An investigation into the ground-living spider communities of Hamsterley forest

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An Investigation into the Ground-living Spider Communities of Hamsterley Forest.

by

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An Investigation into the Ground-living Spider Communities of Hamsterley Forest.

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A study was made of the ground-living spider communities of a commercial forest, using sites at various stages of the management cycle to represent different stages of succession. Clear-felling resulted in an increase in the abundance of large polyphagous cursorial hunters associated with open habitats, and a corresponding reduction in the numbers of small web-building litter species, with a more limited prey range, which characterised the later stages of succession. The most important factor in this change appeared to be the removal of the canopy, resulting in a modification of microclimatic conditions, and degradation of the litter layer. In the first nine years after clear-felling, there were clear and relatively rapid changes in community structure associated with successional age. The observed changes were considered to be mainly due to the increasing vegetation density in this period, which provided both particular structures and a more favourable microclimate for certain species. Associated changes were also found in species richness. abundance, diversity and eveness, which increased during this period. These attributes decreased into late succession, though the pattern was less clear for species abundance, and the oldest sites were less species rich, diverse and even than those of early succession. In late succession, the rate of community change slowed, the most mature sites being very similar in terms of their communities. In general, the differences that did exist were not related to the position of the site on the successional gradient. It was considered that these differences were not due to a single factor, but rather reflected the importance of different factors at each site.

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1. INTRODUCTION.

Coniferous afforestation is the greatest single change in land-use currently taking place in Great Britain, and in 1996 roughly 11% of the land area of mainland Britain was covered with planted forest (Forestry Commission, 1996). The areas most effected by commercial afforestation are the upland areas of England, Wales, and particularly Scotland, in the sub-montane zone (i.e. below the potential tree-line, varying from 650m to 300m in the far north-west). Planting has mainly been on acidic base-deficient substrata, with vegetation types ranging from dry grassland/dwarf shrub heath, to damp grassland and heath or flush bogs and hydrophilous moorland vegetation found on deep blanket bog peats (Ratcliffe, 1986), and in the period from the formation of the Forestry Commission in 1919 to 1996 almost 1 million hectares had been planted (Forestry Commission, 1996). Of the 12% of semi-natural moorland lost since 1945 in six English and Welsh National Parks, 77% had been afforested (Thompson *et al.*, 1988).

The most obvious effect of afforestation is the depletion of the open ground plant and animal communities which existed beforehand (Ratcliffe, 1986), though there are less direct effects on the surrounding communities. Changes in hydrology associated with coniferous afforestation may cause a loss of species in mires and mosses (Butterfield *et al.*, 1995), while birds nesting on habitats that border forests are more likely to fall victim to predators which inhabit the plantations (Thompson, 1987). However, afforestation does have some positive effects. The cycle of management of a plantation produces a range of habitats of varying age and structure, and hence the overall diversity of habitats in the area may be increased (Butterfield *et al.*, 1995). In addition, individual species can profit from the habitats provided by plantations. Both the chequered skipper (*Carterocephalus palaemon*) and the Rannoch looper (*Semiothisa brunneata*) have benefited from the presence of sheltered rides and margins in commercial woodland (Young, 1986), while seed-eating birds such as crossbills (*Loxia curvirostra*) and siskins (*Carduelis spinus*) have increased, likely due to the benefits they derive from the increase in conifer plantations (Bibby, 1987; Petty *et al.*, 1995).

In terms of the effect of afforestation on the animal and plant communities of the upland habitats which they replace certain groups, particularly the birds (Moss *et al.*, 1979; Newton, 1983; Bibby, 1987) and plants (Hill & Jones, 1978; Hill, 1978, 1986), have been studied extensively. Research on invertebrate communities has generally been on ground living groups such as the Carabidae (e.g. Butterfield, 1992; Butterfield *et al.*, 1995) and Araneae (e.g. Downie *et al.*, 1996), though there has been a certain amount of research on the major pest species of commercial forests (Young, 1986; Speight & Wainhouse, 1989).

