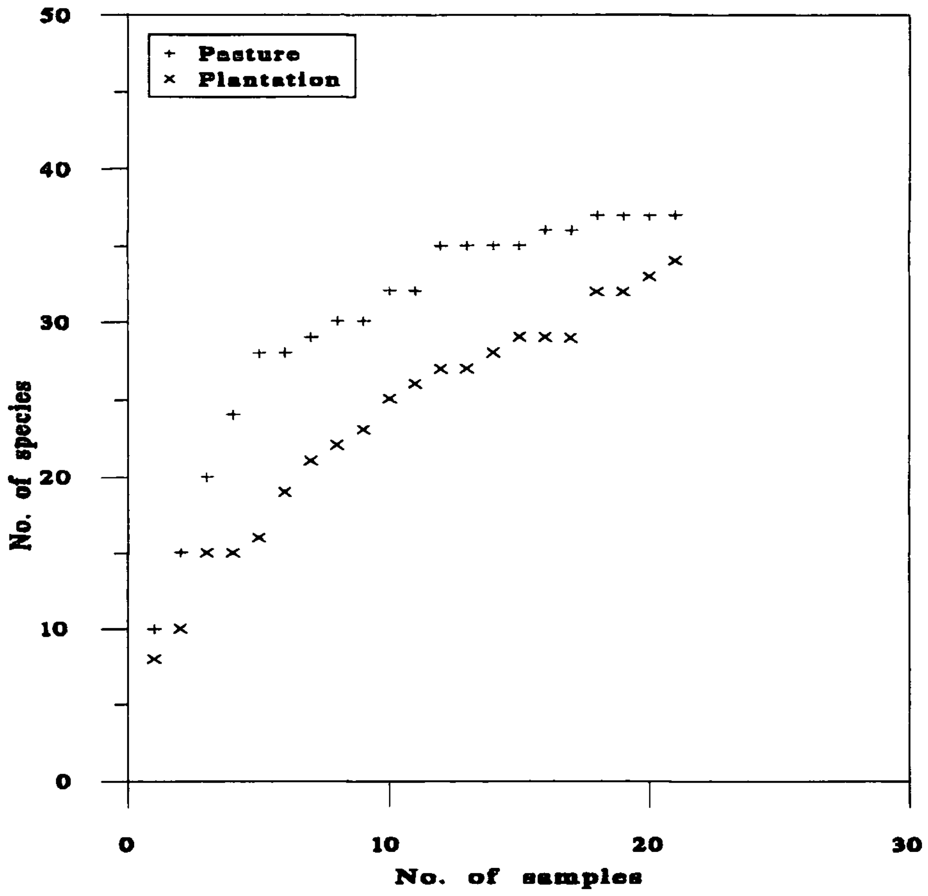


Fig 3.6 Increase in the number of species with increased sampling effort for the pasture and plantation regions either side of the interface at Site 1.

species should increase with number of samples, with a decrease in the rate of new species detected with increased number of samples until a steady state is reached where no new species are detected due to all the species present having been trapped. This is represented by the levelling off of the curve. The results in Fig 3.6 show that neither the pasture or plantation communities were fully sampled, although the pasture curve shows the number of species beginning to level off. The number of species in the plantation are increasing at this point, and therefore the species identified for the plantation side of the interface in this study may not represent the actual community to the same extent as the pasture species. The specimen-species relationship is therefore clearly different in the pasture and the plantation. Fig 3.6 also shows that the number of species collected with increasing sampling effort in the pasture were consistently larger than those from the plantation.

3.1.3 Distribution of spider families and species

At 14m into the pasture (trap A), the dominant spider family is the Lycosidae (Fig 3.7), with Tetragnathidae also of high abundance, and a medium abundance of Linyphiidae. At 12m from the interface, the Lycosidae and Tetragnathidae decrease in abundance, with the Lycosidae decreasing more rapidly so that between 12m and 8m from the interface, Tetragnathidae is the most abundant group, with Linyphiidae beginning to increase between 10m and 8m from the interface to be the second most abundant group. Between 8m and 6m from the interface, the linyphiids increase rapidly (Fig 3.7) in abundance to be the most common group trapped, with lycosids and tetragnathids decreasing in numbers. Between 6m into the pasture and the interface at the boundary, numbers of linyphiids, tetragnathids and lycosids all decrease, but remaining in this order of relative abundance. The linyphiids remain the dominant group in terms of numbers throughout the plantation side of the transect. Thomisidae were only present in the pasture, and only one member of the family Clubionidae was trapped, and this was in the plantation. No family was restricted to the plantation only or to the boundary only. It should be mentioned here that pitfall trapping may not be accurate in measuring the relative abundances of different species or families (see discussion, chapter 5), but the changes in individual family distributions along the transect are more reliable, although activity in different habitat types may be influenced by vegetation structure.

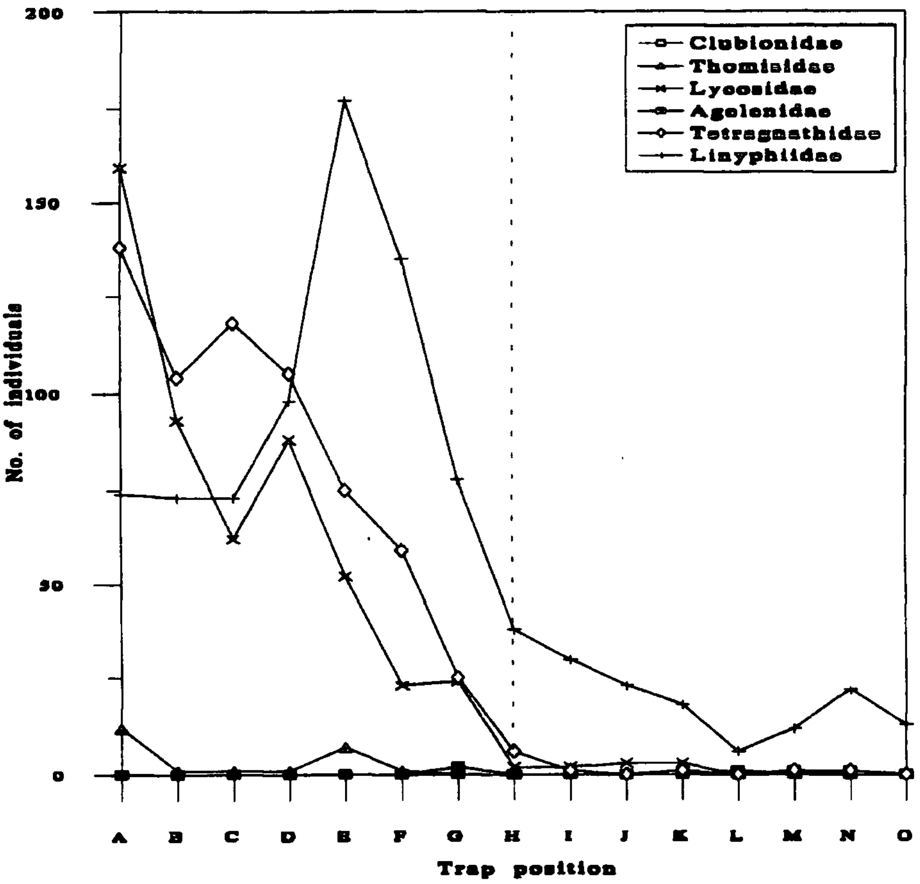


Fig 3.7 Distribution of spider families (data collated from 3 week trapping period) along the Site 1 transect positions, where A to G represent the pasture, H the interface, and I to O the plantation transect regions.

Table 3.3 shows the percentage abundance of the common families (10 or more individuals trapped in total) which make up the community at each transect position. Fig 3.8 shows each transect position and the community composition of common spider families. It shows that the pasture community is dominated by Linyphiidae, Tetragnathidae and Lycosidae, the boundary by Linyphiidae, and the plantation by Linyphiidae. Thomisidae occur only in the pasture.

	Trap														
Family	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Thomisidae	3.5	0.4	0.4	0.4	2.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lycosidae	42.7	38.7	27.4	34.1	18.5	11.2	22.2	7.7	10.5	25.0	25.0	0.0	0.0	9.1	0.0
Tetragnathidae	40.1	43.3	52.9	40.3	26.8	28.8	23.1	23.1	5.3	0.0	0.0	0.0	14.3	0.0	0.0
Linyphiidae	13.7	17.5	19.3	25.2	52.1	59.5	54.6	69.2	84.2	75.0	75.0	100.0	85.7	18.2	100.0

Table 3.3 The abundance (% of total) of common families (totals of species with 10 or more individuals) for Site 1 pasture/plantation transect, where A to G represents the pasture, H the interface, and I to O the plantation regions.

Direct comparisons of catches of individual species from pitfall traps is difficult because the catch is dependent on other factors besides spider population density. Nonetheless, the large differences between catches in some of the species indicate that the habitat differences had dramatic effects on spider community structure. Individual species' distributions were investigated to determine the effect of the sudden change in community type at the interface. The distributions of the common species according to their total numbers are shown in Fig 3.9. Most of these species appear to show an individualistic distribution, tending to prefer one side of the interface to the other. No species appeared to be restricted to the boundary only, although this would not be expected due to its narrow width. most of the species show a degree of overlap (to a greater or lesser extent) into their less-preferred habitat across the interface. It can be seen from the species distributions in Fig 3.9 that the majority of the species show a preference for the pasture habitat. From the

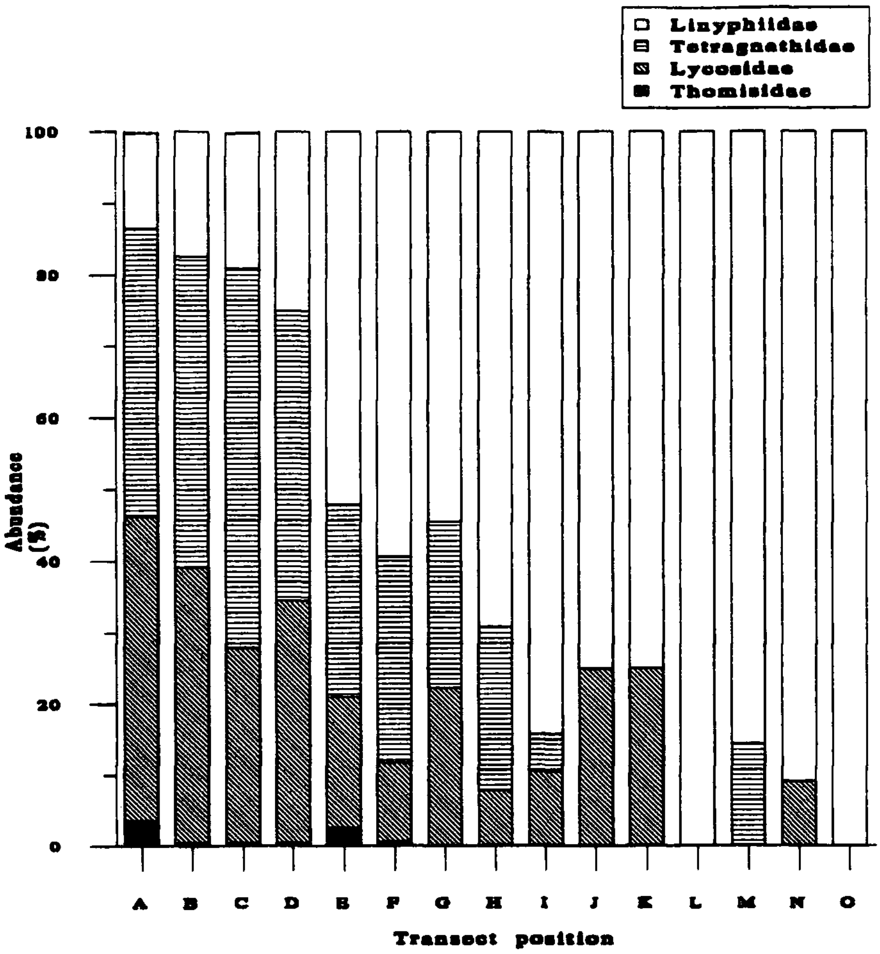


Fig 3.8 Percentage composition of major spider families at each transect position of Site 1 showing the change in abundance, where A to G represent the pasture, H the interface, and I to O the plantation transect regions.

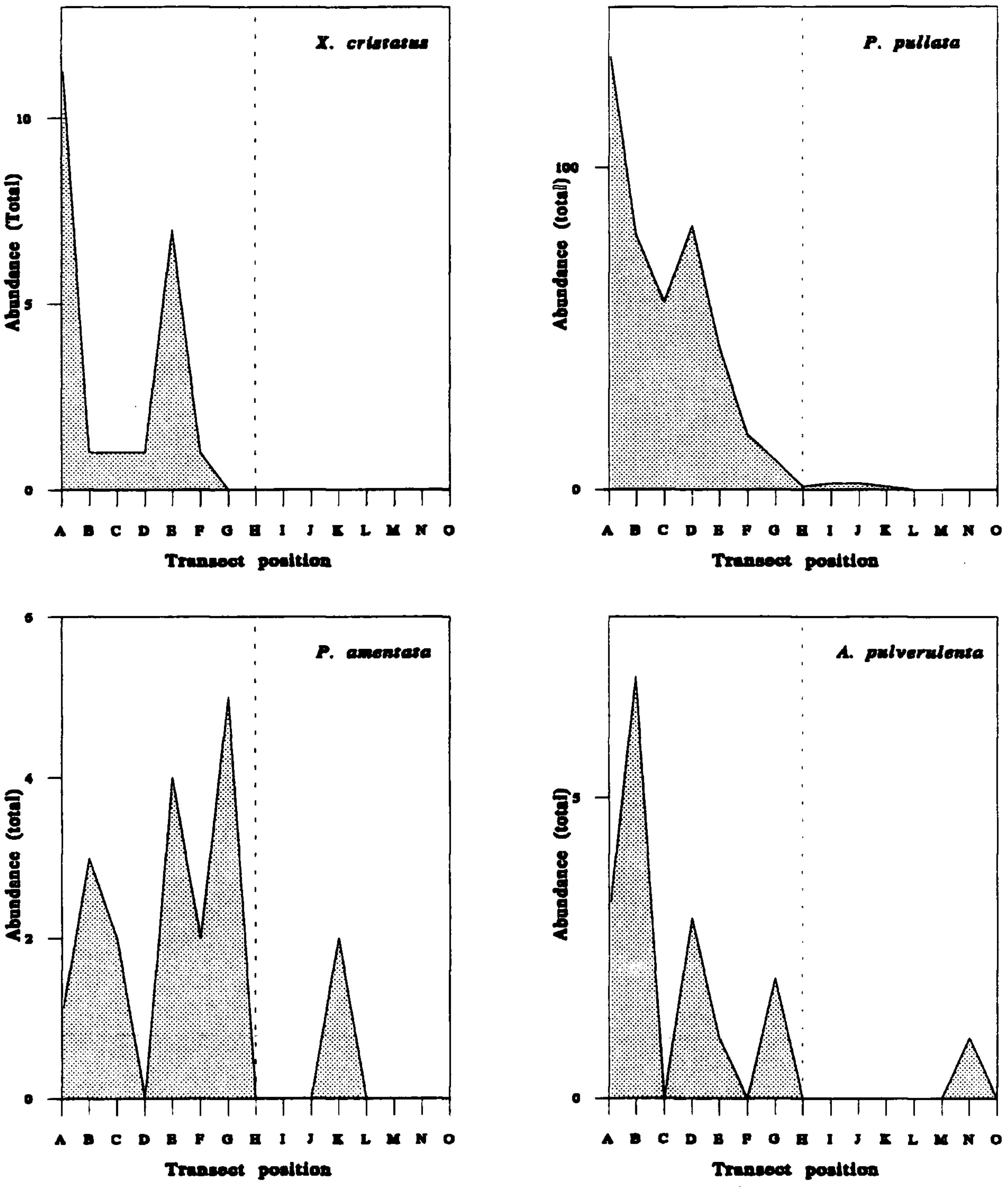
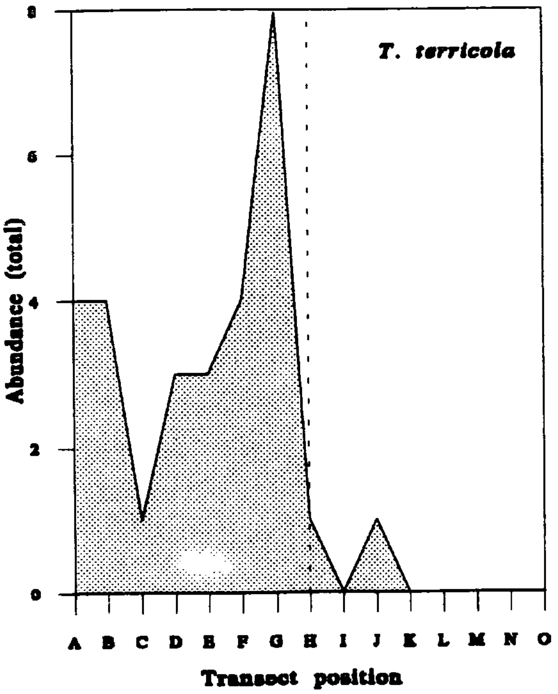
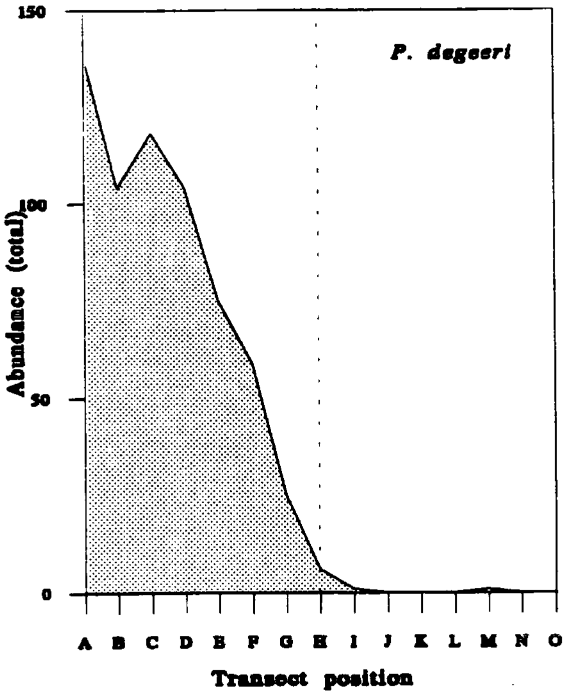
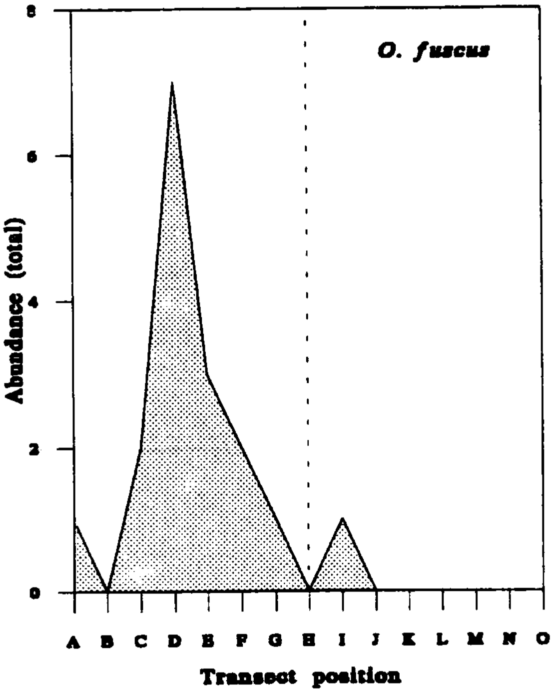
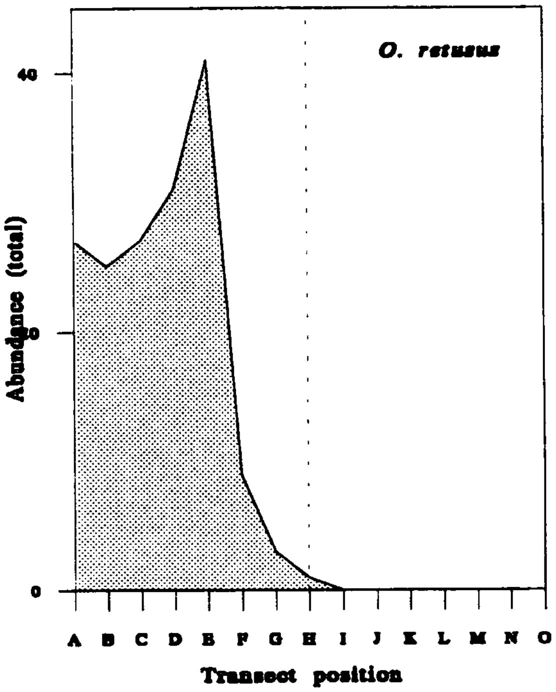


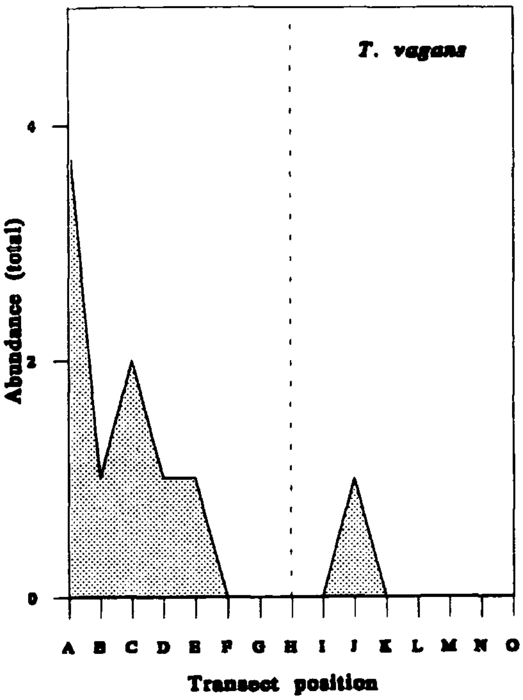
Fig 3.9 Abundance (totals) of common species (10 or more individuals) collected over the 3 week trapping period at each transect position for Site 1 pasture/plantation transect, where A to G represent the pasture, H the interface and I to O the plantation transect regions (continued on following 4 pages).

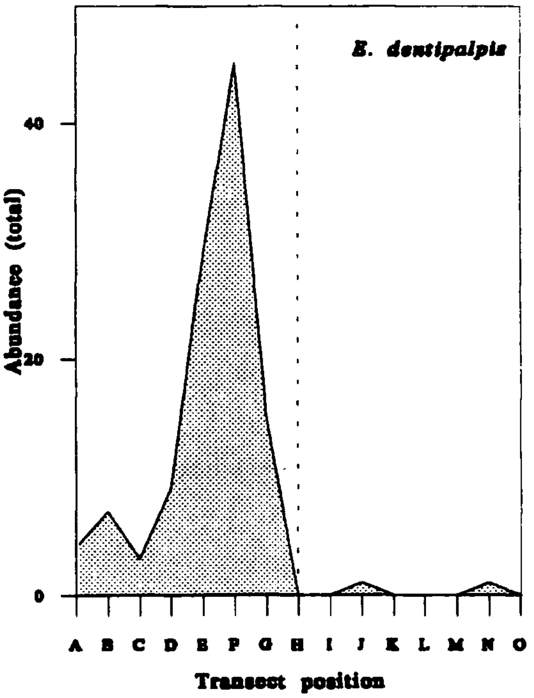

T. terricola
Abundance (total)
8
6
4
2
0
A B C D E F G H I J K L M N O
Transect position

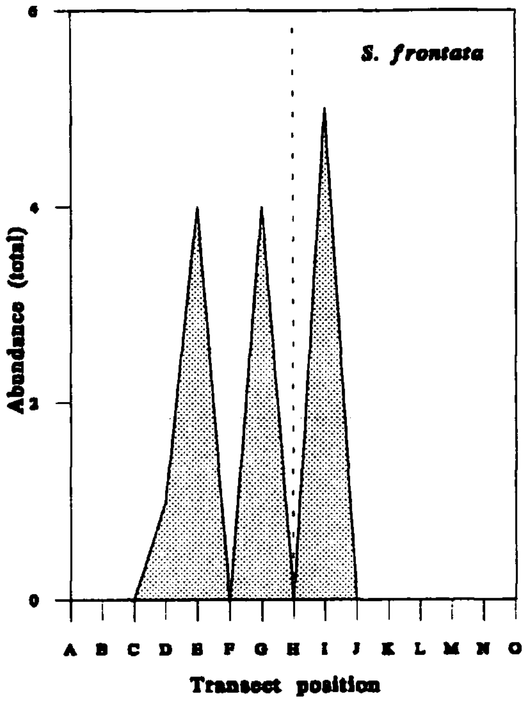

P. degeeri
Abundance (total)
150
100
50
0
A B C D E F G H I J K L M N O
Transect position

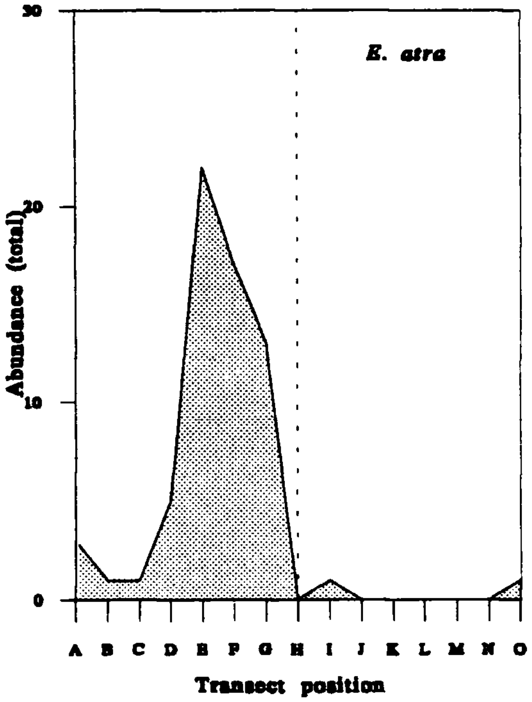

O. fuscus
Abundance (total)
8
6
4
2
0
A B C D E F G H I J K L M N O
Transect position

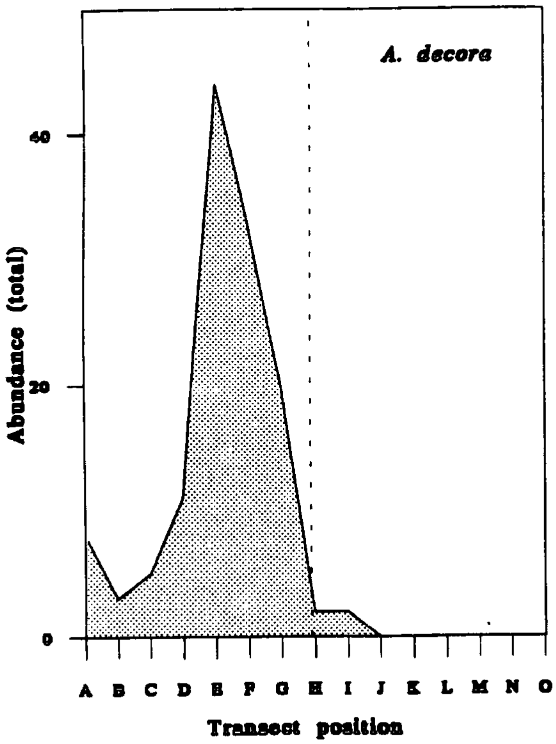

O. retusus
Abundance (total)
40
20
0
A B C D E F G H I J K L M N O
Transect position

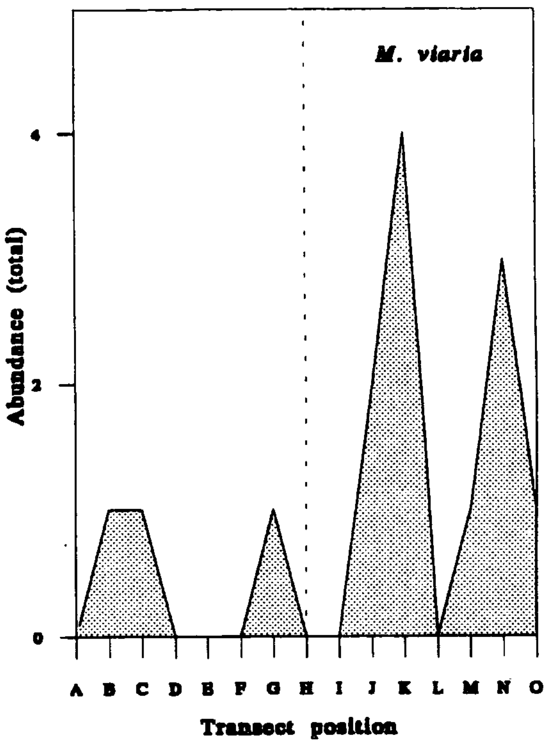

T. vagans
Abundance (total)
0
2
4
A B C D E F G H I J K L M N O
Transect position

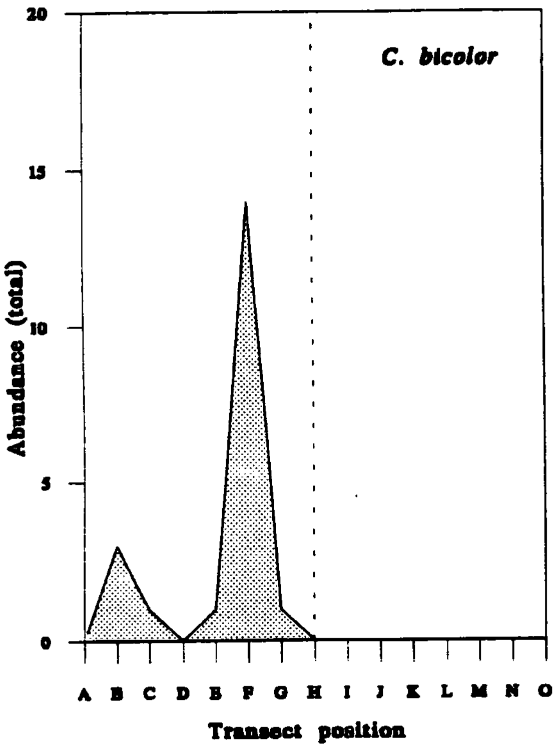

E. dentipalpis
Abundance (total)
0
20
40
A B C D E F G H I J K L M N O
Transect position

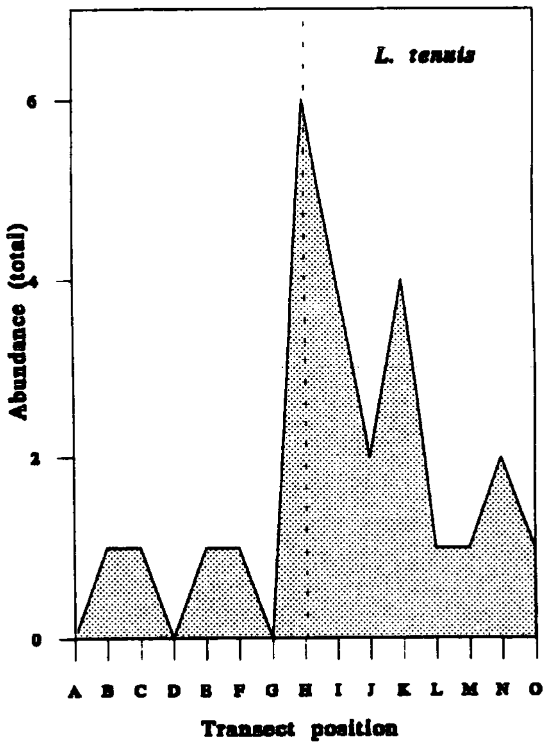

S. frontata
Abundance (total)
0
2
4
6
A B C D E F G H I J K L M N O
Transect position

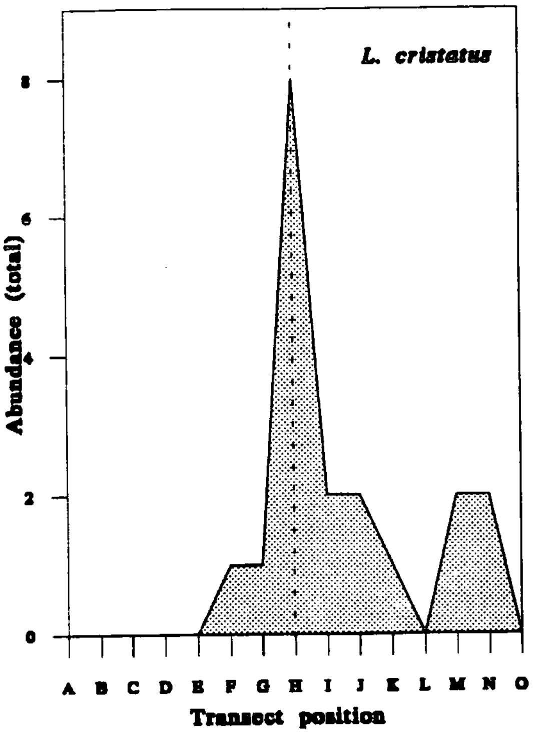

E. atra
Abundance (total)
0
10
20
30
A B C D E F G H I J K L M N O
Transect position

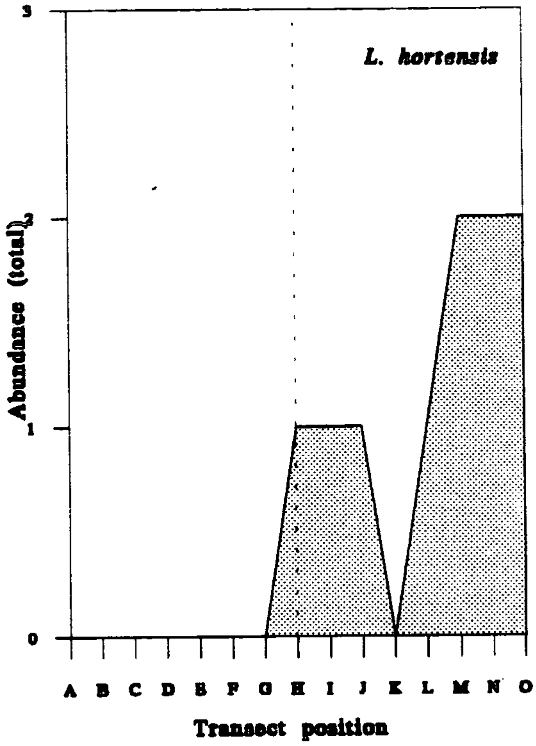

A. decora
Abundance (total)
0
20
40
A B C D E F G H I J K L M N O
Transect position


M. viaria
Abundance (total)
0
2
4
A B C D E F G H I J K L M N O
Transect position


C. bicolor
Abundance (total)
0
5
10
15
20
A B C D E F G H I J K L M N O
Transect position


L. tenuis
Abundance (total)
0
2
4
6
A B C D E F G H I J K L M N O
Transect position


L. cristatus
Abundance (total)
0
2
4
6
8
A B C D E F G H I J K L M N O
Transect position


L. hortensis
Abundance (total)
0
1
2
3
A B C D E F G H I J K L M N O
Transect position

distributions shown, it appears that *Xyticus cristatus*, *Pardosa pullata*, *Pardosa amentata*, *Alopecoesa pulverulenta*, *Trochosa terricola*, *Pachygnatha degeeri*, *Oedothorax fuscus*, *Oedothorax retusus*, *Savignya frontata*, *Erigone dentipalpis*, *Erigone atra*, *Agyneta decora*, and *Centromerita bicolor* show a habitat preference for grassland. All these species, with the exception of *X. cristatus*, show a degree of overlap into the plantation suggesting that although the major habitat of these species is the pasture, temporary movements into the plantation occur as the result of activities such as foraging. Fig 3.9 shows that the species *Lepthyphantes cristatus*, *Microneta viaria*, *Lepthyphantes tenuis* and *Linyphia hortensis* show a preference for woodland. They all show a small degree of overlap into the grassland. It therefore follows that the boundary contains species characteristic of both pasture and plantation habitats.

3.1.4 Similarity Measurements

Quotient of similarity:

An advantage of calculating the quotient of similarity is that it relies on presence/absence data of species, and compares sites according to what species are present or absent. This therefore eliminates the problem that relative abundance data from pitfalls reflects species' activity and trap efficiency for different species, resulting in numbers that may not be comparable between species. Fig 3.10 shows the values for the quotient of similarity (I) as percentages which represent similarities between each transect position. This shows a decrease in similarity of species composition of communities with increasing distance of pitfalls, represented by decreasing values for pitfall pairs. Within-pasture traps show a high degree of similarity to each other, but with this decreasing with increasing distance apart within the pasture. This also applies for within-plantation traps. The average value of similarity between pasture traps is 69%, compared with an average value of 41% for similarity between plantation traps (Fig 3.10). This suggests that the community composition within the pasture is more uniform than that within the plantation. The average similarity values for pasture/boundary and plantation/boundary are 51% and 37% respectively, showing that the species composition of the boundary is more consistent with that of the pasture as opposed to the plantation. The pasture/plantation average similarity is 43%, indicating the dissimilarity between the two habitat types.

A dendrogram constructed by nearest-neighbour clustering of transect regions based on the quotient of similarity is shown in Fig 3.11. This gives a graphical representation of the results, clustering the trap sites according to their similarities in species composition. The similarity values divide the transect into a pasture/boundary cluster, and a plantation cluster.

Trap															
A															
B	64.9														
C	68.6	77.8													
D	66.7	63.2	66.7												
E	68.4	82.9	82.1	82.1											
F	58.8	64.9	80.0	62.9	73.7										
G	51.8	61.9	65.0	65.0	69.8	71.8									
H	33.3	42.4	45.2	45.2	47.1	63.3	45.7								
I	31.3	57.1	42.4	42.4	44.4	43.8	37.8	57.1							
J	26.7	36.4	38.7	25.8	29.4	42.9	28.6	53.9	42.9						
K	14.3	25.8	27.6	13.8	18.8	28.6	24.2	33.3	38.5	50.0					
L	0.0	8.0	8.7	0.0	7.7	18.2	7.4	22.2	20.0	33.3	12.5				
M	3.7	20.0	10.7	7.1	12.1	29.6	18.8	34.8	32.0	52.2	28.6	50.0			
N	13.8	25.0	20.0	13.3	18.2	20.6	29.4	32.0	37.0	56.0	60.9	35.3	42.1		
O	8.0	21.4	23.0	7.6	13.8	16.0	13.3	28.6	43.5	47.6	42.1	30.8	44.4	50.0	
Trap	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**

Average value of similarity (% I) between communities.

	Pasture	Plantation
Pasture	69.0	22.0
Interface	50.7	37.4
Plantation		40.6

Fig 3.10 Values of the quotient of similarity (I) for Site 1 (as %), where A to G represent the pasture, H the interface, and I to O the plantation transect regions.

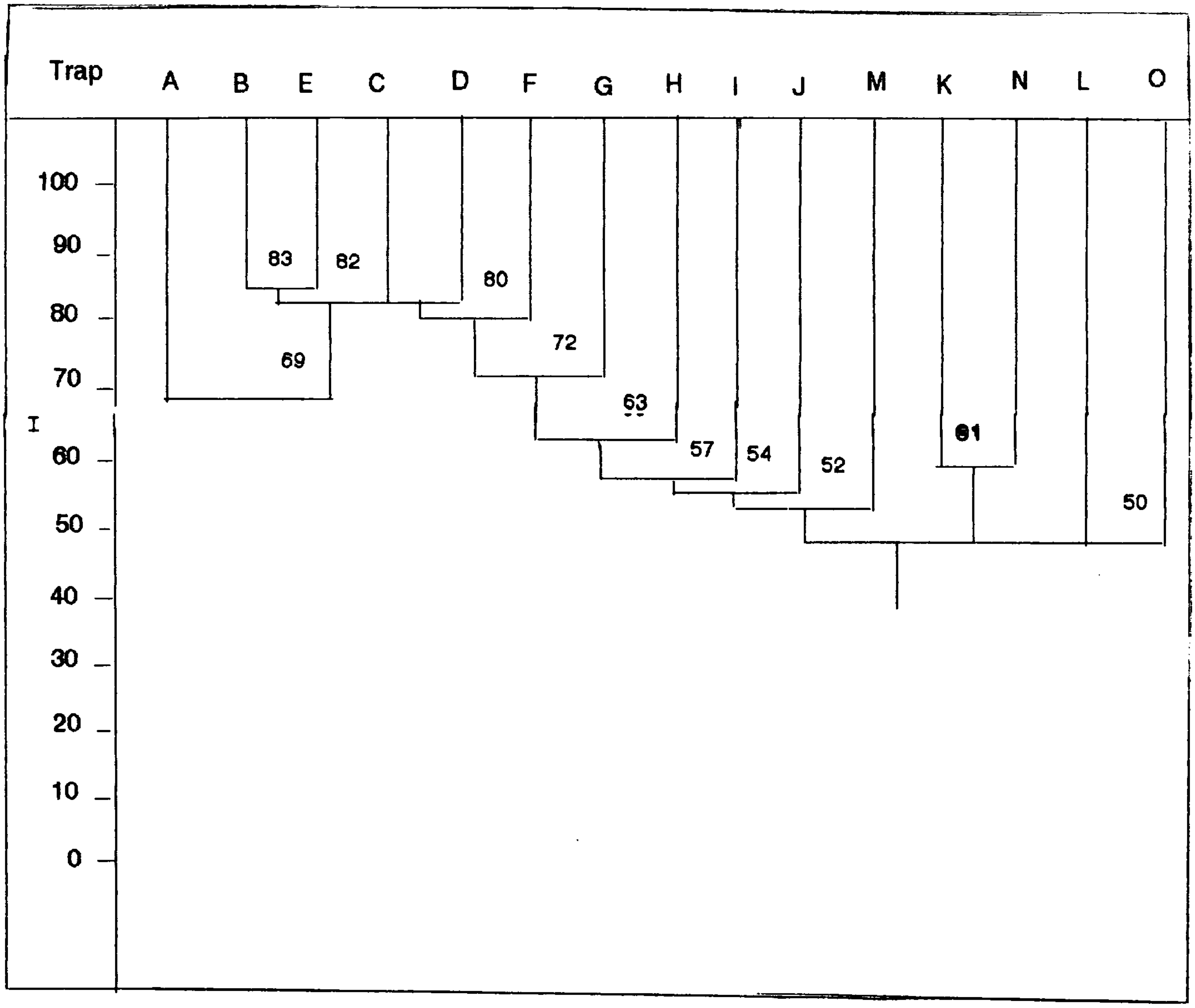


Fig 3.11 Nearest-neighbour clustering of transect regions based on the percentage similarity, Site 1, where A to G represent the pasture, H the interface, and I to O the plantation transect regions.

This emphasises that the species composition of the boundary is more consistent with that of the pasture than that of the plantation. It also demonstrates that the decrease in percentage similarity becomes greater between successive traps in the pasture from trap C through to H. This suggests an increase in some factor that produces a change in community composition towards the interface, probably the effect of the dramatic change in habitat type at the interface.

Chi-squared similarity:

Chi-squared associations are shown in Fig 3.12. Significant associations were found only to occur between within pasture traps and within plantation traps. There were no significant associations between pasture and plantation, demonstrating that the interface produces a dramatic effect on community composition in producing a sudden change in the relative abundance of species, and species composition. A greater proportion of the within pasture traps were significantly associated with each other than the proportion of within plantation traps.

Trap															
A															
B	9.1*														
C	12.2*	20.0*													
D	10.4*	5.0*	27.3*												
E	12.3*	23.9*	22.4*	23.9*											
F	6.2*	9.0*	22.4*	8.2*	16.0*										
G	1.9	5.4*	8.3*	8.3*	10.3*	14.2*									
H	1.9	1.0	1.8	1.8	2.2	8.4*	1.7								
I	0.1	0.0	0.7	0.7	0.8	1.1	0.0	7.0*							
J	0.0	0.0	0.0	0.0	0.0	1.1	0.0	5.8*	1.5						
K	0.6	0.0	0.0	0.9	0.4	0.0	0.0	0.4	1.0	4.7*					
L	1.3	0.2	0.1	1.5	0.3	0.0	0.3	0.1	0.0	1.8	0.2				
M	1.8	0.1	0.0	2.1	1.2	0.0	0.3	0.7	0.2	5.9*	0.1	3.4			
N	0.8	0.0	0.2	1.3	0.8	0.1	0.1	0.1	0.6	7.1*	10.1*	2.2	2.7		
O	0.8	0.1	0.0	1.1	1.9	0.0	0.5	0.2	3.5	4.9*	2.9	0.9	3.7	5.7*	
Trap	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O

Fig 3.12 Values of chi-squared, Site 1 showing significant associations (*) at P=0.05.

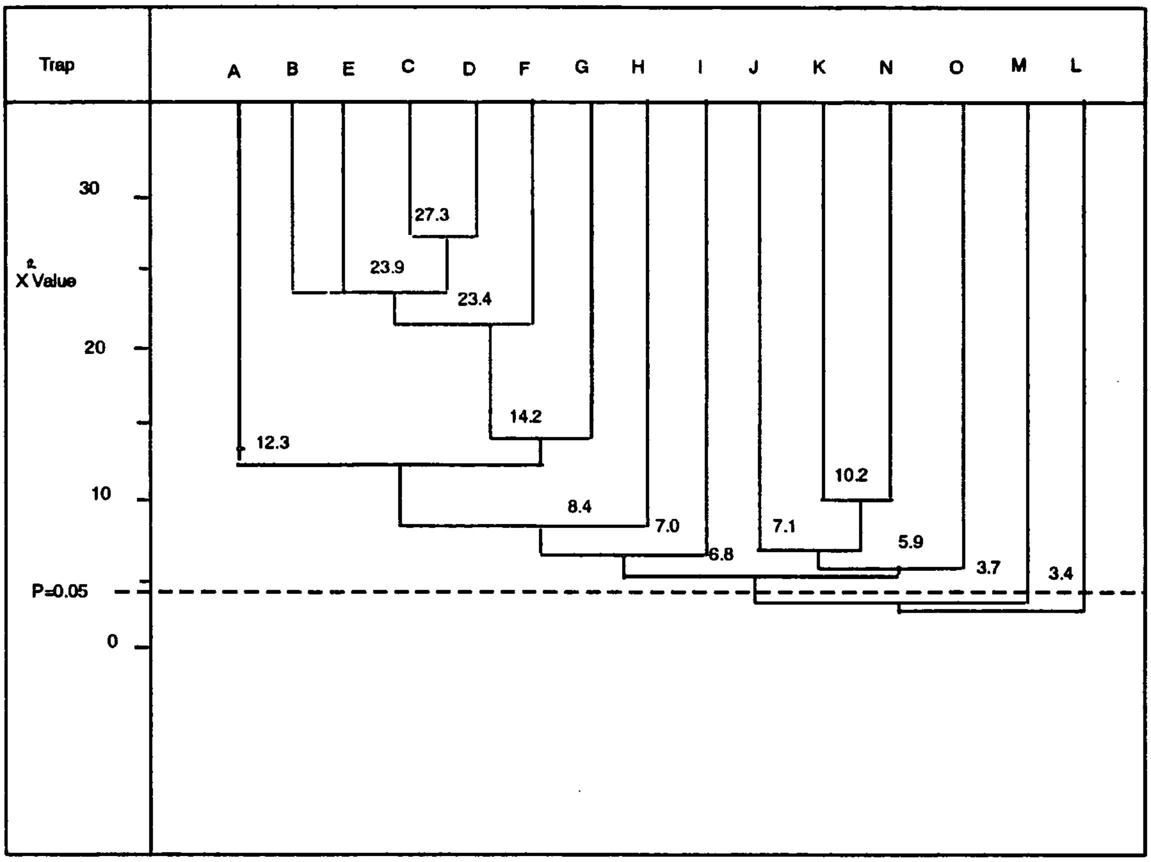


Fig 3.12 Nearest-neighbour clustering of transect regions, based on the chi-squared similarity, Site 2 where A the G represent the pasture, H the interface, and I to O the plantation transect regions.

This again suggests greater uniformity and stability of community structure within the pasture. Fig 3.13 shows a dendrogram constructed as for the quotient of similarity. It shows that some within wood sites were not significantly similar, and also that trap I appears to have a greater affinity towards trap H (at the interface) than to the other plantation traps. Trap H is associated with the first trap either side, suggesting that the community here consists of species from both the pasture and plantation communities.

3.2 Multivariate community analysis

3.2.1 Classification

The aim of this procedure is to group the sites according to the presence and abundance of the spider species so that the similarities of the clustered sites become evident. The classification was made by Hill's indicator species analysis program TWINSPAN (Hill, 1979). The two-way ordered classification showing the relation between samples and species is shown in Table 3.4, and reveals the dichotomies dividing species and sample groups (shown as lines dividing the table). The values indicate a scale of abundance (pseudospecies levels). A dendrogram showing the divisions made by TWINSPAN for site classification, with indicator species at each division, is shown in Fig 3.14. The first division made by TWINSPAN separated the pasture and boundary (group 1 sites) from the plantation woodland (group 2 sites). Spider species more frequent and consistent on grassland were shown to be *Xyticus cristatus, Pardosa pullata, A.lopecosa pulverulenta, Trochosa terricola, Oedothorax fuscus, Oedothorax retusus, Savignya frontata, Erigone dentipalpis, Erigone atra, Agyneta decora, Centromerita bicolor, Pachygnatha degeeri,* and *Pardosa amentata.* Spiders species more frequent and consistent with the woodland plantation were *Microneta viaria*, and *Linyphia hortensis.* Ubiquitous species occurring on all sites were *Lepthyphantes cristatus*, and *Lepthyphantes tenuis.* The first indicator species was *A. decora*, as it was found in group 1 sites but nowhere else. *X. cristatus, C. bicolor, O. fuscus, O. retusus,* and *S. frontata* were other species present in group 1, but did not occur in all of the pitfall sites. *X. cristatus* and *C. bicolor* were only found in the grassland sites of group 1. The fact that in the first division, the first plantation site was classified with the boundary/grassland suggests that grassland species crossed into the plantation to a degree. The second division separates group 1 into grassland (group 3) and boundary (group 4), with *E. dentipalpis* as the

	Site														
Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
X. cristatus	2	1	1	1	1	1									
O. fuscus	1		1	1	1	1	1		1						
O. retusus	2	2	2	2	2	1	1	1							
A. decora	1	1	1	2	2	2	2	1	1						
C. bicolor		1	1		1	2	1								
P. degeeri	3	3	3	3	2	2	2	1	1					1	
S. frontata				1	1		1		1						
E. atra	1	1	1	1	2	2	2		1						1
P. amentata	1	1	1		1	1	1				1				
P. pullata	3	2	2	2	2	2	1	1	1	1	1				
A. pulverulenta	1	1		1	1		1					1			
T. terricola	1	1	1	1	1	1	1	1		1					
T. vagans	1	1	1	1	1					1					
E. dentipalpis	1	1	1	1	2	2	2			1		1			
L. tenuis		1	1		1	1		1	1	1	1	1	1	1	1
L. cristatus						1	1	1	1	1	1	1		1	
M. viaria		1	1				1			1	1	1		1	1
L. hortensis								1	1	1		1	1	1	1

Pasture **Interface** **Plantation**

Table 3.4 Two-way ordered table produced by TWINSPAN, showing the grouping of sites and species. Entries in the table are pseudospecies levels.

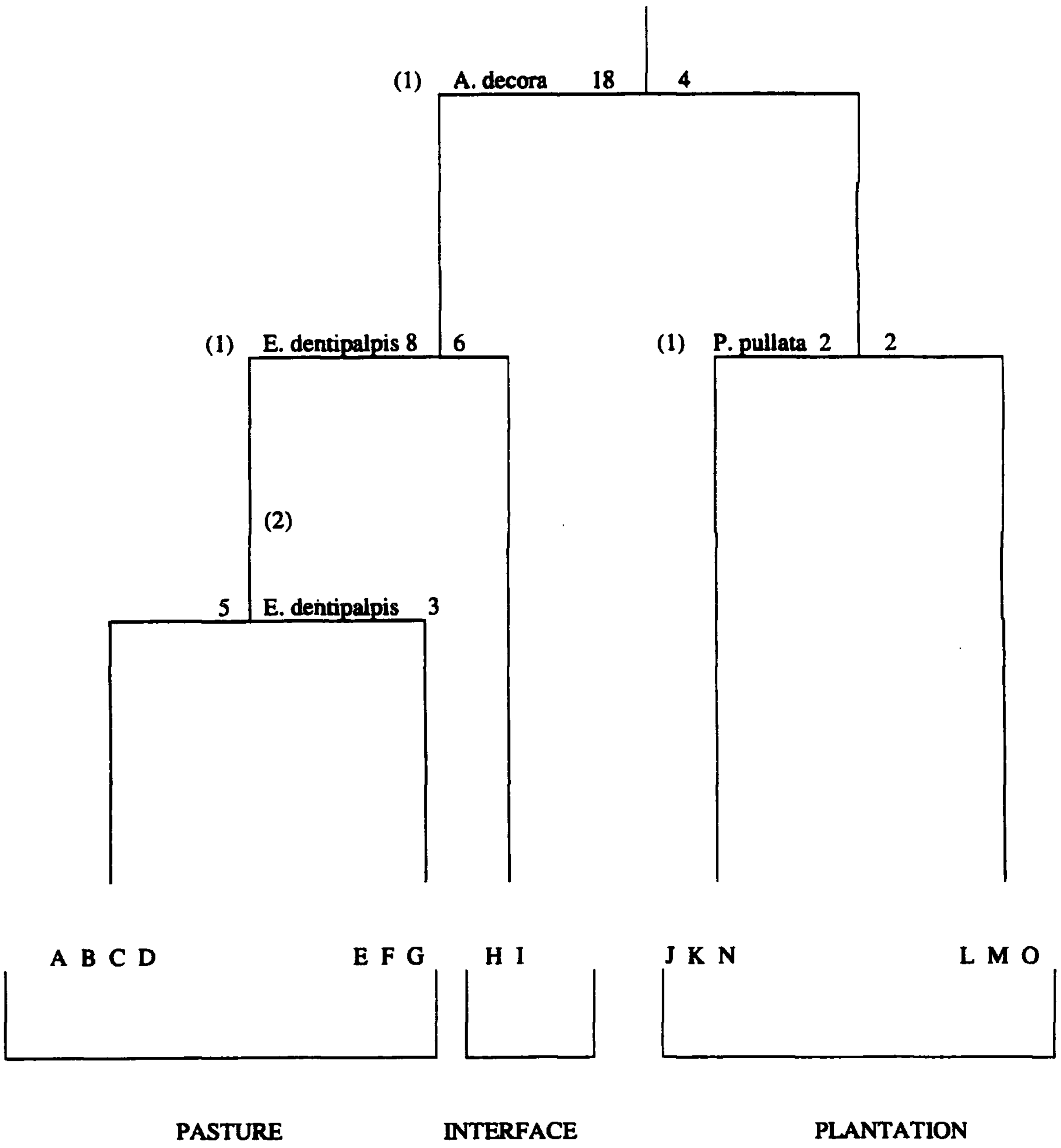


Fig 3.14 Dendrogram produced by TWINSPAN, showing site classification using common spiders. Indicator species with the associated pseudospecies level in brackets ( ) are shown at each stage. Numbers refer to numbers of species. Site 1 pasture/plantation transect.

indicator species for grassland, as it was found on sites A to G, but not sites H and I. Species preferential to the grassland sites were *X. cristatus, T. terricola, E. dentipalpis, C. bicolor, O. retusus, A. decora, P. amentata, E. atra, P. pullata, P. degeeri, A. pulverulenta,* and *Tiso vagans.* Species from group 1 found to be preferential to the boundary following the second division were *L. cristatus* and *L. hortensis. L. hortensis* was a species from the first division shown to be preferential to the plantation, and therefore its appearance in the boundary suggests that it crosses into the grassland habitat to a degree. The second division also separated the plantation sites into 2 groups, each containing 3 pitfall sites. 2 out of the 3 sites in the first group (group 5) were those closer to the boundary (J and K). The 3 sites in group 6 were further into the plantation. *P. pullata* and *E. dentipalpis* were indicator species for group 5, indicating a greater similarity to the grassland and boundary site, as these species were shown in the first division to be preferentially located here. *M. viaria* and *L. hortensis,* 2 species found to prefer the plantation from the first division, were found in the second division to be non-preferential to either of the plantation groups. The third division separates the grassland sites into 2 groups, with group 7 consisting of sites further into the pasture, and group 8 of sites closer to the boundary, with *E. dentipalpis* indicating those closer to the boundary.

In general terms, it is obvious that the second and third subdivisions are not as sharp as the first one, particularly on the plantation side of the transect. The scarcity of species belonging to a single group is evident, and reflects the fact that communities are identified by the relative abundances of species rather than sets of species, thus showing the individualistic nature of communities (Krebs 1985). This pattern has been observed for spiders (Coulson and Butterfield 1986).

The results of indicator species analysis suggest a link between the habitat preferences of the spiders and the vegetation, since the first division makes a clear distinction between the grassland and plantation sites. Although the results suggest that there are some structural or edaphic factors which have an influence on the spider community, a more quantitative approach is needed in order to establish if the influence is real.

3.2.2 Ordination:

To assess the relationships between the spiders and the measured environmental variables, ordination of the sites and species were made using canonical corresponcence analysis (CANOCO). An advantage of using direct ordination techniques is that it allows exploratory data analysis of many environmental variables simultaneously, thereby allowing their relative imporatance to be assessed by their effects on the populations. It results in the production of ordination diagrams of samples, species, and environmental variables which optimally display how community composition varies with the environment (Ter Braak 1988). The environmental variables used in this analysis were results from vegetation structural measurements (section 2.2.3) which were vertical vegetation density, frequency of vertical vegetation structures, frequency of horizontal vegetation structures; and soil moisture content. Scores were given according to habitat type (plantation 1; interface 2; pasture 3). The environmental variables are shown in Table 3.5.

Env.								Trap							
Var	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
SM	21.4	29.2	31.9	27.7	23.6	32.8	27.1	19.1	23.6	25.9	28.5	31.4	31.0	24.1	37.3
VVD	23.8	23.8	22.5	22.5	22.5	23.8	22.5	25.0	16.3	15.0	15.0	12.5	0.0	0.1	0.0
FHS	16.0	21.0	16.0	17.0	10.0	18.0	11.0	25.0	15.0	15.0	13.0	16.0	0.0	2.0	0.0
FVS	25.0	25.0	25.0	25.0	25.0	25.0	25.0	25.0	15.0	22.0	24.0	20.0	0.0	2.0	0.0
HS	3.0	3.0	3.0	3.0	3.0	3.0	3.0	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Table 3.5 Environmental variables (Env. var) for Site 1 pasture/plantation transect, where A to G represent the pasture, H the interface, and I to O the plantation transect regions. SM=% soil moisture; VVD=vertical vegetation density; FHS= frequency of horizontal vegetation structures; FVS=frequency of vertical vegetation structures; HS=habitat score (3=pasture, 2=interface, 3=plantation).

Eigen values (λ) for the ordination, which give relative indication of the amount of community variation explained by each axis were 0.473, 0.087 ,0.056, and 0.047 for the first to fourth axes respectively. These results suggest that the first two axes explained most of the between-site differences in spider communities. The axis 1 scores appeared to be related to habitat type (grassland or woodland), since the plantation sites had the highest axis 1 scores, and the pasture sites the lowest. In this study, the species-environment weighted correlation coefficients produced by CANOCO were 0.986; 0.910; 0.896 and 0.911 for axes 1 to 4 respectively. Axis 1 species correlations with the environmental variables are shown in Fig 3.15. Results suggest that axis 1 is most highly correlated with vegetation structure. Vertical vegetation density, vertical vegetation frequency, and horizontal frequency gave r-values of 0.922, 0.891, and 0.615 respectively. With 19 degrees of freedom (number of species-2), these are all significant at the 0.01 level. The soil moisture r-value is not significantly correlated with axis 1. Axis 2 is most highly correlated with soil moisture content, (r=0.523, significant at the 0.05 level with 19 df), suggesting that out of the environmental variables measured, separation of species and sites along the second axis is mainly due to this. This is consistent with results obtained in a study of habitat preferences of grassland spiders (Rushton, Topping and Eyre 1987) where results produced by Detrended Correspondence Analysis (DECORANA) suggested that management regime and site wetness were the major factors influencing spider communities (management is considered to affect spider communities by altering the structural diversity of the habitat).

Fig 3.16a displays the ordination diagram of the sample scores and centroids of the habitat type variables on axes 1 and 2. The quantitative environmental variables are represented by arrows which point roughly in the direction of maximum variation in value of the corresponding variable. Their length relative to each other indicates their relative importance. The first axis (λ_1=0.473) is seen to separate the pasture sites from the plantation sites. From the left of the diagram, the first centroid (◊) is for the pasture, the second for the interface, and the third for the plantation regions. The second axis (λ_2=0.087) doesn't appear to separate the sites, although the pasture sites are more clustered than those of the plantation. The low eigenvalue suggests that this axis does not exhibit much of the over all community variation. Fig 3.16b shows the ordination diagram based on species, to which the environmental variables represented by the arrows in Fig 3.16a may be applied. The species are represented by points, approximate to their optima, in the ordination space, as determined by the supplied environmental varables. The species are grouped such that those to the left of axis one were found more commonly or exclusively in the pasture, and those to the right were found more commonly or exclusively in the plantation. The species ordination plot shows a distinct group of 14 species with axis 1 scores below zero, suggesting that they preferred the managed

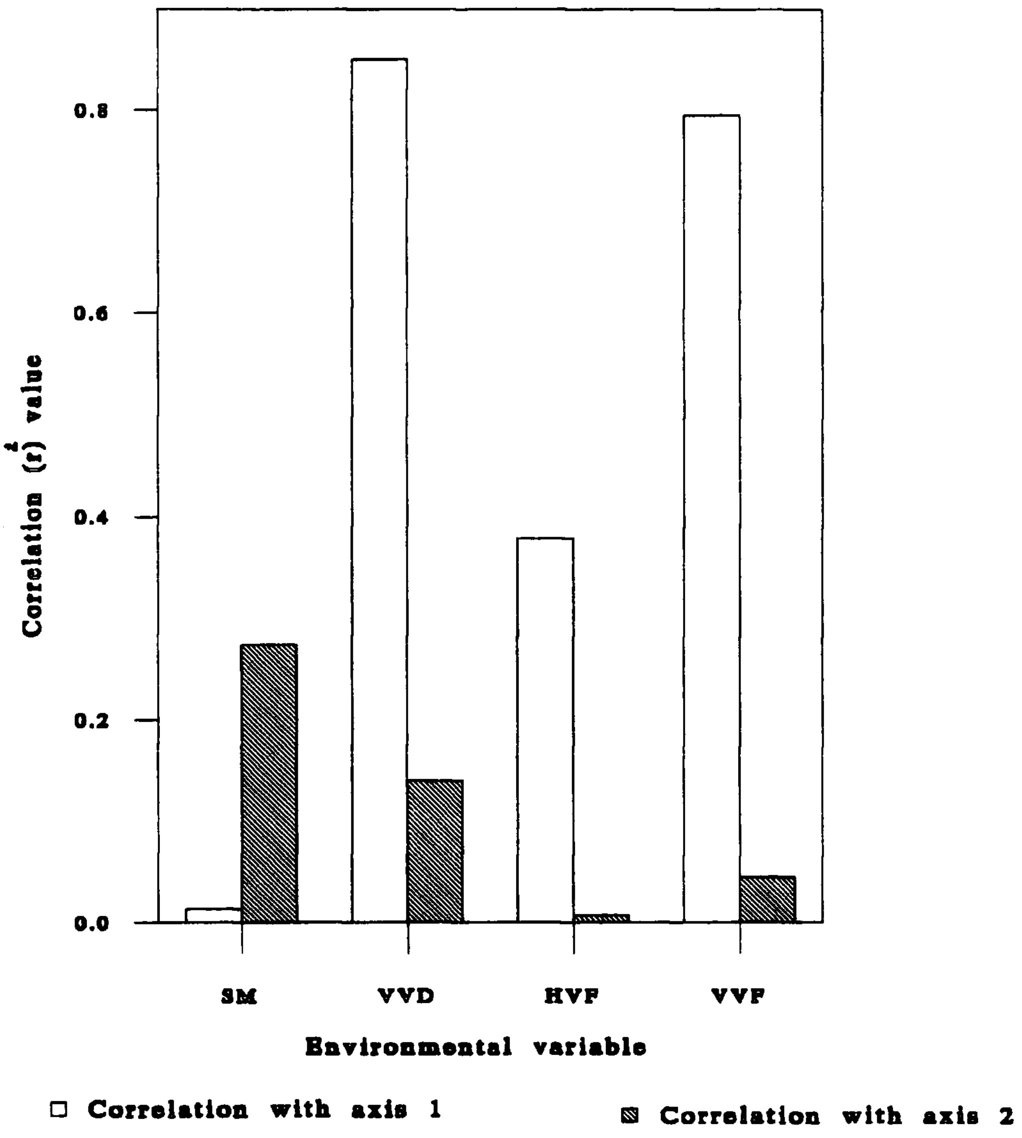
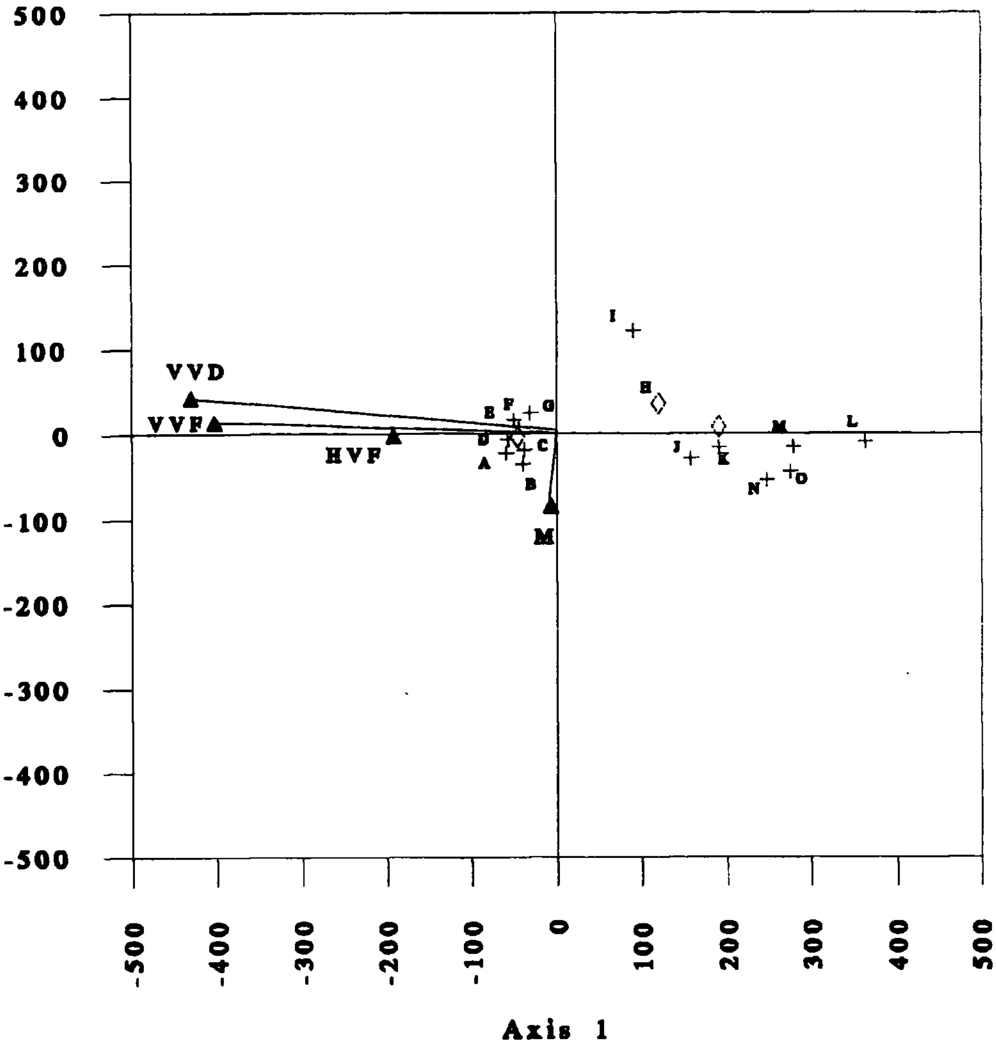
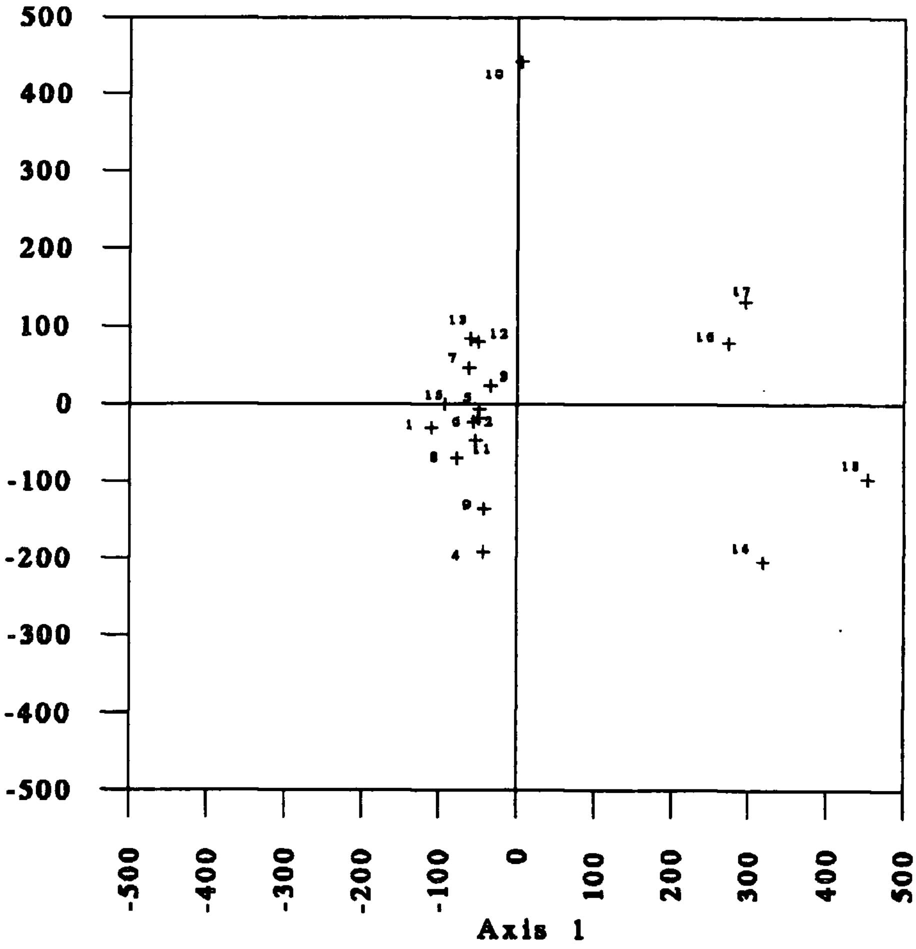


Fig 3.15 Correlation of environmental variables with the two main axes of variation in species produced by CANOCO. SM=%soil moisture; VVD=vertical vegetation density; HVF=frequency of horizontal vegetation structures; VVF=frequency of vertical vegetation structures.



VVD vertical vegatation density; VVF frequency of vertical vegetation structures; HVF frequency of horizontal vegetation structres; M % soil moisture. ◊ represents centroids of habitat type (see text).

Fig 3.16a Ordination diagram of samples, produced by canonical correspondence analysis of common spider species from Site 1. Environmental variables are represented by arrows which point in the direction of maximum variation, with length relative to importance.



1 X. cristatus; 2 P. pullata; 3 P. amentata; 4 A. pulverulenta; 5 T. terricola; 6 P. degerri; 7 O. fuscus; 8 O. retusus; 9 T. vagans; 10 S. frontata; 11 E. dentipalpis; 12 E. atra; 13 A. decora; 14 M. viaria; 15 C. bicolor; 16 L. tenuis; 17 L. cristatus; 18 L. hortensis.

Fig 3.16b Ordination diagram of species, produced by canonical correspondence analysis of common spider species from Site 1.

pasture habitat containing greater vegetational structural diversity. These species were *Xyticus cristatus* (Thomisidae), *Pardosa pullata, Pardosa amentata, Trochosa terricola, Alopecosa pulverulenta* (Lycosidae), *Pachygnatha degeeri* (Tetragnathidae), *Oedothorax retusus, Tiso vagans, Erigone dentipalpis, Erigone atra, Agyneta decora*, *Centromerita bicolor,* and *Savigyna frontata* (Linyphiidae). *E. atra, E. dentipalpis,* and *O. fuscus* are species typical of more open, managed sites (Rushton, Topping and Eyre 1987). *Microneta viaria, Lepthyphantes tenuis, Lepthyphantes cristatus,* and *Linyphia hortensis* had axis 1 scores above 250, indicating a preference for the undisturbed plantation sites.

The wide separation in axis 1 scores indicates that these two groups of species did not occur together with any frequency on the the sites sampled. There appears to be no intermediate group of species, suggesting that no species was equally abundant in both of the habitat types. This indicates the effect resulting from the abrupt change at the interface on the relative abundance of spider species in the community.

The range in axis 2 species scores was also large, although the lower eigenvalue attributes less importance to the factors contributing to this axis.

To investigate whether the observed differences could be accounted for by chance, a Monte Carlo permutation test was used on the data (Ter Braak 1988). This is a test carried out in CANOCO by randomly permuting the sample numbers in the environmental data: the environmental data are randomly linked to the species data, giving rise to a "random data set." For each random data set, CANOCO calculates a test statistic (this study used the trace statistic which is the sum of all eigenvalues). If the species react to the current environmental variables, then the test statistics calculated from the data-as-observed will be larger than most of the test statistics calculated from the random data. If the observed value is amongst the 5% highest values, then the species are significantly related to the environmental variables.

The 99 random data sets generated by random permutation of pitfall sites all yielded a lower eigenvalue than the axis 1 eigenvalue. It is therefore concluded that there are significant differences in axis 1 environmental variables (P= 0.01), which affect the distribution of spider species.

CHAPTER 4

SITE 2 RESULTS

A table showing the total numbers of each invertebrate group collected is shown in Appendix 5. A species list for the spiders identified from Site 2, using correct nomenclature, is presented in Appendix 6. Subsequent references to species in the text will use the abbreviated form. Appendix 7 shows the total numbers of each of these species. Table 4.1 shows the numbers of the 19 most common species (where 10 or more individuals were recorded). Including rare species, a total of 1212 spiders was collected, and included 51 species and 7 families. The crop samples contained 527 individuals, representing 36 species and 5 families. Those from the wood contained 457 individuals representing 39 species and 7 families. Samples from the boundary contained 228 individuals representing 21 species and 5 families. The samples size of the boundary was 1/7 that of either crop or wood and therefore cannot be compared directly. For the same sample area, the number of individuals trapped in the boundary may be expected to be 7x228=1596, a value greater than that for either the crop or wood communities. A total of 9 species were found in the crop only, 15 species in the wood only, and 26 species were found in both habitats. One species (*Alopecosa pulverulenta*) was found in the boundary only, although a total of only two individuals were recorded.

4.1 Community Analysis

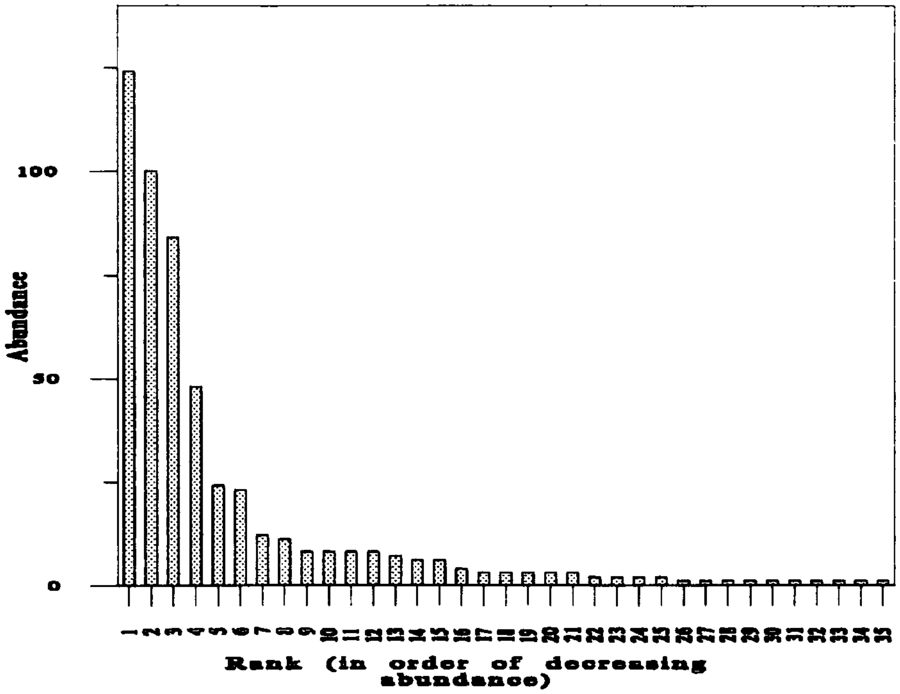
4.1.1 Species abundance relationships

Rank abundance plots showing the patterns of species abundances for the community on each side of the interface were constructed (Figs 4.1a and 4.1b). The distribution shows a high number of rare species, intermediate numbers of more common species, and low numbers of common species, characteristic of the log series distribution. When the crop and woodland are compared, the wood shows lower dominance, due to the lower abundance of the most common species, and higher eveness, due to a smaller range in abundance between species. This is expected to result in a higher diversity for this community.

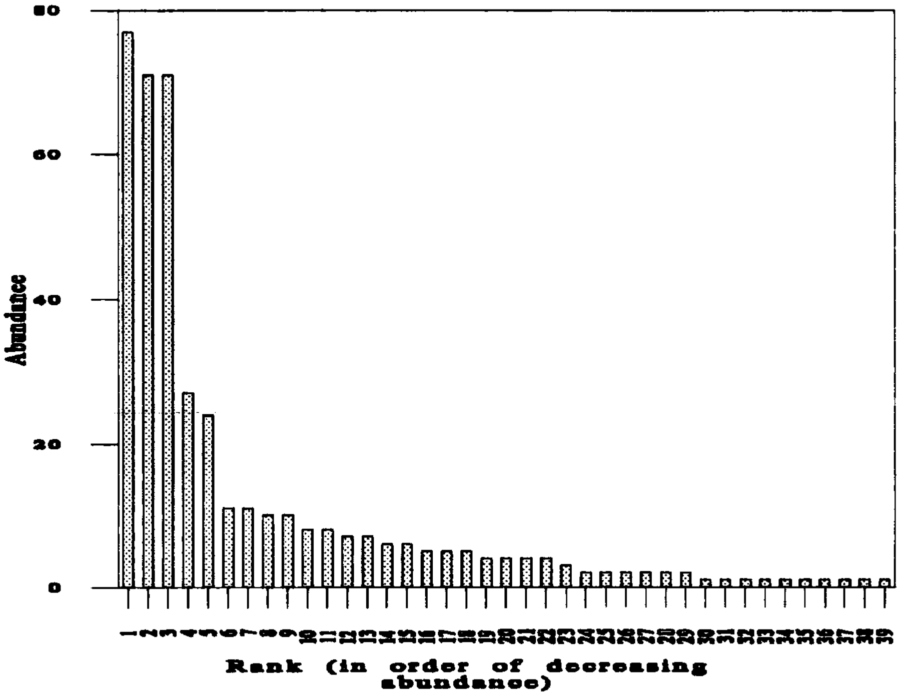
Figs 4.2a and 4.2b show the log abundance/species rank plots for the crop and woodland respectively. Both graphs deviate from the geometric distribution which would produce a straight line.

Species	Trap															
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	Tot
Gnaphosidae																
Micaria pulicaria	0	0	0	0	0	0	0	6	2	0	8	0	0	0	0	16
Clubionidae																
Clubiona lutescens	0	0	0	0	0	0	1	2	1	3	1	0	2	1	3	14
Thomisidae																
O. praticola	0	0	1	0	0	0	0	1	4	2	4	1	3	8	2	26
Lycosidae																
Pardosa amentata	5	7	27	23	7	5	26	131	23	2	6	8	8	16	8	302
Trochosa terricola	0	0	2	0	1	1	2	5	4	0	1	0	1	1	1	19
Linyphiidae																
Ceratinella brevis	0	0	0	1	0	1	6	5	11	8	3	3	0	1	1	40
Walckenaeria cuspidata	2	0	0	0	1	0	3	1	3	1	2	0	0	0	0	13
Oedothorax fuscus	6	2	1	0	2	0	0	1	2	2	0	0	1	0	0	17
Monocephalus fuscipes	1	0	0	1	1	0	0	0	3	2	1	1	0	4	0	14
Savigyna frontata	3	7	2	2	1	7	2	2	3	1	0	1	1	0	0	32
Diplocephalus latifrons	2	1	0	0	0	3	6	4	4	1	0	1	2	2	0	26
Diplocephalus picinus	0	2	0	0	4	40	38	35	29	7	7	6	10	8	4	190
Erigone dentipalpis	3	2	0	1	0	1	1	1	0	1	0	0	0	0	0	10
Erigone atra	20	12	7	3	2	3	1	2	2	0	1	0	0	1	0	54
Diplostyla concolor	5	15	13	17	25	17	32	21	27	12	14	10	7	3	4	222
Stemonyphantes lineatus	1	0	1	0	0	0	0	1	2	0	1	0	0	3	1	10
Lepthyphantes tenuis	4	2	2	4	7	2	2	0	2	0	1	0	1	0	1	28
Lepthyphantes cristatus	0	0	0	0	0	1	1	0	2	0	1	4	0	1	0	10
Lepthyphantes tenebricola	0	1	2	0	0	0	0	0	1	4	0	1	0	0	1	10

Table 4.1 Totals of common spider species (10 or more individuals collected over the 3 week trapping period), Site 2 crop/woodland transect, where A to G represent the crop, H the interface, and I to O the woodland transect regions.



a



b

Fig 4.1 Rank abundance plots of numbers of specimens of each species, Site 2, a=crop, b=woodland.

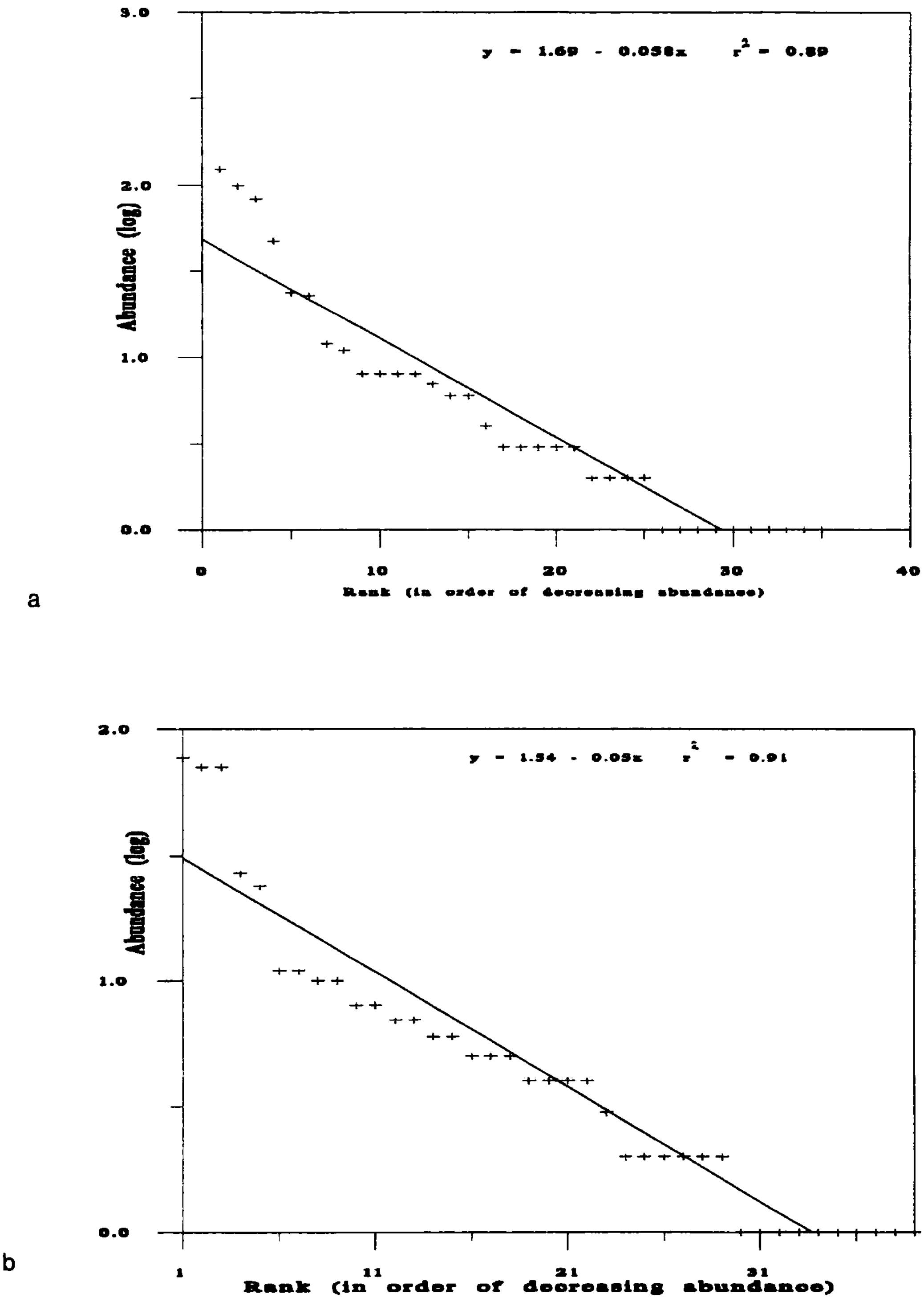


Fig 4.2 Log abundance distribution of ranked species for Site 2, a=crop, b=woodland.

4.1.2 Diversity

Fig 4.3 shows the total number of spiders trapped at each transect point for the three weeks combined. It shows a fairly uniform abundance in the crop until a distance of 4m from the interface (trap position F) where numbers rise to a peak at the interface. Between the interface and 4m into the wood (trap position I), the numbers decline again to abundances similar to those found in the crop. At 2m either side of the interface (trap positions G and I), the numbers in the crop and wood are fairly even, but beyond this the drop in numbers is more rapid in the wood then in the crop (Traps I and J compared with traps G and F in Fig 4.3). This general pattern was reflected in the totals for each separate week suggesting that this was a real effect.

The peak at H suggests that this is a more favourable habitat than the wood or the crop, and could be due to structural diversity or vegetation density. It is also a position from where species may migrate into the crop or the wood. It may also serve the purpose as a refuge for crop species from the more harsh and unstable crop environment. Chi-squared analysis carried out on the species totals between successive pitfalls in the transect resulted in differences as shown in Fig 4.3. The results indicate a significant increase in numbers from 6m either side of the interface to the interface, where the highest numbers occurred (see Fig 4.3 for details). This suggests that the interface has a positive influence on the number of spiders for a distance of 6m into the habitats on either side.

Table 4.2 shows the number of spiders, species richness, and the values of Simpson's diversity index for each transect position

Species richness: The number of species caught at each transect position is shown in Fig 4.4 . The species richness shows a peak in the boundary habitat, with the highest value at I on the woodland side of the interface. The crop generally has lower species richness than the wood.

Species diversity: Fig 4.5 shows the change in diversity (Simpson's index) along the transect. It shows a pattern of fairly constant levels in the crop, with a drop in diversity at the interface, followed by a rapid rise in the wood to a fairly constant level higher than in the crop. The woodland spider diversity appears more constant than that of the crop. This may reflect insability of the crop communtiy, where species migrate into and out of the crop environment, resulting in a changing species diversity.

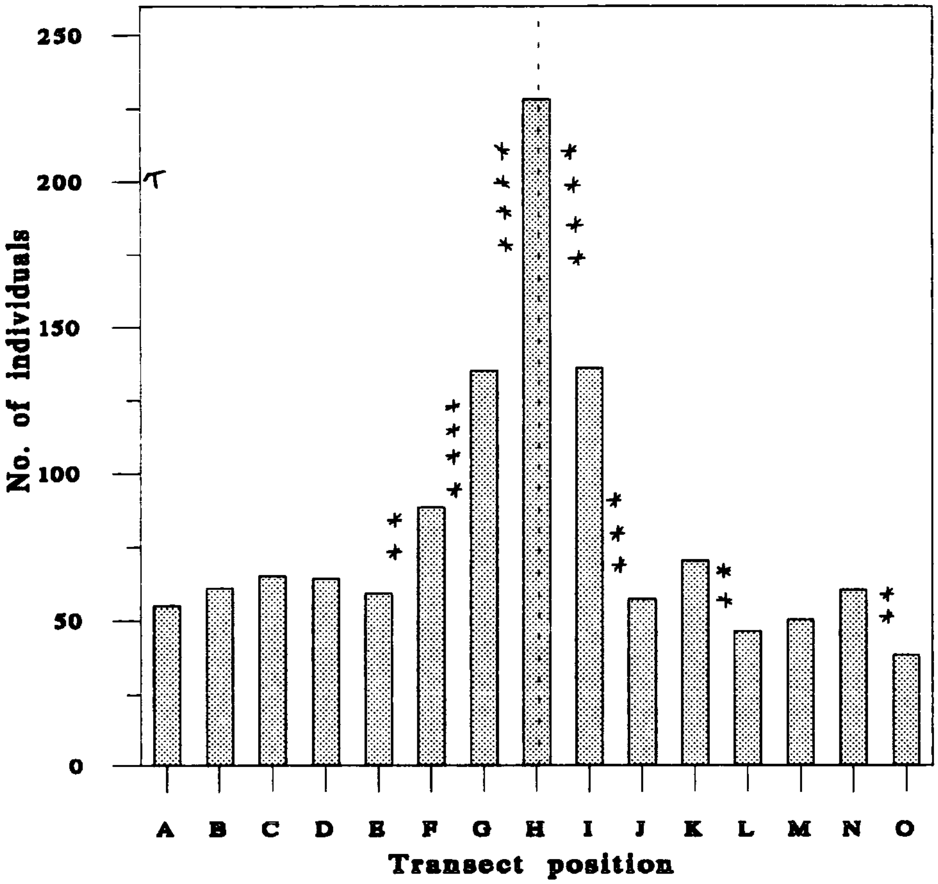


Fig 4.3 Total number of spiders recorded for each transect position over the three week trapping period for Site 2, where A to G represent the crop, H the interface, and I to O the woodland transect regions. Significant differences between successive traps as calculated by chi-squared analysis are shown, where the significance levels are:**** (P=0.005), *** (P=0.001), ** (P=0.05), * (P=0.01) with 1 df.

Trap	N	S	Diversity
A	54	13	1.70
B	59	17	1.95
C	65	14	1.46
D	60	12	1.42
E	55	14	1.39
F	87	17	1.33
G	134	22	1.70
H	226	21	0.99
I	133	24	2.03
J	53	18	2.19
K	55	18	2.06
L	42	16	2.01
M	42	15	1.99
N	55	17	1.94
O	35	15	2.15
Tot	1155	52	1.97

Table 4.2 Number of spiders (N), species richness (S), and diversity (Simpson) for transect position totals (immatures not included), Site 2 crop/woodland transect. where A to G represent the crop, H the interface, and I to O the woodland transect regions.

The number of individuals found in the crop and wood habitats were similar, but the wood showed higher species richness, therefore resulting in higher diversity.

To see if the total spider community had been sampled, plots were made for the crop and wood separately of sample number against number of species, as for Site 1. The results in Fig 4.6 show that both the crop and woodland species appear to be well represented in total shown by the levelling off in the number of species with increased number of samples. Fig 4.6 also shows that the number of species collected with increasing sampling effort in the woodland were consistently larger than those from the crop.

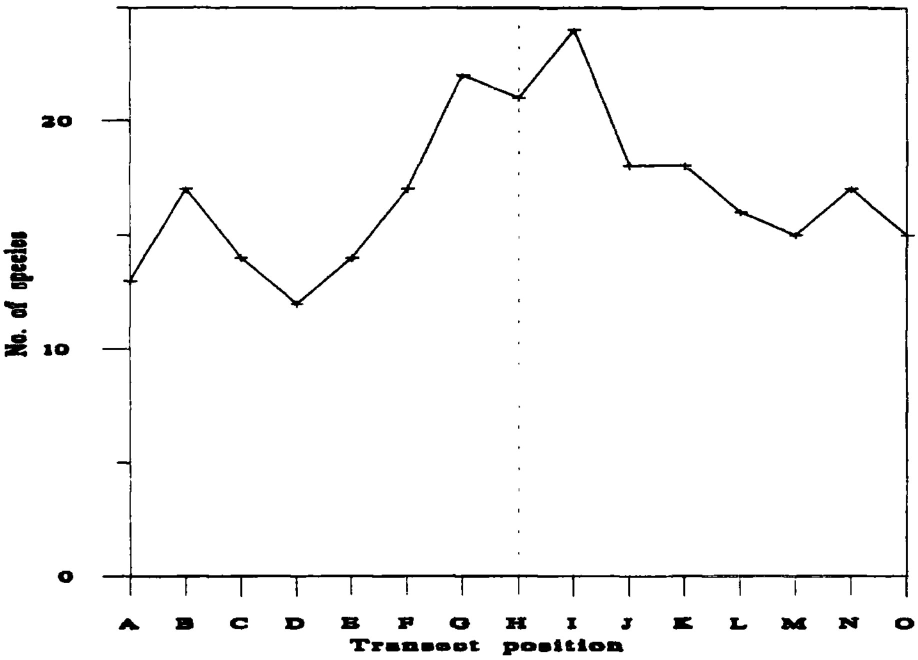


Fig 4.4 Species richness at each transect position, Site 2, where A to G represent the crop, H the interface and I to O the woodland transect regions.

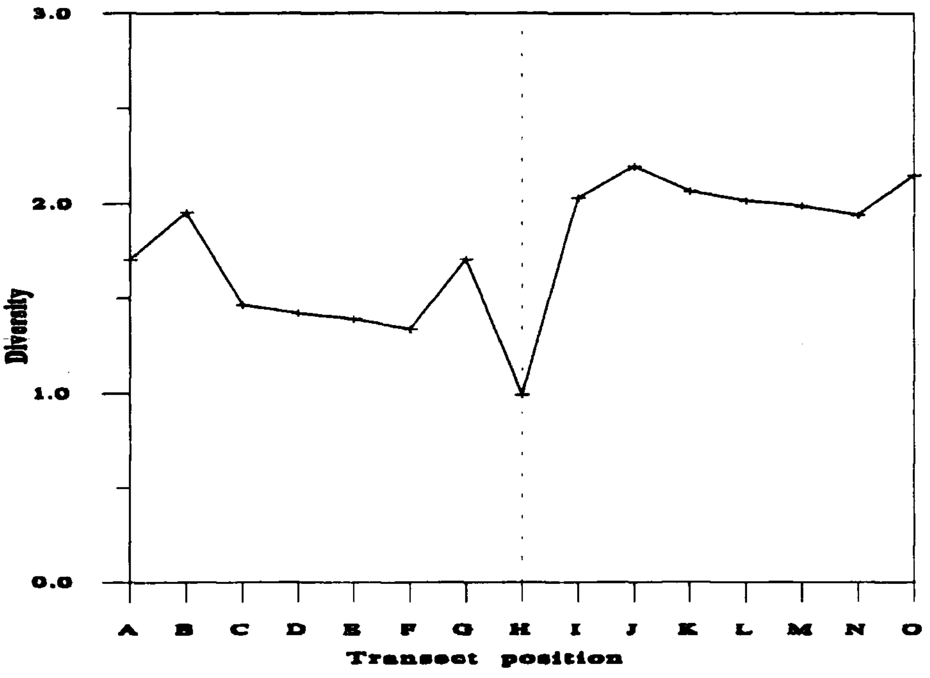


Fig 4.5 Change in diversity as measured by Simpson's index for Site 2, where A to G represent the crop, H the interface, and I to O the woodland transect regions.

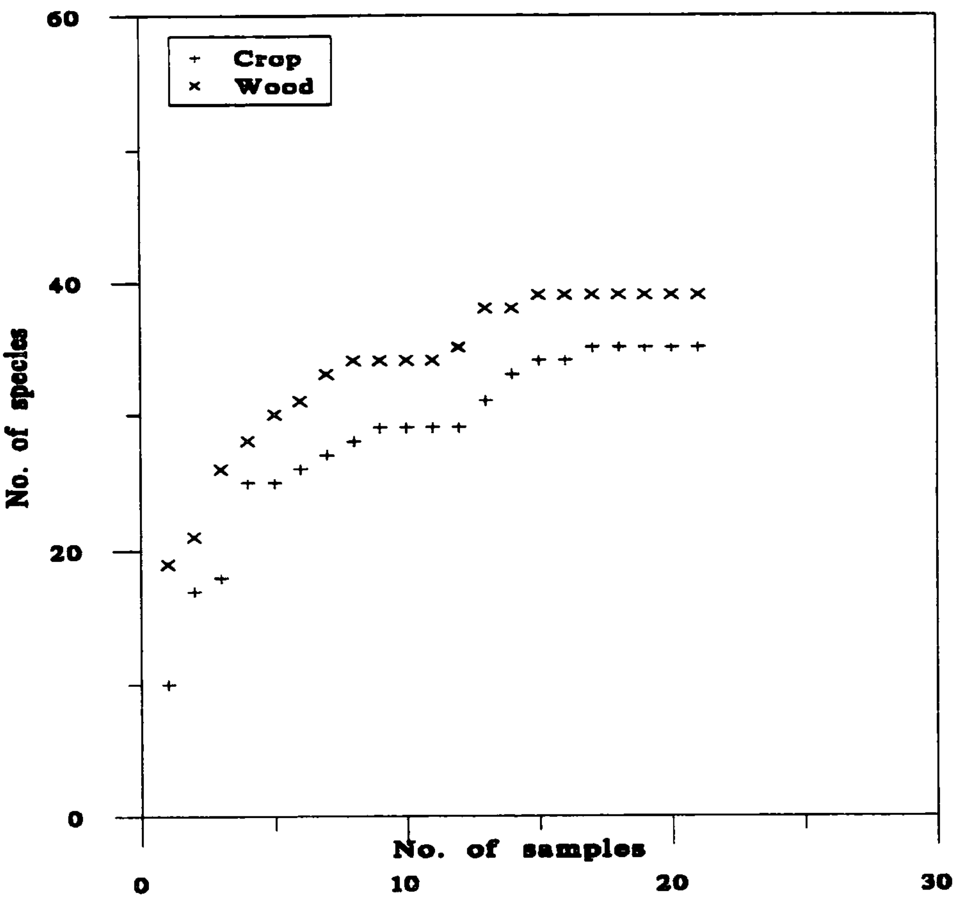


Fig 4.6 Increase in the number of species with increased sampling effort for the crop and woodland regions either side of the interface at Site 2.

4.13 Distribution of spider families and species

In the crop, the dominant family is the Linyphiidae, with the Lycosidae as the second most abundant group (Fig 4.7). Low numbers of Tetragnathidae and Thomisidae are also present. Linyphiid numbers rise to a peak at position G, 2m from the interface, immediately on the edge of the crop. Between this position and H, at the interface, there is a slight decline in ther abundance. The numbers of lycosids show a rapid increase between F (4m from the interface) and H (at the interface) to become the most dominant group at H with greater abundance than the linyphiids. Between H and I (2m into the wood), linyphiid numbers rise to a peak similar to that at G, beyond which there is a rapid decline to J (4m into the wood) and then a gradual decline through the remaining wood sites at abundance levels similar to that in the crop. Linyphiids remain the dominant group through the wood. The abundance of lycosids shows a rapid drop from H to I, similar to that between H and G, and remain at relatively low levels throughout the wood. Also present in the boundary and wood were small numbers of Gnaphosidae, Clubionidae, Thomisidae and Tetragnathidae. Gnaphosidae and Clubionidae are groups which were not represented in the crop. Table 4.3 shows the percentage abundance of the common spider families (species with 10 or more individuals trapped in total) which make up the community at each transect position.

Fig 4.8 shows each major habitat type and the community composition of spider families.It shows that the crop is dominated by the Linyphiidae, with a fairly large percentage of lycosids. The boundary is dominated by lycosids with linyphiids also making up a large proportion of the community. The wood is dominated by linyphiids, and the community here has more families represented (5 families compared with 3 for the boundary and 3 for the crop). Tetragnathidae were represented only in the crop, Gnaphosidae only in the boundary and wood, and Clubionidae and Thomisidae only in the wood. No families were restricted to the boundary habitat.

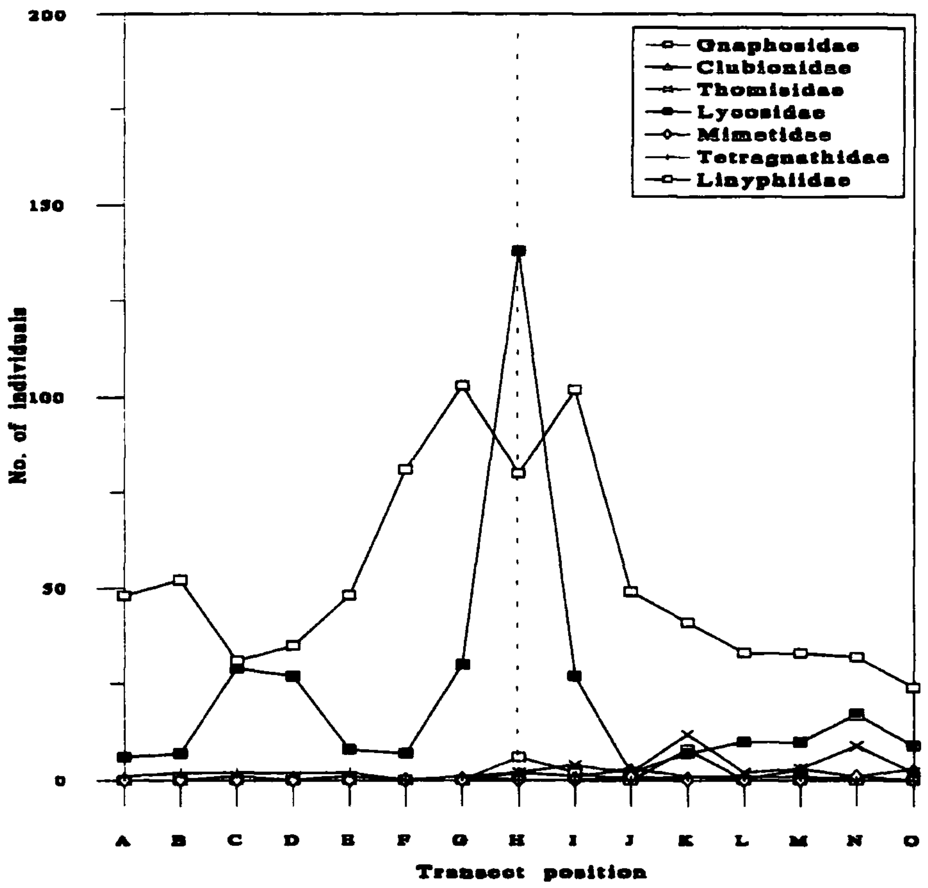


Fig 4.7 Distribution of spider families (data collated from 3 week trapping period) along the Site 2 transect positions, where A to G represent the crop, H the interface, and I to O the woodland transect regions.

Species	Trap														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Gnaphosidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	1.6	0.0	15.7	0.0	0.0	0.0	0.0
Clubionidae	0.0	0.0	0.0	0.0	0.0	0.0	0.83	1.0	0.8	6.5	2.0	0.0	5.6	2.0	11.5
Thomisidae	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.5	3.2	4.3	7.8	2.8	8.3	16.0	7.7
Lycosidae	9.6	13.7	50.0	44.2	15.7	7.4	23.1	62.4	21.6	4.3	13.7	22.2	25.0	34.7	34.6
Linyphiidae	90.4	86.3	48.3	55.8	84.3	92.6	76.1	33.3	72.8	84.9	60.8	75.0	61.1	47.3	46.2

Table 4.3 The abundance (% of total) of common families (totals of species with 10 or more individuals) for Site 2 crop/woodland transect, where A to G represent the crop, H the interface, and I to O the woodland regions.

The distributions of the common species according to their total numbers are shown in Fig 4.9. Most of these species appear to show an individualistic distribution, showing a preference for a particular side of the interface. No species appeared to be restricted to the boundary only, and most show a degree of overlap from one habitat into the next.

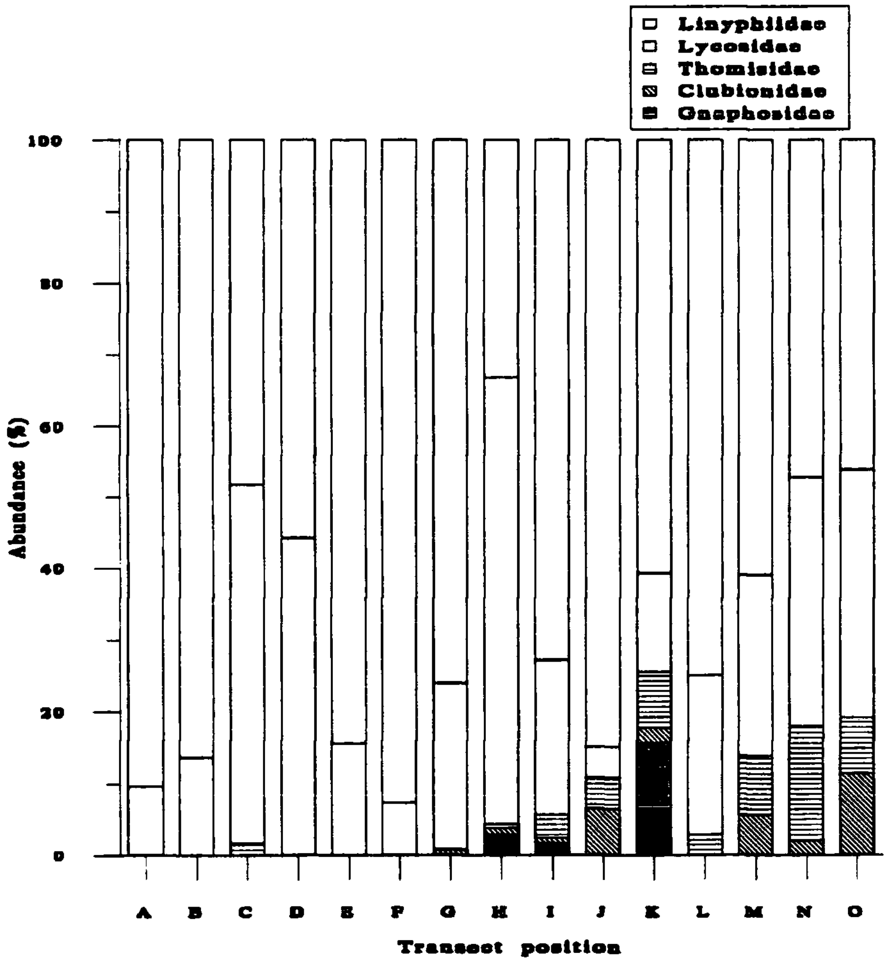


Fig 4.8 Percentage composition of major spider families at each transect position of Site 2 showing the change in abundance, where A to G represent the crop, H the interface, and I to O the woodland transect regions.

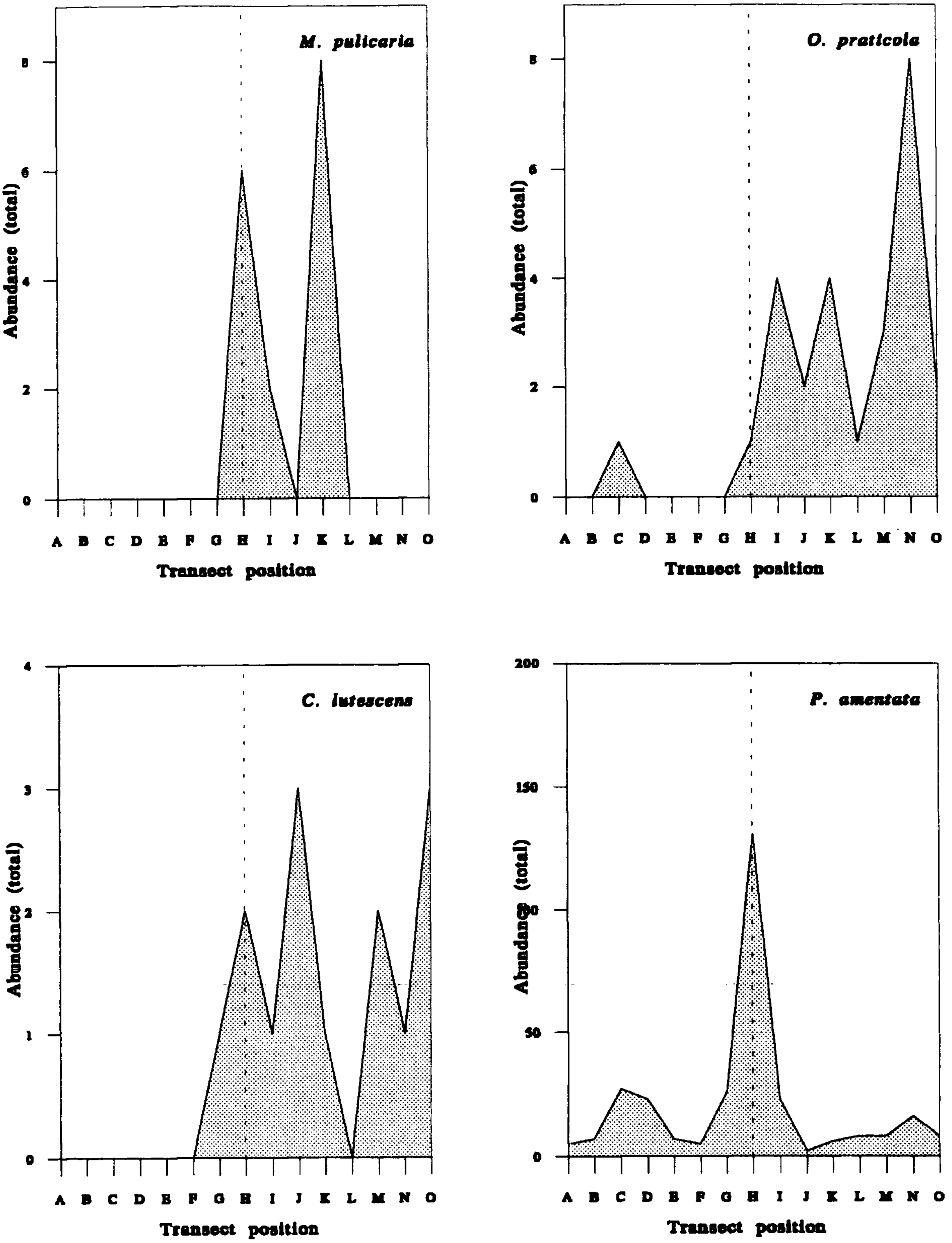
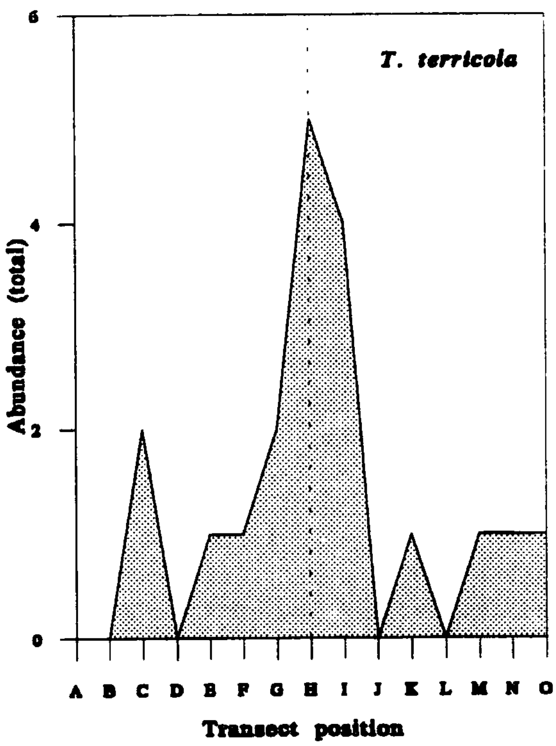
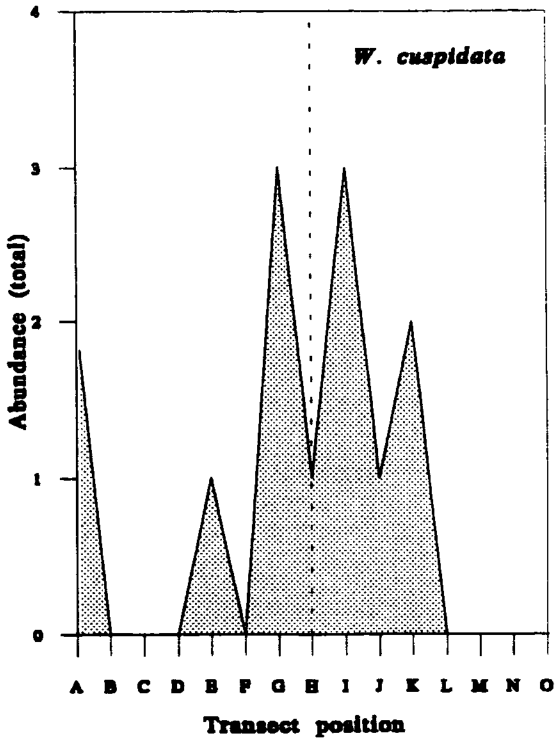
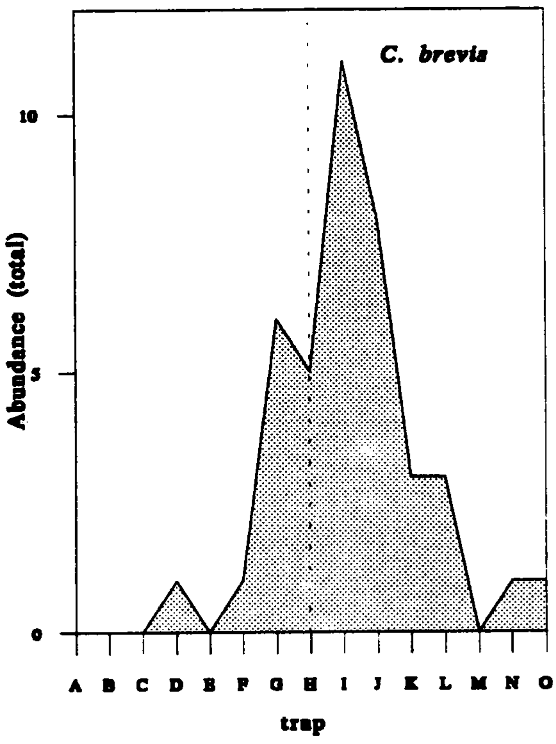
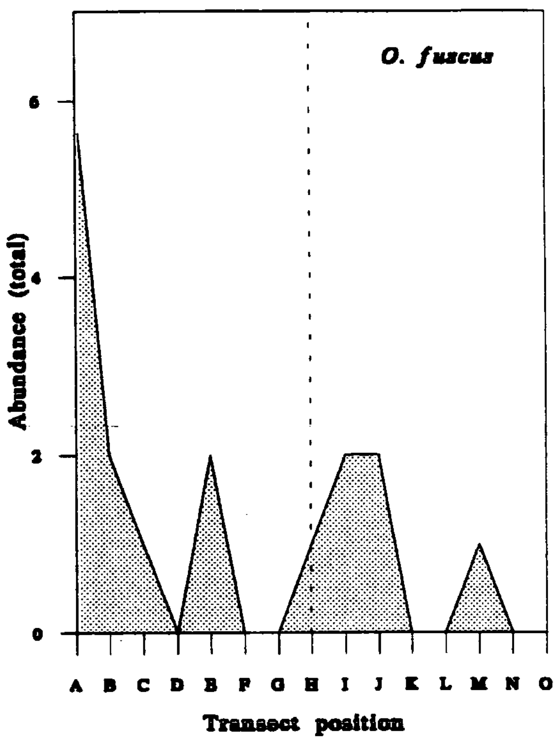


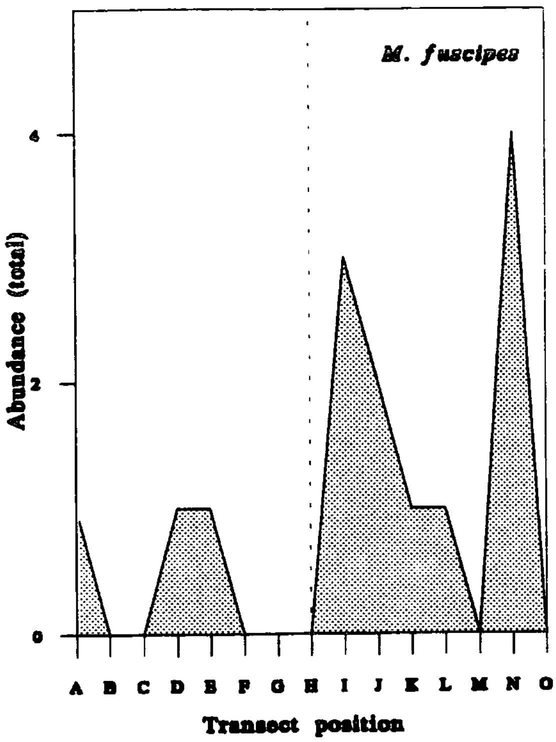
Fig 4.9 Abundance (totals) of common spider species (10 or more individuals) collected over the 3 week trapping period at each transect position for Site 2 crop/woodland transect, where A to G represent the crop, H the interface, and I to O the woodland transect regions (continued on following 4 pages).

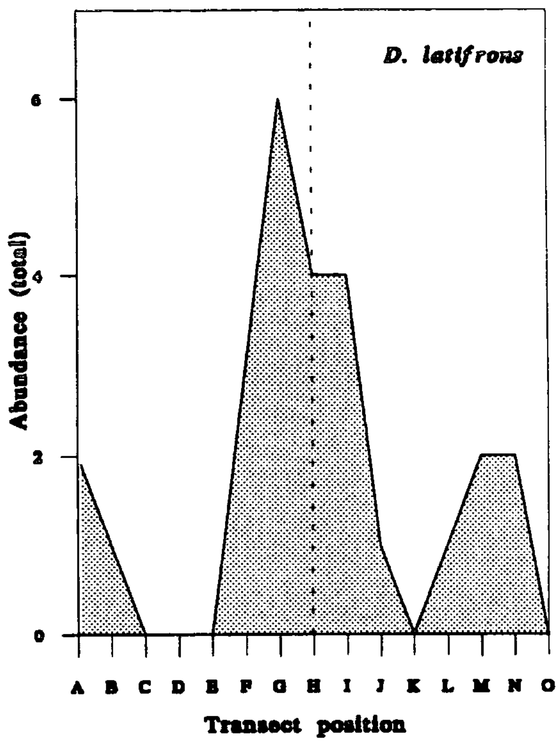

T. terricola
Abundance (total)
0
2
4
6
A B C D E F G H I J K L M N O
Transect position

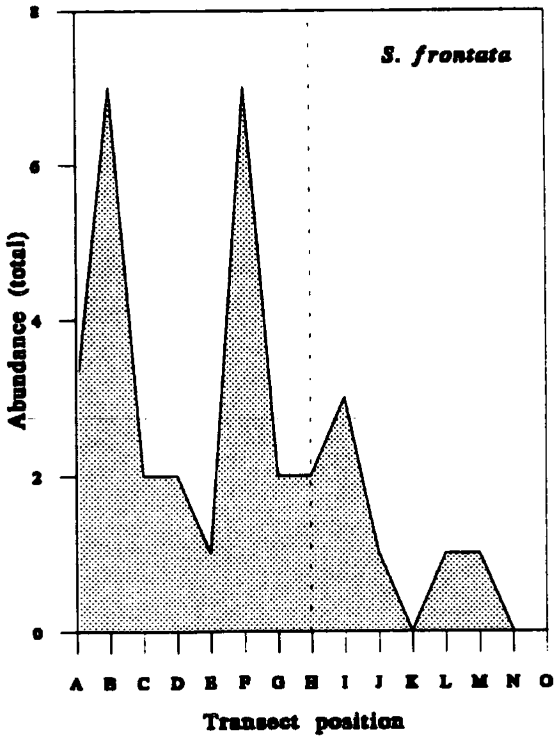

W. cuspidata
Abundance (total)
0
1
2
3
4
A B C D E F G H I J K L M N O
Transect position

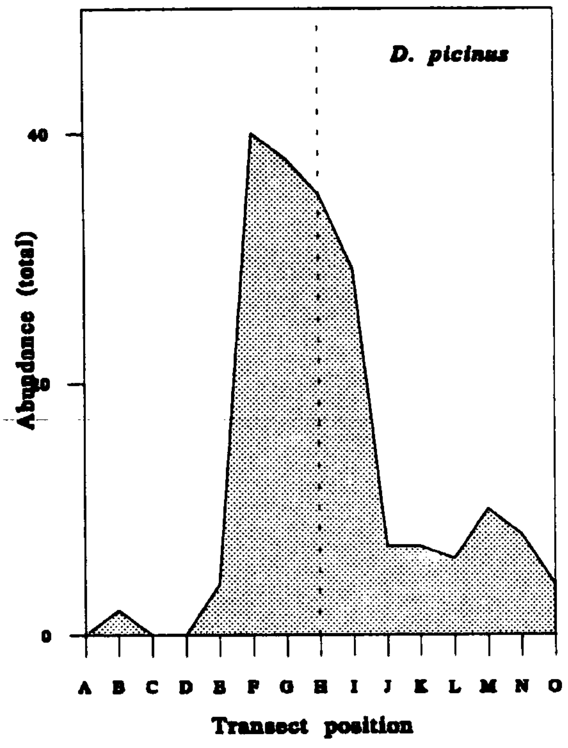

C. brevis
Abundance (total)
0
5
10
A B C D E F G H I J K L M N O
trap

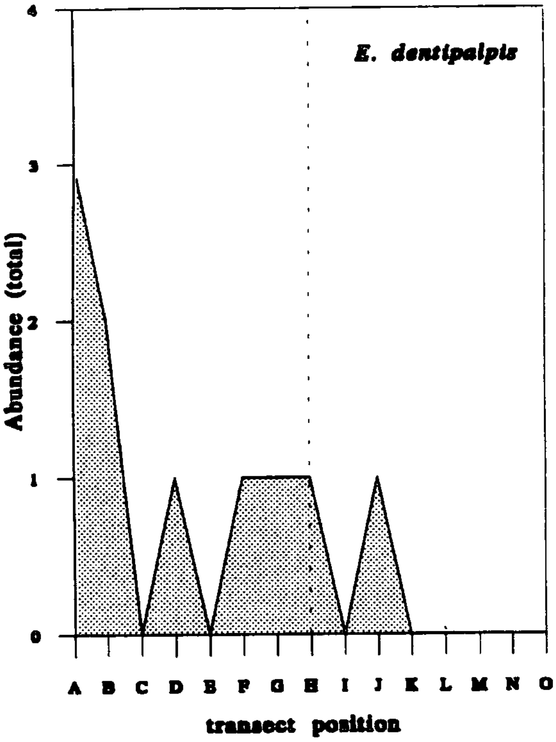

O. fuscus
Abundance (total)
0
2
4
6
A B C D E F G H I J K L M N O
Transect position

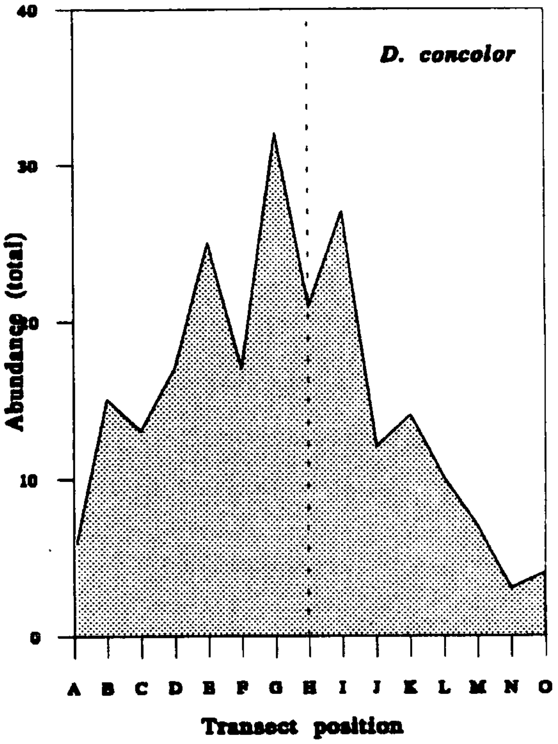

M. fuscipes
Abundance (total)
0
2
4
A B C D E F G H I J K L M N O
Transect position

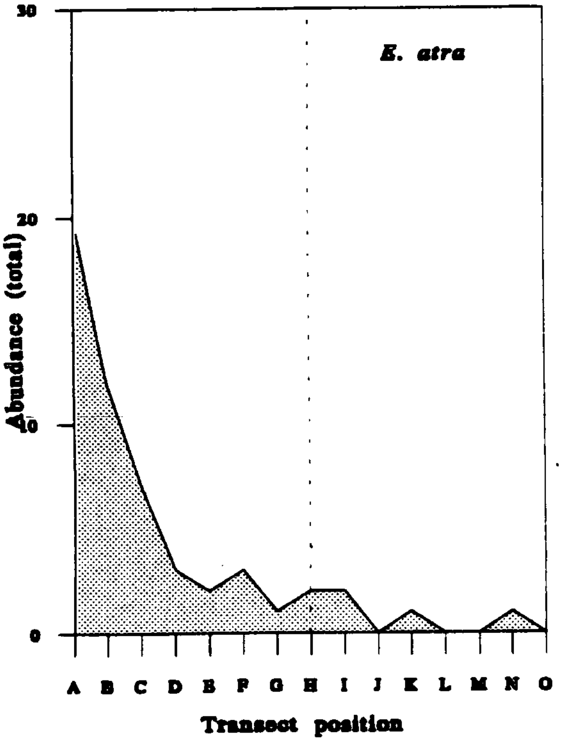

D. latifrons
Abundance (total)
0
2
4
6
A B C D E F G H I J K L M N O
Transect position

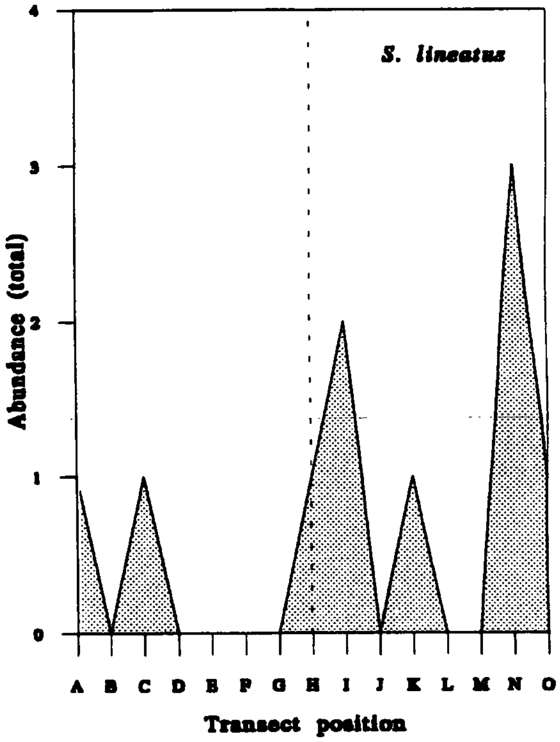

S. frontata
Abundance (total)
0
2
4
6
8
A B C D E F G H I J K L M N O
Transect position

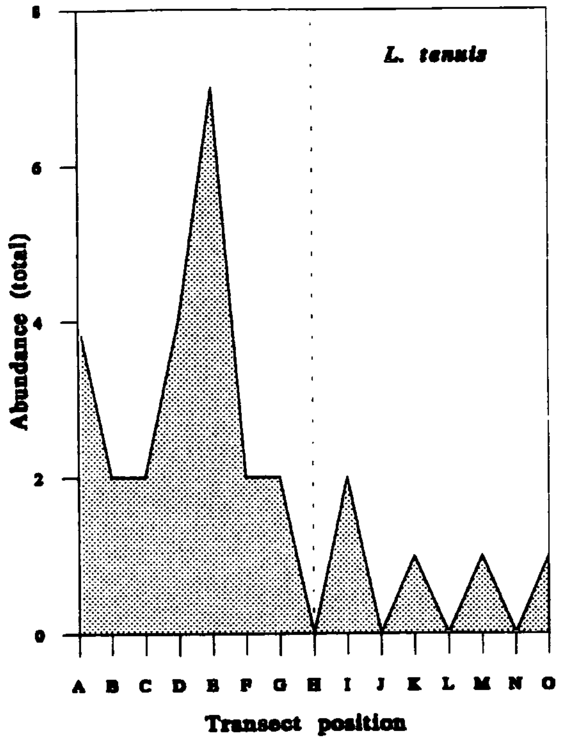

D. picinus
Abundance (total)
0
20
40
A B C D E F G H I J K L M N O
Transect position

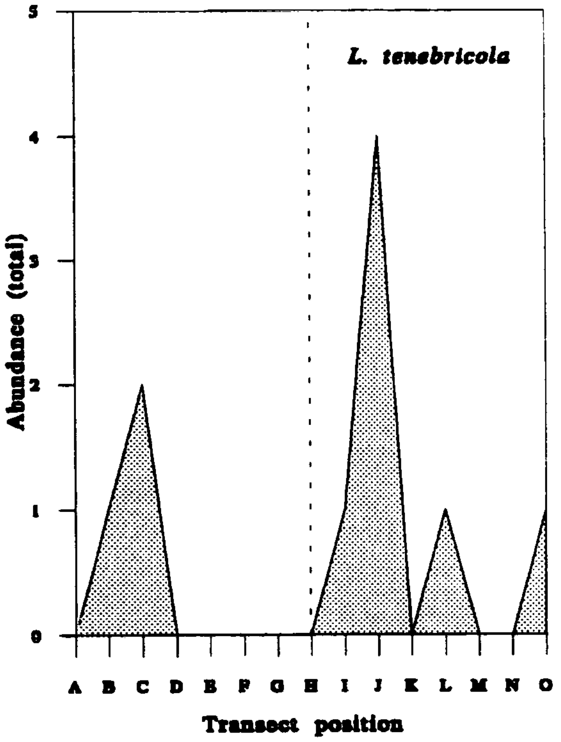

E. dentipalpis
Abundance (total)
0
1
2
3
4
A B C D E F G H I J K L M N O
transect position

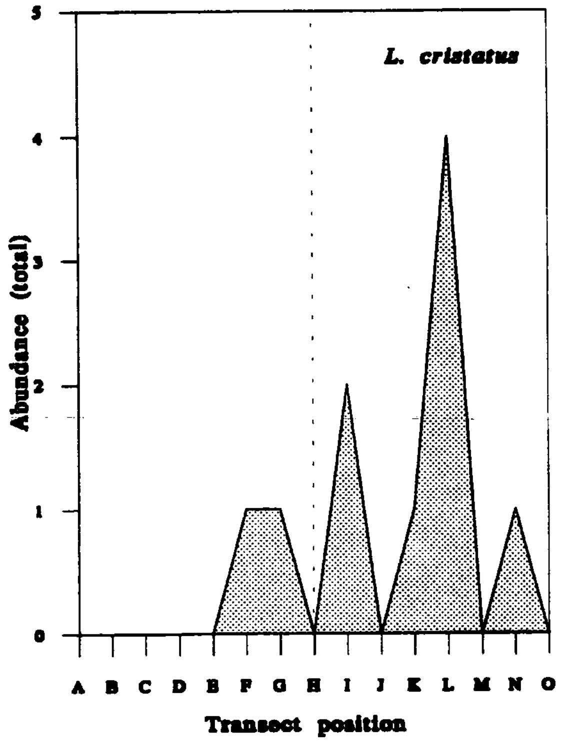

D. concolor
Abundance (total)
0
10
20
30
40
A B C D E F G H I J K L M N O
Transect position


E. atra
Abundance (total)
0
10
20
30
A B C D E F G H I J K L M N O
Transect position


S. lineatus
Abundance (total)
0
1
2
3
4
A B C D E F G H I J K L M N O
Transect position


L. tenuis
Abundance (total)
8
6
4
2
0
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
Transect position


L. tenebricola
Abundance (total)
5
4
3
2
1
0
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
Transect position


L. cristatus
Abundance (total)
5
4
3
2
1
0
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
Transect position

4.1.1 Similarity measurements

Quotient of similarity:

Fig 4.10 shows the values of the Søensen quotient of similarity (I) as percentages which represent similarities between each transect position, and Fig 4.11 shows clustering of transect regions in a dendrogram.

Trap															
A															
B	66.7														
C	61.5	58.1													
D	64.0	55.2	61.5												
E	66.7	58.1	64.3	53.9											
F	53.3	52.9	58.1	64.3	58.1										
G	51.4	51.3	50.0	66.7	50.0	71.8									
H	52.9	42.1	45.7	36.4	47.1	52.6	66.7								
I	54.1	43.9	53.6	40.0	54.1	53.7	56.6	66.7							
J	37.2	48.5	43.8	40.0	50.0	45.7	50.0	61.5	61.9						
K	45.2	28.6	43.8	40.0	50.0	45.7	50.0	61.5	71.4	50.0					
L	34.5	36.4	43.8	42.9	33.3	54.6	52.6	48.7	60.0	58.8	52.9				
M	42.9	43.8	48.3	37.5	48.3	42.4	54.1	55.6	56.4	48.5	42.4	51.6			
N	40.0	29.4	38.7	34.5	40.0	52.9	51.3	57.9	73.2	51.4	62.9	54.6	50.0		
O	28.6	31.3	44.4	29.6	34.5	37.5	43.2	55.7	63.2	54.6	60.6	45.2	53.3	56.3	
Trap	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O

Average value of similarity (%I) between communities

	Crop	Woodland
Crop	58.9	43.3
Interface	59.1	56.2
Woodland		58.2

Fig 4.10 Values of the quotient of similarity (I) for Site 2 (as%), where A to G represent the crop, H the interface, and I to O the woodland transect regions.

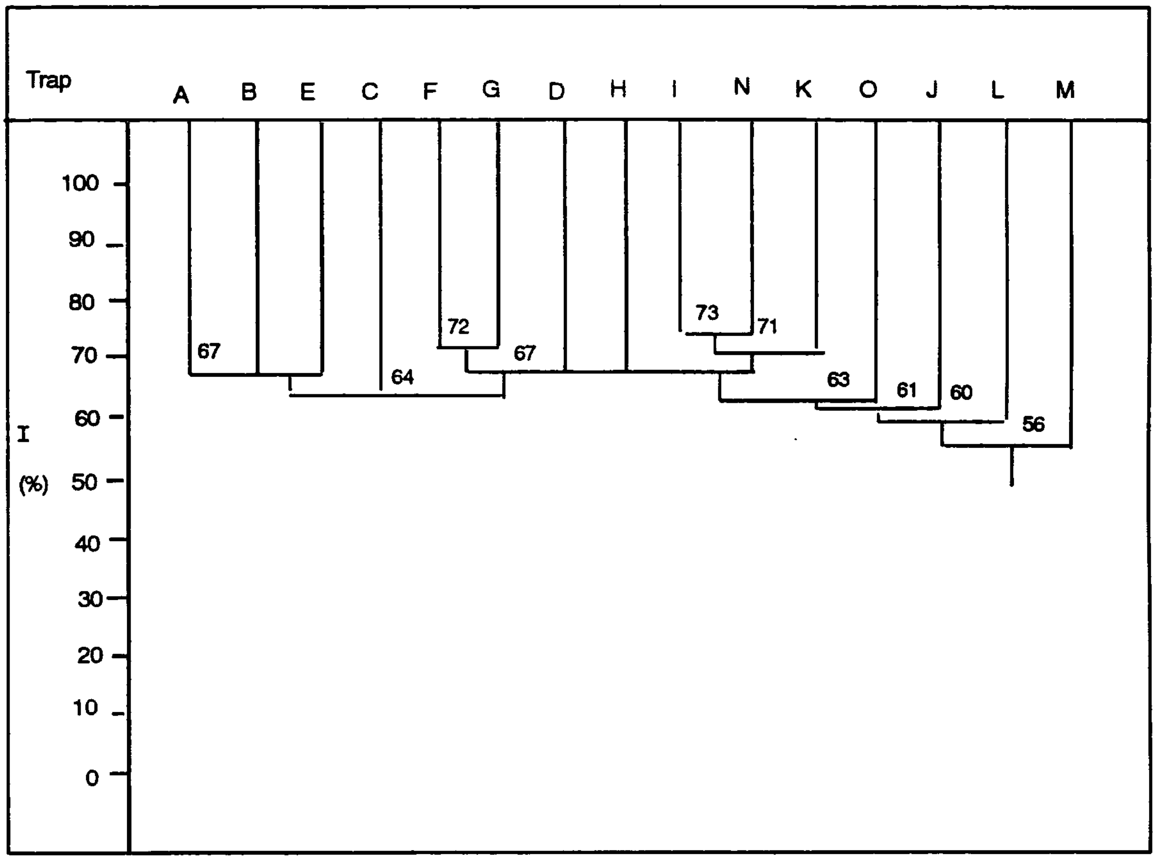


Fig 4.11 Nearest-neighbour clustering of transect regions based on the percentage similarity, Site 2, where A to G represent the crop, H the interface, and I to O the woodland transect regions.

This shows a decrease in similarity of species composition of communities with increasing separation distance of pitfalls, represented by decreasing values for pitfall pairs. Within-crop traps show a high degree of similarity to each other, but with this decreasing with increasing distance apart within the crop. This also applies for within-woodland traps. The average value of similarity between crop traps is 59%, and 56% for similarity between woodland traps (Fig 4.10). The average similarity values for crop/boundary and woodland/boundary are 59% and 58% respectively, suggesting that the species composition of the boundary shows a high degree of similarity to both the communities of either side, indicating that species from crop and woodland contribute equally to the community composition of the boundary. The average similarity value between crop and woodland is 43% indicating the dissimilarity between the crop and woodland habitat according to spider species composition. Therefore, although each habitat contributes species to the boundary habitat, large numbers of species characteristic of one side do not stretch very far into the habitat across the interface, thus indicating the dramatic effect of a sudden change in habitat type at the community interface on spider species abundances and community composition on opposite sides.

Chi-squared similarity:

Chi-squared associations are shown in Fig 3.12, and clustering of sites is represented as a dendrogram in Fig 3.13. Significant associations were found to be mainly between within crop sites and between within woodland sites, although some cross similarity did occur (i.e. between A and I; A and J; E and I; and F and L). This indicates that there are species common to both habitats, and that species cross the interface to a certain extent. Trap H at the interface is significantly associated with the woodland traps (except L), and only with two of the crop traps. This suggests that the community composition of the boundary shows higher similarity to the woodland habitat (this was not shown by the quotient of similarity). The fact that very little cross-similarity was indicated between the crop and woodland either side of the interface suggests that the interface produces a dramatic change in the community composition of spider species due to the sudden change in habitat type.

Trap															
A															
B	12.4*														
C	9.7*	6.5*													
D	11.3*	6.0*	9.7*												
E	10.2*	6.5*	10.7*	5.6*											
F	4.7*	3.2	6.5*	11.3*	6.5*										
G	3.5*	1.7	2.4	13.8*	2.4	13.7*									
H	4.2*	0.1	1.2	0.1	1.7	2.3	7.8*								
I	4.7*	0.1	3.4	0.5	4.0*	2.2	1.5	6.9*							
J	4.7	1.9	1.0	0.8	2.8	0.9	1.1	5.9*	5.6*						
K	1.7	0.1	1.0	0.8	2.8	0.9	1.1	5.9*	12.5*	1.7					
L	0.1	0.0	0.9	1.5	0.0	4.1*	2.1	1.4	5.8*	5.9*	3.2				
M	1.4	0.9	2.7	0.5	2.7	0.6	3.5	4.3*	4.5*	2.0	0.6	3.4			
N	0.6	0.0	0.3	0.1	0.6	3.2	1.7	4.5*	15.0*	2.4	7.8*	4.1*	2.7		
O	0.1	0.1	1.9	0.0	0.1	0.1	0.5	4.3*	8.5*	4.3	7.3*	1.4	4.3*	5.2*	
Trap	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O

Fig 4.12 Values of chi-squared for Site 1, showing associations between transect regions, where *=significantly associated at P=0.05. A to G represent the crop, H the interface, and I to O the woodland transect regions.

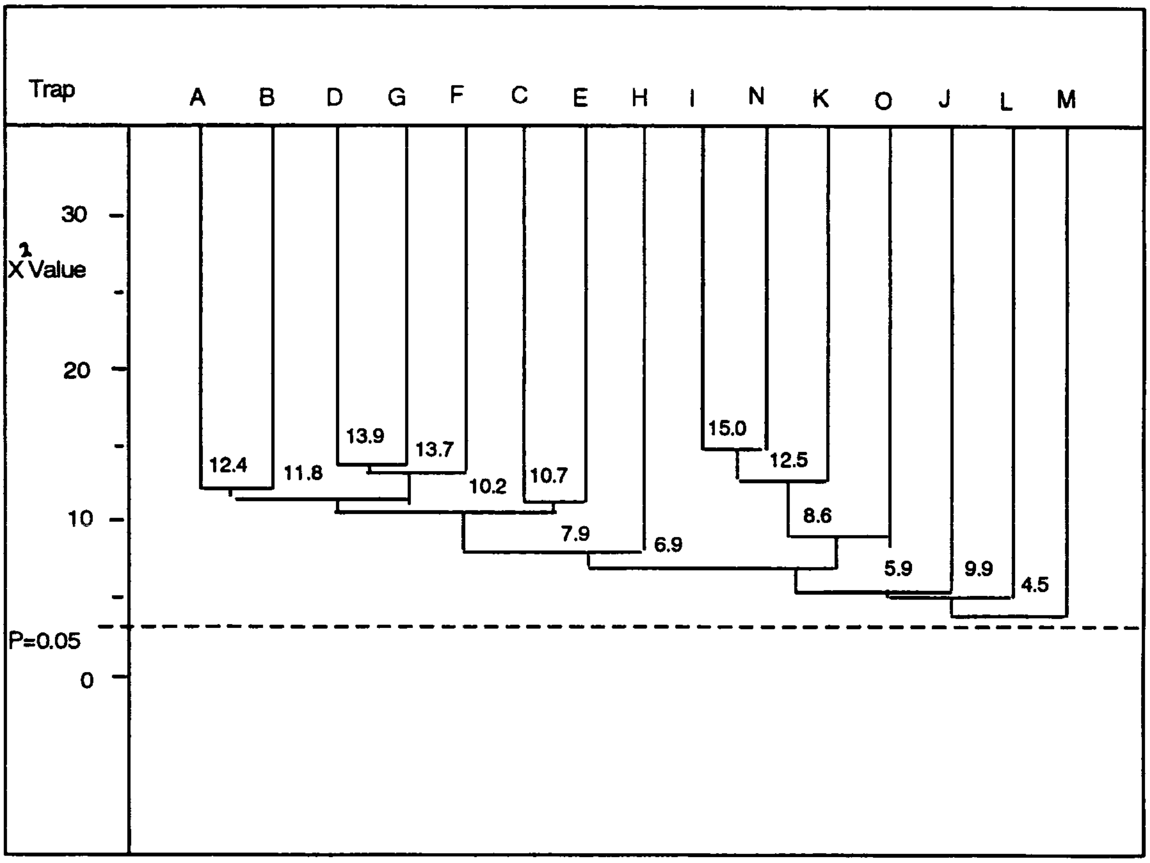


Fig 4.12 Nearest-neighbour clustering of transect regions based on the chi-squared similarity, Site 2, where A to G represent the crop, H the interface, and I to O the woodland transect regions.

3.2 Multivariate community analysis

3.2.1 Classification

The aim of this procedure is to group the pitfall sites according to the presence and abundance of the spider species so that the similarities of the clustered sites becomes evident. The classification was made by Hill's indicator species analysis program TWINSPAN (Hill 1979). Table 3.4 shows the ordered two-way classification, revealing the relationships between species and samples, where the lines indicate the divisions made by TWINSPAN. A dendrogram showing the divisions made for site classification, with indicator species at each division, is shown in Fig 4.14. The first division made by TWINSPAN separated the woodland and boundary sites plus the first two crop sites, from the remaining crop sites. Spiders more frequent and consistent in the woodland/boundary were shown to be *Micaria pulicaria, Clubiona lutescens, Oxyptila praticola, Trochosa terricola, Ceratinella brevis, Monocephalus fuscipes, Diplocephalus latifrons, Diplocephalus picinus*, and *Lepthyphantes cristatus*. Spiders more frequent and consistent in the crop were shown to be *Oedothorax fuscus* and *Erigone atra*. The first indicator species were *C. lutescens* and *L. cristatus*, which indicated the woodland/boundary group of traps (F to O). The fact that in the first division, the boundary was classified with the woodland sites suggests that the boundary spider fauna showed higher similarity to the woodland than to the crop community (this is consistent with the results of the chi-squared similarity calculations, section 4.1.4). Crop sites F and G near the edge of the crop were also classified with the woodland/boundary in the first division, suggesting that woodland species penetrated the crop environment to a certain degree.

The second division separates group 2 into woodland (group 4) and crop/boundary (group 5), with trap M classified with group 5. This indicates that only a proportion of the woodland species occur in the boundary and the first few metres of the crop. *Monocephalus fuscipes* was the indicator for group 4 (woodland), and *Diplocephalus picinus* the indicator for group 5 (boundary/crop traps G and F). The second division also separates the crop into two groups, with *Pardosa amentata* indicating traps C and D. The third division divided the wood (group 4) into two, and group 5 into separate boundary and crop sites. *O. praticola* was the indicator species for the boundary, as it was only very rarely found in the crop.

	Trap														
Species	J	L	I	K	N	O	H	M	F	G	D	A	B	C	E
M. pulicaria			1	1			1								
C. lutescens	1		1	1	1	1	1	1		1					
L. cristatus		1	1	1	1				1	1					
O. praticola	1	1	1	1	1	1	1	1			1				
C. brevis	1	1	2	1	1	1	1		1	1		1			
D. picinus	1	1	2	1	1	1	2	2	2	2				1	1
P. amentata	1	1	2	1	2	1	3	1	1	2	2	2	1	1	1
T. terricola			1	1	1	1	1	1	1	1	1				1
W. cuspidata	1		1	1			1			1			1		1
D. latifrons	1	1	1		1		1	1	1	1			1	1	
S. lineatus			1	1	1	1	1				1		1		
M. fuscipes	1	1	1	1	1							1	1		1
L. tenebricola	1	1	1			1					1			1	
S. frontata	1	1	1				1	1	1	1	1	1	1	1	1
E. dentipalpis	1						1		1	1		1	1	1	
D. concolor	2	2	2	2	1	1	2	1	2	2	2	2	1	2	2
O. fuscus	1		1				1	1			1		1	1	1
E. atra			1	1	1		1		1	1	1	1	2	2	1
L. tenuis			1	1		1		1	1	1	1	1	1	1	1

Woodland/Interface Crop

Table 4.4 Two-way ordered table produced by TWINSPAN, showing the grouping of sites and species. Entries in the table are pseudospecies levels.

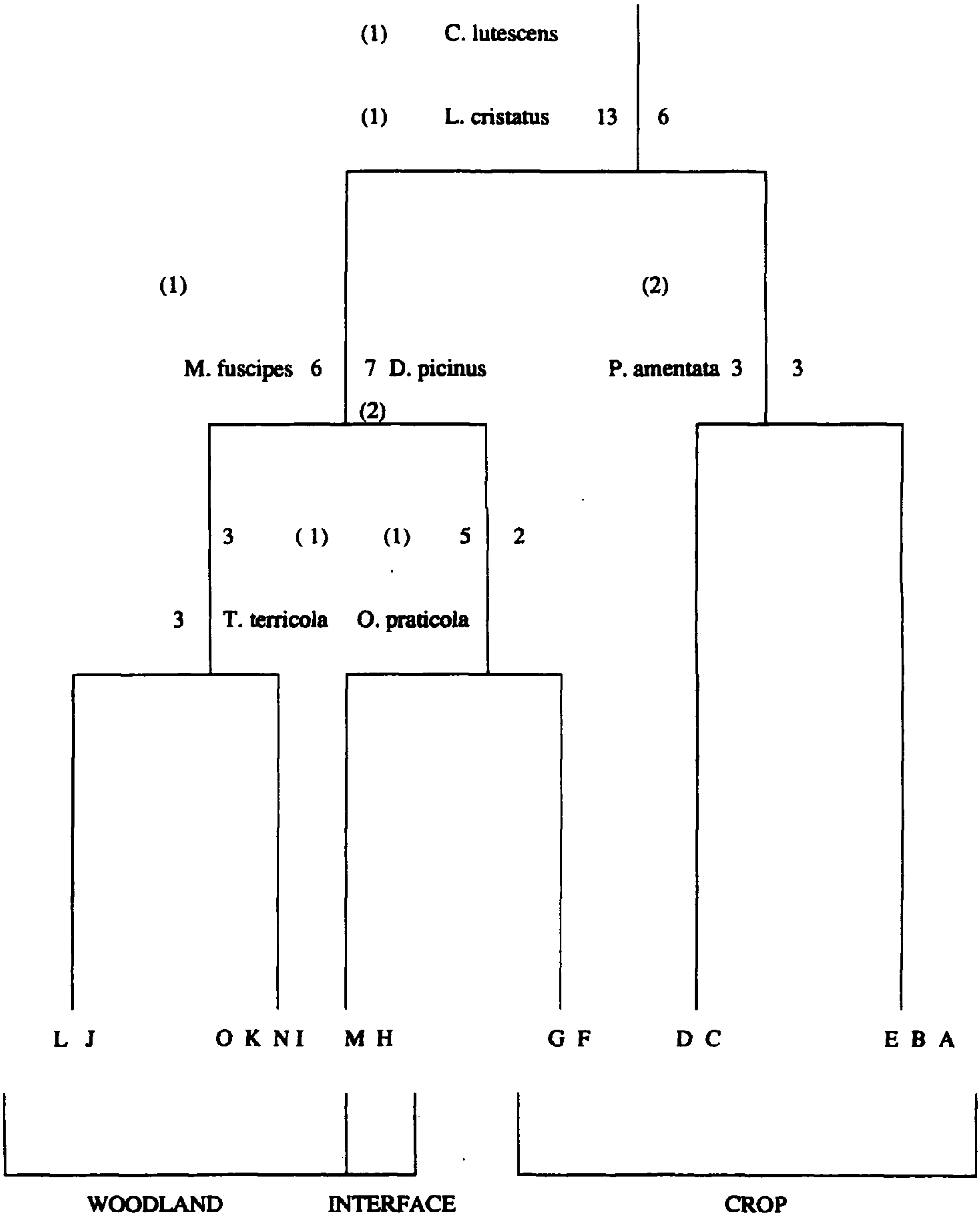


Fig 4.14 Dendrogram produced by TWINSPAN, showing site classification using common spiders. Indicator species with the associated pseudospecies level in brackets ( ) are shown at each stage. Numbers refer to numbers of species. Site 2 crop/woodland transect.

As with Site 1, it can be seen that the second and third divisions are not as sharp as the first one. The results suggest a link between the habitat preferences of the spiders and the vegetation, since the divisions make distinctions between the crop, boundary and woodland sites. therefore, ordination of the sites and species were carried out to assess the relationships between the spiders and measured environmental variables.

4.2.2 Ordination

Ordination of the pitfall sites and species were made using CANOCO, as for Site 1.The environmental variables are shown in Table 4.5

Env.	Trap														
Var	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
SM	21.2	23.3	24.2	19.2	18.3	20.9	25.1	26.1	29.9	24.0	44.4	29.3	22.6	39.5	33.5
VVD	20.0	90.0	23.8	21.3	22.5	22.5	22.5	17.5	25.0	25.0	20.0	17.5	20.0	10.0	15.0
FHS	12.0	10.0	17.0	5.0	2.0	9.0	22.0	25.0	25.0	25.0	25.0	25.0	10.0	19.0	5.0
FVS	25.0	25.0	25.0	25.0	25.0	25.0	25.0	25.0	25.0	25.0	25.0	14.0	20.0	20.0	24.0
HS	4.0	4.0	4.0	4.0	4.0	4.0	4.0	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Table 4.5 Environmental variables (Env. Var) for Site 2 crop/woodland transect, where A to G represent the crop, H the interface, and I to O the woodland transect regions. SM=% soil moisture; VVD=vertical vegetation density; FHS=frequency of horizontal vegetation structures; FVS=frequency of vertical vegetation structures; HS=habitat score (4=crop, 2=interface, 1=woodland).

Eigenvalues for the ordination, which give some indication of the amount of community variation explained by each axis were 0.177; 0.068; 0.051 and 0.042 for the first to fourth axes respectively. These results suggest that the first two axes explained most of the between-site differences in spider communities. As for Site 1, the axis 1 scores appeared to be related to habitat type (crop or woodland), since woodland sites had the highest axis 1 scores, and crop sites the lowest. In this study, the species-environment weighted correlation coefficients produced by CANOCO were 0.945; 0.931; 0.923 and 0.819 for axes 1 to 4 respectively. Axis 1 species correlations with the environmental variables are shown in Fig 4.15.

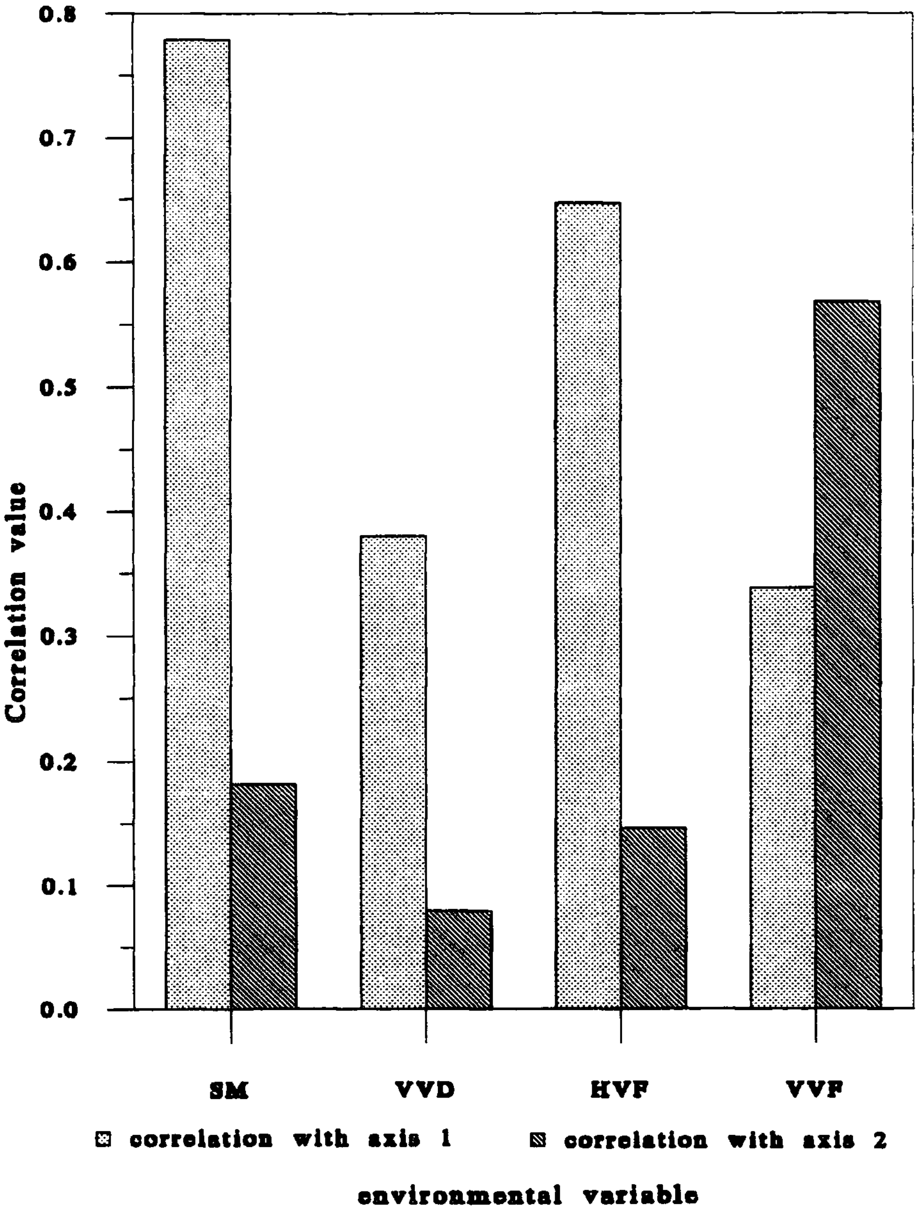
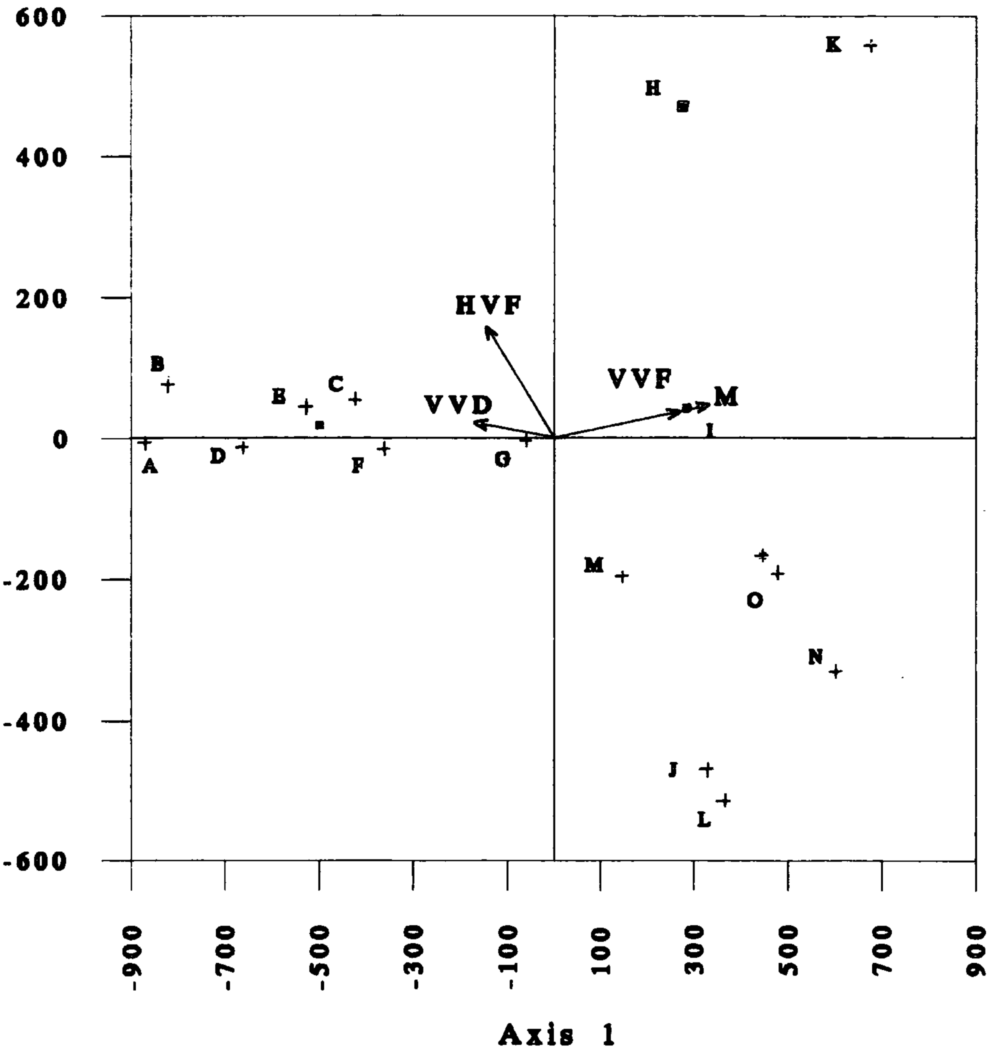


Fig. 4.15 Correlation of environmental variables with the two main axes of variation in species produced by CANOCO. SM=% soil moisture; VVD=vertical vegetation density; HVF=frequency of horizontal vegetation structures; VVF=frequency of vertical vegetation structures.

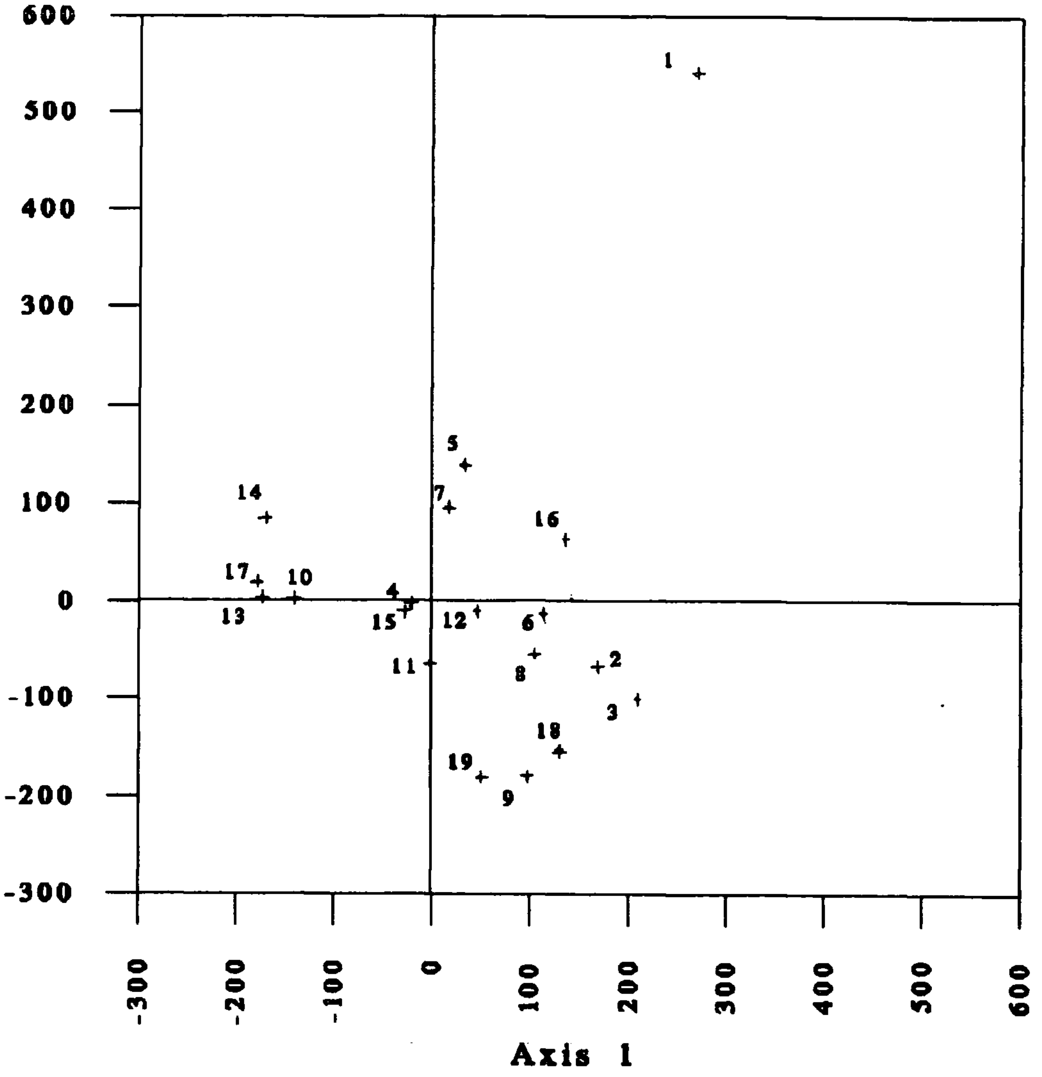
Results suggest that axis 1 is most highly correlated with moisture and the vertical vegetation frequency (r-values of 0.082 and 0.804 respectively, with 19-2=17 df, significant at the 0.01 level). Although the vertical vegetation density and the horizontal vegetation frequency have lower r-values (0.616 and 0.581 respectively) they are also significant at the 0.01 level with 17 df. Axis 2 is most highly correlated with horizontal vegetation frequency, with an r-value of 0.754, significant at the 0.01 level with 17 df. The other environmental variables are not significantly correlated with axis 2.

Fig 4.16a displays the ordination diagram of the sample scores and centroids of the habitat type variables on axes 1 and 2. The environmental variables are represented by arrows which point in the direction of maximum variation in value of the corresponding variable with relative length indicating relative importance. The first axis (λ_1=0.178) is seen to separate the crop sites A to G from the interface and woodland sites H to O. From the left of the diagram, the first centroid (•) is for the crop, the second (at H) for the interface, and the third for the woodland regions. The close proximity of the centroids for the interface and the woodland on axis 1 indicates the similarity of these habitats according to species composition. Soil moisture is seen to be greater in the woodland, with the more exposed habitat type of the crop having lower values. The second axis (λ_2=0.068) separates the woodland sites to a greater degree than the crop sites. Therefore, environmental variables contributing to axis 2 were more varied in the woodland. The variable most highly correlated with axis 2 is the horizontal vegetation density. Because the woodland contained a greater variety of plant structures and species, it would be expected to vary more in vegetation structure than the crop which consisted of a uniform vegetation type of high vertical structure and lower horizontal structure. Fig 4.16b shows the ordination diagram based on species, to which the environmental variables represented by arrows in Fig 4.16a may be applied. The species are represented by points in the ordination space, leading to approximate values of the weighted averages of the species with respect to the environmental variables. The species are grouped such that those to the left of axis 1 were found more commonly or exclusively in the crop, and those to the right were found more commonly or exclusively in the wood. This plot does not show the same discrete grouping of species along the first axis as in Site 1 species ordination. This suggests a greater amount of overlap of species into the adjoining community, and indicates a more gradual change in species composition and their relative abundance in the community across the



VVD vertical vegetation density; VVF frequency of vertical vegetation structures; HVF frequency of horizontal vegetation structures; M % soil moisture; ▪ represents centroids of habitat type (see text).

Fig 4.16a Ordination diagram of samples, produced by canonical correspondence analysis of common spider species from Site 2. Environmental variables are represented by arrows which point in the direction of maximum variation, with length relative to importance.



1 *M. pulicaria*; 2 *C. lutescens*; 3 *O. praticola*; 4 *P. amentata*; 5 *T. terricola*; 6 *C. brevis*; 7 *W. cuspidata*; 8 *O. fuscus*; 9 *M. fuscipes*; 10 *S. frontata*; 11 *D. latifrons*; 12 *D. picinus*; 13 *E. dentipalpis*; 14 *E. atra*; 15 *D. concolor*; 16 *S. lineatus*; 17 *L. tenuis*; 18 *L. cristatus*; 19 *L. tenebricola*.

Fig 4.16b Ordination diagram of species, produced by canonical correspondence analysis of common spider species from Site 2.

transition. From axis 1 separation, it appears that *Micaria pulicaria* (Gnaphosidae), *Clubiona lutescens* (Clubionidae). and *Oxyptila praticola* (Thomisidae) prefer sites with greater moisture content, as found in the woodland sites towards the right of the ordination diagram in Fig 4.16. Interestingly, these species are the larger sized species which were trapped, and perhaps cannot tolerate the drier conditions as well as the linyphiids. It is possible that species found in the woodland prefer sites with a litter layer that provides a greater abundance of prey, or sites more suitable for web construction. On the other hand, these species may simply be slow at recolonising arable sites following ploughing. Species found to prefer drier conditions, as found in the crop towards the left of the ordination diagram in Fig 4.16b were *Erigone atra, Erigone dentipalpis, Lepthyphantes tenuis,* and *Savigyna frontata.* These species are known to be highly mobile, invasive species, particularly *E. atra* and *E. dentipalpis* which are often the first species to colonise new habitats such as arable fields (Rushton, Topping and Eyre 1987), and newly reclaimed polders (Meijer 1977). Species intermediate between the extremes were mainly linyphiids: *Diplostyla concolor, Diplocephalus latifrons, Walckenaeria cuspidata, Diplocephalus picinus, Lepthyphantes tenebricola, Oedothorax fuscus, Monocephalus fuscipes, Ceratinella brevis, Stemonyphantes lineatus, Lepthyphantes cristatus,* and the two lycosids *Pardosa amentata* and *Trochosa terricola.* These species do not appear to show a clear cut preference for a particular side of the interface.

To investigate whether the observed differences could be accounted for by chance, a Monte Carlo permutation test was used on the data (Ter Braak 1988). The 99 random data sets generated by random permutation of pitfall sites yielded 4 eigenvalues that were greater than the axis 1 eigenvalue. It is therefore concluded that there are significant differences in axis 1 environmental variables (P=0.04), which affect the distribution of spider species.

CHAPTER 5

DISCUSSION

The results obtained from this study of the effects of an abrupt change in habitat type on spider communities suggest that an interface between two contrasting habitat types has a pronounced effect on the distribution of spiders, their abundances and community composition. It also appears that the effects vary according to the ecological situation, depending on the habitat either side of the interface, and of the boundary habitat itself. This is shown in Sites 1 and 2 where the respective interfaces generally have different effects on the spider numbers, their distribution and diversity. Because of these different patterns, I shall initially discuss each site separately, and then compare and contrast the sites and suggest reasons for any differences or similarities revealed from the results. Firstly, however, it is necessary to discuss some of the limitations imposed by pitfall trapping on community studies.

5.1 Pitfall trapping

The trapping of surface-active arthropods using pitfalls is used extensively in ecological studies to provide information on the occurrence, abundance and activity of species. They provide a continuous sample, and large catches can result, representing many species, and thereby allowing rapid and efficient collection of data amenable to statistical analysis. Pitfall traps are commonly used by arachnologists, although the validity of their use is questionable. A review of the literature by Southwood (1978) revealed that the catch was dependent upon other factors in addition to abundance. It is generally appreciated that the capture rate in pitfalls depends on both population density and on activity. Studies have indicated that pitfalls would only represent abundance accurately if activity were constant between species, and such a study by Topping and Sunderland (1992) found that the relative abundance of species in pitfall traps from a winter wheat field did not mirror that found in the community. However, whilst there appeared to be little relationship between pitfall and density samples in numerical species composition, this did not preclude the possibility that pitfall traps might reflect changes in individual species over time. This therefore would also apply to the distribution of species in space, as investigated in the present study. The difficulty in distinguishing changes in activity from changes in numbers is particularly acute in ephemeral habitats (Topping and Sunderland 1992), where changes in abundance may be marked due to the instability of the vegetational community structure. However, this factor does not invalidate comparisons between sites.

Similarly, an increase in numbers caught in a trap does not necessarily mean that the catches are reflecting a change in density. The observed pattern could be due to pitfalls recording increased activity associated with mate searching, female dispersal, searching for oviposition sites, and foraging for food.

Baars (1979) studied catches in pitfall traps in relation to mean densities of carabid beetles, and found that for two beetles, relative to their densities, one species was eight times more likely to be trapped. Variation in vegetation density was found to have species specific effect on the catch. Trap efficiency (unrelated to activity) is therefore also important and may vary between species and habitats. Video studies on carabid beetles show that different species have different abilities to escape from pitfall traps (Halsall and Wratten 1988). These differences are also likely to occur between various spider taxa, particularly in comparing families such as ground-foraging lycosids and web-building linyphiids. Trap efficiency may also vary between males and females of the same species.

The use of pitfall trapping in the study of ground-dwelling invertebrates has been the subject of much debate. The major criticisms are that catches reflect animal activity as well as population density, and that they are also dependent on environmental features such as vegetation cover (Greenslade 1964). However, pitfall trapping has been demonstrated as an effective method to acquire an accurate representation of the spider species composition of structurally complicated habitats.

The alternatives to pitfall trapping also have drawbacks. For example, a study by Uetz and Unzicker (1976) concluded that pitfall trapping gave a better estimate of the total number of species in a community than quadrat sampling. Quadrat sampling should provide an absolute density measure, but is influenced by the activity of animals in the brief time span when the sample is taken. Results are also influenced by the presence of the investigator, since many spiders escape capture by running away when approached. Uetz and Unzicker (1976) conclude that limiting the method to cursorial forms, like wandering spiders, may diminish sampling error due to differential species activity. Similarly, just as trap efficiency applied to a pitfall reflects the probability that a spider having fallen into the trap cannot escape, it could also be taken to represent the probability of retention in a sampler's hand, or extraction in a thermal extraction apparatus. Also, just as the likelihood of a spider falling into a pitfall depends on its activity. the probability of its capture by hand is greatly increased by its activity rendering the specimen more noticeable to the researcher (Curtis 1980). Therefore, the types of distortions which may be reflected in pitfall trapping are also applicable to the other sampling methods employed by ecological arachnologists. The high numbers of species recorded in pitfall traps coupled with their continuous nature of their sampling argue in favour of their use, and provided that the limitations are understood, are a useful tool in the analysis of community composition. Pitfall trapping was therefore used in the present study to investigate how the numbers of individuals and species composition of communities changed across an interface between two habitat types, but not between species at a particular site, thus avoiding the comparison of the relative abundance of different species. In the multivariate techniques used for classification, if relative densities are not considered at all, much information is lost because rare and abundant species are given the same weight. However, if the differences in catchability remain constant between sites to be compared, and the samples are used to indicate differences in habitat, these techniques may be considered satisfactory. Another factor to be considered is the fact that many communities are identified by relative abundances rather than by discrete groups of populations, suggesting that it is misleading to base the classification and ordination analyses on presence and absence data only, because when presence and absence data are used the same weight is given to species which are present in high and low numbers, even though these differences could be representing real differences in habitat preference.

A problem that arises in this study is that the vegetation structure varied considerably between sites, and catches are considered to be dependent on this (Greenslade 1964) in that it resists invertebrate locomotory activity. Because this resistance of the vegetation is also an effect of management/disturbance of the community (an important factor in this study), pitfalls were considered suitable. Furthermore, a larger number of catches would be expected in the plantation than in the pasture of Site 1 due to the lower vegetational resistance of the first category. However, the number of catches in the pasture was significantly higher, despite the greater abundance of ground vegetation.

5.2 Site 1

5.2.1 Community analysis

Site 1 shows a reduction in the spider abundance from the pasture through to the plantation habitat, from a total of 384 individuals at A to 13 individuals at O, collected over the three week trapping period (Appendix 3). Numbers at the interface were significantly lower at the P=0.005 level (using chi-squared analysis, Fig 3.3) than all of the pasture positions, even the first position 2m into the pasture. The numbers in the plantation remained low, and the first position 2m into the plantation was not significantly different from the interface in the total numbers of spiders recorded. This results in the community on the pasture side of the interface having significantly higher numbers of spiders than the plantation side (at the P=0.005 level, using chi-squared analysis). The abrupt change in habitat type at the interface appears therefore to have a negative influence on numbers in the pasture, resulting in significant reductions (from the chi-squared analyses, Fig 3.3) between successive traps at 6m, 2m and 0m from the interface.

Species richness also decreased progressively from the pasture through to the plantation, with the number of species at the interface (13) intermediate between that of the pasture (mean=19) and the plantation (mean=11). Although a greater number of species were present in the pasture, species diversity was lowest here (mean=1.51), and highest in the plantation (mean=2.38). This is probably partly due to the higher numbers in the samples from the pasture. The interface showed a diversity intermediate between pasture and plantation (1.91). These results show that there is a definite 'edge-effect' of the abrupt change in habitat type between pasture and plantation at Site 1 which influences the species richness and diversity of the spider community within a small area.

Results for the community composition, the distribution of spider families and their relative abundances at different positions of the transect, show a change in dominance from on side of the interface to the other, with some groups located at only one side. Lycosidae and Tetragnathidae were dominant families in the pasture, but replaced by Linyphiidae on approaching the interface. At the interface, and throughout the plantation, linyphiids remained the dominant family. Thomisidae were restricted to the pasture habitat only. The lycosid and tetragnathid species dominant in catches from the pasture were *Pardosa pullata, Pardosa amentata, Alopecosa pulverulenta, Trochosa terricola* (Lycosidae), and *Pachygnatha degeeri* (Tetragnathidae). The two species with by far the highest numbers were *P. pullata* and *P degeeri*. *P. amentata* and *P. degeeri* are known to have preferences for moderately disturbed sites such as hay meadows (Rushton, Topping and Eyre 1987). Numbers of different species were not compared statistically due to the limitations imposed on the accuracy of relative abundance counts from pitfall studies (section 5.1). However, the higher dominance of some species does indicate that higher numbers were present. Linyphiid species present in high abundance in the pasture included *Oedothorax retusus, Erigone dentipalpis, Erigone atra,* and *Agyneta decora. Erigone* and *Oedothorax* species are known to be highly invasive species (e.g. Rushton, Topping and Eyre 1987), and are often the first species to colonise new habitats such as agricultural areas, including pasture and crop fields. Numbers of each of these species were shown to fall abruptly at the interface, or just beyond the interface in the plantation. This indicates a high degree of habitat selectivity for a certain habitat type of these species. Other linyphiid species which occurred predominantly or exclusively in the pasture were *Oedothorax fuscus, Tiso vagans, Centromerita bicolor,* and *Savignya frontata.* These species are also typical of grassland sites, and *T. vagans* occurs particularly on improved, well vegetated grassland sites (the pasture in this study was only lightly grazed, and was fairly well vegetated, developing into a hay meadow later in the season). The species of Thomisidae present in the pasture was *Xyticus cristatus.* This species is typical of moderately disturbed pasture sites (Rushton, Topping and Eyre 1987). Occasional catches of Agelenidae and Therididae were made in the pasture, but not in the plantation.

Of the dominant Linyphiidae family in the plantation, the main species were *Microneta viaria, Lepthyphantes tenuis, Lepthyphantes cristatus,* and *Linyphia hortensis. M. viaria* is characteristically found in detritus, particularly in woodland (Merrett, Locket and Millidge 1953). *L. cristatus* occurs amongst moss, grass and undergrowth, and *L. hortensis* in hedges and lowland woodland vegetation (Merrett, Locket and Millidge 1953). *L. tenuis* is a species known to occur in a variety of situations, and to colonise ephemeral or disturbed sites (Rushton, Luff and Eyre 1989), and was also present (although in smaller numbers) in the pasture. This suggests that it showed preference for the plantation habitat, but did cross the interface to a certain extent. The significance of wandering by the linyphiids on this scale is difficult to assess, as they are not active hunters but catch their prey in webs. In part, capture in pitfalls may be indirectly related to feeding in that it represents movement to a new site for web building, but much of it is probably related to sexual searching by the male (Williams 1962).

Occasional catches of Clubionidae and Agelenidae were also made in the plantation.

The results from this study indicate that most of the spider species from Site 1 show a preference for one side of the interface where they are most abundant, but in most cases smaller numbers were located on the less preferred side, often in only the first few trap positions into that habitat. This is probably the result of species dispersal, foraging in hunting species, and mate searching.

5.2.2 Similarity measurements

The Sørensen and chi-squared indices of similarity were calculated to visualise the effects of local faunal exchange between the habitat types. The spider populations showed the highest homogeneity between traps within each habitat, and stronger dissimilarities between habitats. This again emphasises the 'edge-effect' of the interface in producing an abrupt change in the species composition of spider communities. The general pattern is of a decrease within the one habitat type of community similarity with increased trap distance, with similarity decreasing towards the interface, and the largest drop in similarity at the interface, followed by a continuing gradual decrease throughout the habitat on the other side. The fact that similarity values between the two communities is very rarely zero indicates that some population exchange does occur between the neighbouring habitats.

5.2.3 Classification

To establish that the particular habitat types of the transect could be characterised by the species present, and their abundances, TWINSPAN was carried out on the data. The dendrogram produced (Fig 3.14) divided the transect into three distinct areas : pasture, interface and plantation, thereby suggesting distinct community compositions for each of these regions. The first division was the strongest, with *Agyneta decora* (Linyphiidae) indicating the grassland/interface group. TWINSPAN classification of pitfall sites indicated that the three transect regions of Site 1(pasture, interface and plantation) have characteristic spider communities associated with them in terms of species present and their abundances. The main discrimination was between the pasture and plantation which produced discrete groups at the first division. This suggested that components of the habitat structure and/or management history were the major factors determining the differences in the spider community either side of the interface.

Habitat structure has been shown to be important in the habitat selection of beetles (Buse 1988), where a marked correlation was found between the number of beetles found in a trap and the number or diversity of plant species around it. This was due to the greater variety of microhabitats available for the beetle species when more plant species were present, with each species exhibiting a preferred habitat type. It has been shown in birds (MacArthur and MacArthur 1961) that diversity of species depends on the diversity of foliage height and density rather than on species composition. Available evidence (e.g.

Duffey 1978) suggests that certain easily acquired components of habitat description, especially structure, floristics, history, management, area and climatic features are important factors in understanding the occurrence and status of a particular spider species in a specific locality. Greenstone (1988) found spider web diversity to be highly correlated with vegetation tip height diversity in a study of scrub- and meadow-inhabiting web spider species assemblages.

5.2.4 Ordination

Ordination of the results using canonical correspondence analysis, which relates environmental parameters directly to the axes representing the species in an ordination space, showed that pitfall sites were separated along the first ordination axis according to the extent of vegetation structure. Sites in the pasture had higher vegetation structure (as shown by the direction of the arrows in the ordination space, Fig 3.16a). The sites showed significant differences in the axis 1 environmental variables, as revealed by a Monte Carlo permutation test, and this affected the distribution of species as shown in Fig 3.16b. Species showing a preference for the pasture were located towards the left of axis 1, where vertical vegetation density, frequency of vertical vegetation structures, and frequency of horizontal vegetation structures were higher. Those preferring the plantation were located towards the right where the vegetation structure was less diverse.

Numerous studies where spiders have been classified and ordinated according to site preferences in grasslands have indicated the importance of vegetation structure in determining species' distributions, with the vegetation structure affected by management practices such as grazing (Duffey 1978, 1988; Siepel *et al.* 1989; Gibson, Hambler and Brown 1992; Rushton and Eyre 1992). In most cases, the importance of management has been directly related to its effect on vegetation structure: short, intensively used grasslands have fewer spider species than long, undisturbed grasslands because the diversity and number of sites suitable for web construction is lower in short grassland, and there is less available niche space within the vegetation.

The most obvious conclusion to be drawn from the results of the classification and ordination analyses is that the differences in the spider communities present on the sites sampled along the transect of Site 1 in the present study appeared to be dependent on vegetation structure. This was influenced by the degree of habitat management/interference, where the pasture was a managed site undergoing disturbance through grazing and the later development of a hay meadow. In comparison, the plantation remained undisturbed. Results revealed that a greater number of species preferred the higher vegetational structural diversity of the pasture habitat to the sparse ground-level vegetation of the plantation. A total of 72% of the common species were located on the left of the origin of axis 1 in the ordination space, and 28% were located to the right (Fig 3.16b). This is probably partly due to the fact that the pasture was only grazed lightly and hence the vegetation was fairly high. Therefore, the diversity and number of sites available for web construction and niche availability were higher in the pasture than in the plantation for ground-inhabiting species. The results therefore demonstrate the importance of vegetation structure as a habitat component mediating the effects of management.

Studies have shown that other non-vegetation mediated aspects of management may also be of importance. For example, Rushton and Eyre (1989) showed that the way in which intensively grazed pasture was utilised influenced the communities present, with silage production favouring ground-web producing species. Siepel *et al.* (1989) found that low fertilisation levels resulted in the highest number of individuals in grassland.

The results of ordination suggested that out of the environmental variables measured, after vegetation structure, soil water content was the next important variable influencing the spider community composition. Site wetness has often been cited as a a major factor influencing spider communities (e.g. Coulson and Butterfield 1986; Rushton *et al.* 1987; Rushton and Eyre 1992).

5.3 Site 2

5.3.1 Community analysis

Site 2 shows fairly uniform spider abundance within the crop and woodland, with a dramatic increase at the interface (from 55 at A in the crop, to 228 at the interface, and 38 at O in the woodland). (Appendix 6). Numbers of spiders at the interface were significantly higher at the P=0.005 level (using chi-squared analyses, Fig 4.3) than numbers in any of the crop or woodland positions, even the pitfall sites 2m into the crop and 2m into the woodland. From 6m into the crop and 6m into the woodland, significant increases were found in spider numbers between successive traps towards the interface. The interface therefore appears to have a positive influence on numbers in the crop and woodland.

Species richness (Fig 4.4) showed the same pattern of an increase in the number of species from the crop (mean=16) and woodland (mean=18) towards the interface (21). Species diversity was lower in the crop (mean=1.56) than in the woodland (mean=2.33) where the highest diversity was recorded, indicating that the sudden change in habitat type at the interface had a definite effect on the spider community within a small area. A drop in species diversity occurred at the interface to 0.99, despite the higher number of species located here. This was probably due to the significantly higher numbers of individuals recorded here (Fig 4.3). Spider diversity has been significantly associated with habitat structure (Duffey 1978), and many workers have reported associations between plant diversity and successional stages in determining species diversity. Spider diversity and abundance have been correlated with the physical structure of the litter (Uetz 1979). Increased spider diversity found in the woodland in the present study may be due to the greater diversity of plant structures, and the deeper litter layer that has developed in comparison with the crop where a fairly uniform vegetation structure existed and disturbance through ploughing and cultivation prevents the development of a litter layer.

The community composition of spiders along the transect for Site 2 reveals that the distribution of spider families and their abundances show a change in dominance from linyphiids in both the crop and woodland to lycosids at the interface. Lycosidae occurred throughout the crop and woodland, Thomisidae predominantly in the woodland, and Gnaphosidae and Clubionidae exclusively at the interface and in the woodland. The crop community consisted mainly on linyphiids, which are known as colonisers of ephemeral habitats. The species of Linyphiidae most common in the crop were *Erigone atra, Oedothorax fuscus, Savignya frontata*, and *Lepthyphantes tenuis.* They are typical of disturbed habitats such as arable crops and are aeronauts allowing rapid recolonisation following disturbance through the behaviour of 'ballooning'. Species such as *O. fuscus* and *Erigone* species are thermophiles which benefit from the microclimate of short turf (deKeer *et al.* 1989), such as found in early crop establishment. The dominant lycosid was *Pardosa amentata*, which is an aeronaut as a juvenile, and is known to prefer sites exposed to light (Merrett, Locket and Millidge 1953). Species of Linyphiidae and the lycosid *P. amentata* have been found to be indicative of high fertilisation (Siepel *et al.* 1989), and the barley field in the present study was fertilised on two dates prior to the study period.

Diplostyla concolor, the linyphiid trapped in the greatest numbers in the crop was also highly abundant at the interface and throughout the woodland. In this situation, it was a ubiquitous species, showing no preference for a particular habitat in the transect region. ***Pardosa amentata*** was also ubiquitous, being common in the woodland as well as the crop, with a peak in numbers at the interface. This suggests that the boundary habitat was most favourable to this species, and from here, migration occurred into the woodland and crop habitats. Other species occurring throughout the transect were *Walckenaeria cuspidata, Oedothorax fuscus, Monocephalus fuscipes, Diplocephalus latifrons Diplocephalus picinus, Lepthyphantes cristatus, Lepthyphantes tenebricola* (Linyphiidae), and *Trochosa terricola* (Lycosidae). Of these, *D. picinus* and, to a lesser extent, *D. latifrons* increased in abundance towards the interface. These species are typical of sites with dense undergrowth (Merrett, Locket and Millidge 1953). Species preferring the woodland were *Micaria pulicaria* (Gnaphosidae), *Clubiona lutescens* (Clubionidae), *Ceratinella brevis* and *Stemonyphantes lineatus* (Linyphiidae). *M. pulicaria* is a characteristic woodland species, and *C. lutescens* shows preference for moist places, grasses, bushes and trees in woodland.

Many of the species exhibited a preference for one side of the interface, although most were seen to cross into the less-preferred habitat to a certain extent where they occurred in smaller numbers. A few species were ubiquitous and some of these indicated a preference for the boundary habitat.

5.3.2 Similarity measurements

The Sφrensen and chi-squared indices of similarity were calculated to visualise the effects of local faunal exchange between habitat types. As for Site 1, the spider populations exhibited the highest homogeneity within each habitat type, and stronger dissimilarities between habitats. However, the effect of the abrupt change in habitat change at the interface in Site 2 does not appear as dramatic as for Site 1, as many comparisons remained above 50% similarity for the Sφrensen index (Fig 4.10). In addition, four significant associations between sites A and I, A and J, E and I, and F and L, across the interface were revealed by chi-squared analysis (Fig 4.12). This indicates greater population exchange between the two habitat types across the interface at Site 2 than at Site 1. However, the general pattern of a gradual decrease in similarity within a habitat with increased trap distance with similarity decreasing towards the interface still applies, with the largest drop at the interface and a continuing gradual decrease throughout the habitat on the other side.

5.3.3 Classification

To establish that the particular habitat types of the transect could be characterised by the species present and their abundances, TWINSPAN was carried out on the data. The dendrogram produced (Fig 4.4) divided the transect into crop and woodland regions. The first division was the strongest, and separated the crop form the woodland/interface, with the first two traps of the crop classified with the woodland. The fact that the division between woodland and crop was not sharply defined (in comparison with Site 1 where there was clear separation of pasture and plantation in the first division) again suggests a greater degree of population exchange across the interface. The classification of the first two crop traps with the woodland/interface suggests that it is the woodland species that were contributing to the crop habitat. This indicates that the woodland and boundary were important sites for some crop species, perhaps providing overwintering sites and a refuge for crop colonisers during disturbance.

The separation of the majority of the crop sites from the woodland group by TWINSPAN indicates that the areas do have characteristic spider communities associated with them in terms of species present and their abundances relative to their abundances in other regions of the transect. This suggested that (as with Site 1), components of habitat structure mediated through management history or degree of habitat disturbance were the major determinants of the differences in spider communities either side of the interface.

5.3.4 Ordination

Ordination of the data using CANOCO revealed that pitfall sites were separated along the first ordination axis with the crop sites to the left of the origin, and woodland sites to the right (Fig 4.16a). Axis 1 was most highly correlated with soil moisture and the frequency of vertical vegetation structures. Vertical vegetation density and frequency of vertical structure were also significantly correlated with the first axis. the sites showed significant differences in the axis 1 environmental variables, from a Monte Carlo permutation test, which affected the distribution of species shown in Fig 4.16b. It therefore appears that the habitat characteristics of soil moisture and vegetation structure determined the distribution of spiders in Site 2. These factors were probably mediated by the degree of management. Results revealed that a greater number of the common species (63%) were located on the right (woodland sites) of the ordination space, and 37% to the left (crop sites). The crop sites made up a highly managed habitat where seasonal ploughing, planting, cultivation, crop growth and harvesting imposes continual change on the habitat structure with periods of dramatic disturbance, thereby affecting the spider community present. The species located in the crop were shown by this study to be those characteristic of ephemeral habitats, where recolonisation of the field would have occurred during the crop establishment. On the other side of the interface, the semi-natural woodland was undisturbed and species located here were often characteristic woodland species. Soil moisture content was lower in the crop, indicating the more exposed conditions, and therefore species here must have been able to tolerate lower moisture levels. The absence of Gnaphosidae and Clubionidae in the crop may therefore have been due to an intolerance to water loss, or a lack of vegetational structural diversity, as although vertical vegetation density was high, this was made up of vertical structures (stems).

Another factor is the use of fertiliser in the management regime. Kajak (1978) studied the influence of NPK fertiliser treatment on the density, biomass and locomotory activity of spiders. Results suggested that the spider community responds to fertiliser treatment by changes in numerical dominance of species. Larger species (Lycosidae) were replaced by smaller ones (Linyphiidae), and as a result the mean spider biomass and locomotory activity of spiders was reduced in fertilised plots. There were no changes observed in the species diversity of spiders, as values of Simpson's species diversity index were very similar in fertilised and unfertilised plots. Results also found that the concentrations of N and P were higher in the bodies of spiders collected in fertilised plots, and was more pronounced in the bodies of larger spiders than in smaller ones. In the present study therefore, the dominance in the crop by linyphiids and the absence of many of the larger species (Thomisidae, Gnaphosidae, Clubionidae) may have been partly due to the fact that two fertiliser treatments were applied to the crop prior to the study period. Within the woodland, the increased variety of vegetation structure compared with the uniformity of the crop, and the deeper litter layer observed, and increased soil moisture content provided conditions more suitable for species of Gnaphoside, Clubionidae and Thomisidae. Those species characteristic of the crop were then excluded to a certain extent from the woodland sites characteristic of a later successional stage.

5.4 Comparison of Site 1 and Site 2 results

Site 1 consisted of an abrupt change in habitat type from pasture to plantation, represented by a dramatic change in vegetation structure at the interface. This produced a negative influence on total spider abundance in the pasture, but no significant influence was observed on the plantation numbers where abundance was consistently lower. It also resulted in a general gradual decline in spider species richness from the pasture to the plantation, and an increase in diversity. The interface itself did not exhibit and dramatic divergence from the general trends. This also applied to the spider family distributions where alteration in dominance and numbers showed a gradual change from one habitat to the next across the interface. Different species showed preferences for different sides of the interface according to their habitat requirements. It therefore appears that the interface at Site 1 produces a 'soft-edge' effect where influences extent into both habitats, producing a gradual change in spider communities. This was because most species occurred in lower abundance on the less-preferred side. however, a 'hard-edge' effect occurred for some species which were located entirely on one side. Classification and ordination techniques did produce a definite difference between the communities either side of the interface, indicating the importance of habitat structure and management in influencing the spider community composition

In contrast, at Site 2 the interface consisted of a boundary zone of dense vegetation, approximately 2m wide. This habitat produced a positive influence on total spider abundance in the crop and in the woodland. It also resulted in a definite increase in species richness, and diversity in the woodland habitat was higher than the crop on the other side of the interface. Spider family composition of communities showed that the crop and woodland were dominated by the same group (Linyphiidae), but the interface was the only position dominated by the Lycosidae. As for Site 1, different species showed preferences for different sides of the interface, depending on their habitat requirements. However, there were some definite ubiquitous species (which was not the case for Site 1), and some species showed preference for the boundary habitat, unlike Site 1 (probably due to the higher vegetational diversity of the Site 2 boundary, and the fact that it represented an ecotone rather than the narrow interface habitat of Site 1). The habitat change at the interface of Site 2 therefore produced a 'soft-edge' effect on most species, i.e. ones which occurred in both habitats but to a lesser extent on the less preferred side. A 'hard-edge' effect was shown for a few species which occurred only on one side on the interface, and an 'ecotone' effect on a few species which increased in abundance at the interface.

Results obtained from the two Sites indicate that different spider species respond in different ways to a change in habitat type at an interface between pasture and plantation and between barley and woodland communities. The vegetation structure is a major determining factor of species distributions, and the width of the interface habitat and its vegetation structure also has an important impact on species abundances and spider communities present.

5.5 Applications of spider conservation in farmland

5.5.1 Conservation of semi-natural habitats in farmland

The presence of undisturbed habitats in farmland is considered to significantly influence the spider fauna of cultivated land (Duelli 1990), and the importance of sites such as hedgerows and grassy strips as overwintering sites for surface dwelling arthropods has been indicated (Sotherton 1984). The pasture and barley fields in the present study were shown to be fairly rich in spider species, and one possible explanation is the influx of species from adjacent semi-natural areas such as the woodland. in intensively cultivated areas, therefore, a mosaic landscape consisting of small habitat patches may yield maximum levels of species richness (Duelli 1990). Consequently, the conservation of semi-natural areas such as woodland, or even strips or patches of natural vegetation can contribute towards the protection of genetic resources. It must be noted, however, that species richness is not always the prime concern of nature conservation. For example, remnants of endangered habitats such as peat bogs or heathland may subsist in otherwise cultivated areas and contain highly endangered specialised species which cannot cope with an influx of large numbers of ubiquitous species. Fragmentation of such areas may well increase species diversity at the expense of a few, but particularly interesting species.

The conservation of semi-natural areas such as woodlands and hedgerows in farmland may be of importance in the field of biological control, particularly in the provision of an over-wintering habitat for spiders to recolonise crop fields from. Nyffeler and Benz (1988b) studied the predation by wolf spiders in winter wheat. *Pardosa agrestis, P. amentata*, and *P. palustris* were observed to be predaceous on harmful cereal aphids, suggesting that they may be of beneficial value. Linyphiidae (*Erigone* and *Oedothorax* species) were found to dominate the spider faunas on the ground surface of winter wheat field and hay meadows (Nyffeler and Benz 1988a), and were observed to be generalist predators of small, soft-bodied arthropods. Collembola and aphids were the most frequent prey.

Although numerous studies on the spider fauna of European cereal fields and grasslands exist, the role of spiders as natural control agents of insect pests is still largely unknown. Table 5.1 shows a summary of the most highly ranked spider species identified as aphid predators in field based studies in the UK (after Jepson 1989).

Species
LINYPHIIDAE
Bathyphantes gracilis
Erigone atra
Erigone dentipalpis
Lepthyphantes tenuis
Meioneta rurestris
Millariana inerrans
Oedothorax apicatus
Oedothorax fuscus
Oedothorax retusus
TETRAGNATHIDAE
Pachygnatha degeeri
LYCOSIDAE
Pardosa pullata

Table 5.1 A brief summary of the most highly ranked beneficial spider species identified as aphid predators in field-based studies in the UK (after Jepson 1989).

5.5.2 Uses of spider community data in nature conservation

Classification and ordination techniques of multivariate analysis of communities allows description of the factors influencing spider community faunas. A further development is the use of predictive discriminant procedures (e.g. Rushton and Eyre 1992) to assign sites to habitat groups on the basis of measured environmental variables. the ability to predict spider community type on the basis of environmental variables may be a useful tool in environmental impact assessments, especially in the monitoring of changes in land use which affect vegetation structure and spider community composition. In this way, spiders may be of value as an 'indicator group' for some aspects of management effects or environmental change. For example, the spider communities of intensively managed pastures or arable fields may reflect surrounding land use patterns and spider community data may be of use in assessing the environmental impact of large scale changes in land use such as those brought about by changes in agricultural policy. However, it must be appreciated that the spider community may provide only part of the information needed, and differences between invertebrate groups imposes limitations on the use of a single taxonomic assemblage. It must also be noted that the success of multivariate techniques depends on having measured relevant environmental factors. This is one of the main problems with the use of these techniques, as there is no way to know with complete certainty that the most relevant factors were measured. Similarly, it is not possible to discover in retrospect if an important environmental variable has been disregarded.

5.3.3 Concluding statement

The results of the present study indicate that in agricultural habitats, where there exist fragments or areas of semi natural or undisturbed habitats, the spider community composition according to the species present, richness and diversity may be significantly altered. The effect of an abrupt change in habitat structure produces different responses in different species. The majority show a preference for one habitat type on one side of an interface, some are ubiquitous and occur in both communities, and some occur most abundantly in the boundary habitat separating the two communities. The main contributory factors to spider distribution were found to be the components of vegetation structure, mediated through habitat management and disturbance.

Fragmentation and insularisation of natural habitats in cultivated landscapes reduces the possibilities for genetic exchange between subpopulations vital for survival. Invertebrate species present tend to be highly mobile species, well adapted to living in temporary habitats. However, nature conservation is mainly concerned with the less well-adapted forms (Duelli *et al.* 1990), the large number of species which have become rare due to the drastic changes of land use.

Studies on the effects of habitat boundaries on invertebrate populations is useful to determine the consequences of agricultural practices on communitiy composition, and to establish the importance of semi natural areas. Multivariate classification and ordination enables the most likely factors determining the species distributions and their relative importance to be identified.

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