The management of a commercial forest, with its cycle of felling and replanting, produces habitats of varying age, from immediately after felling to mature plantation, contained within a relatively limited area and as such provides an excellent opportunity to study a simplified woodland succession on replicated plots. As a consequence, a number of studies have used managed forests to study the processes related to change along a successional gradient. Downie *et al.*, (1996), studying the effect of a pasture-plantation ecotone on ground-living spiders in northern England, found that the abundance of spiders was greater in the pasture than in the adjacent plantation, while species richness was similar in both habitats. Niemalä *et al.*, (1996) investigating the effect of habitat heterogeneity on the abundance of forest floor invertebrates in the southern Finnish taiga, showed that both species richness and abundance were greater in the spider communities of early successional habitats than those of mature forest, while Pajunen *et al.*, (1995), studying the structure of spider communities in old-forest fragments in the same region, found that both species richness and abundance were lower in these fragments than in the surrounding managed forest, presumably due to the more heterogeneous nature of the latter. In contrast, Coyle (1981) found that clear-cutting produced a marked reduction in abundance, and to a lesser degree in species richness, in the spider communities of a southern Appalachian forest, though the clear-cut communities were more diverse than those of the preceding forest due to an increase in species eveness in the former. The observed changes in this case were considered to be due to the removal of the forest canopy and reduction in litter depth after clear-cutting. Similarly, McIver *et al.*, (1992), considered that the extent of tree cover and litter depth were important factors in determining the occurrence of species along a successional gradient in a coniferous forest in western Oregon, and both Pajunen *et al.* (1995) and Niemalä *et al.* (1996) stressed the importance of tree cover in influencing community change.

In addition to changes in the structure of communities, and associated attributes such as species richness and abundance, along successional gradients, the species which make up these communities have been shown to exhibit trends in life history, dispersal ability, reproductive output and morphological diversity in response to the prevailing conditions during succession. Hence both Brown & Southwood (1983) and Brown (1985), studying secondary succession in southern England, found that generation time in exopterygote herbivores was shorter during early succession than in later stages, while dispersal ability decreased from early to mid-succession and then increased again into late succession. In addition both of these studies found that niche breadth, considered in terms of the range of food plants fed upon, decreased along the successional gradient. In terms of morphological diversity a number of studies have shown that the range of variation in both size and shape increases along the successional gradient (e.g. Brown 1982; Brown & Hyman, 1986).

Spiders are a useful group for investigating the way in which species accumulate in differently aged and managed areas (Gibson *et al.*, 1992). Not only do they occur in high densities and have a well known taxonomy, they also have a wide range of structural and microclimatic requirements, and as such the structure of their communities are sensitive to changes in the physical environment. In addition, they also exhibit a range of life-cycle strategies which might be expected to have relatively predictable trends along a successional gradient. The purpose of the present study was to investigate the changes which occurred in both the structure and attributes of spider communities, and the strategies exhibited by their constituent species, along a simplified successional gradient, and to this end sites were selected to represent various stages in the successional process from recently clear-felled to mature coniferous plantation. In addition, the effect of a habitat boundary on spider community attributes, and on the distribution of individual species, was investigated.

2. STUDY AREAS.

2.1. Hamsterley Forest.

The main part of this study was carried out in Hamsterley Forest in Weardale (national grid reference, NZ 0030), approximately 32 km south west of Durham City, and covering an area of roughly 2000 ha between 150-425m in the eastern Pennines.

The underlying geology of the area is largely Millstone grit (roughly 95%), though there are small areas of carboniferous limestone, and an igneous intrusion of basalt, the Hett dyke, runs roughly east-west across the site. Soils consist largely of typically upland types, mainly gleys and brown earths, though there are smaller areas of podzols, ironpan and flushed peat.

The land was purchased by the Forestry Commission in 1927, and initial planting took place between this date and 1951, with felling of the first rotation crop beginning in the late 1960's. The figures below show the proportional land-use of the forest in 1992:

Coniferous woodland	82.5%
Broad-leaved woodland	8.0%
Pastures and meadows	4.5%
Conservation areas	2.0%
Recreational grassland	1.0%
Forest rides and roads	2.0%

(Forestry Commission, 1992)

2.1.1. Study Sites.

The approximate location of the 11 sites sampled at Hamsterley Forest are shown in Fig.1, while Table 1 gives summary information for each site. Sampling of the spider communities at these sites took place in 1992, but assessment of vegetation density was not able to take place until 1994.

(1) Restocked.

Site 1.

Situated at the south-eastern edge of Hamsterley Forest, at an altitude of approximately 310m, this site was planted in 1928, felled in 1983-84, and replanted in 1985 with Sitka Spruce (*Picea sitchensis*). This site had the densest vegetation layer of any site sampled (609 touches per 50 quadrats) with 95% cover in 1992. At this time the vegetation was dominated by grasses, and this was also the case in 1994, when the dominant species were *Deschampsia flexuosa* (34% of vegetation cover) and *Holcus lanatus* (17%). The soil organic content at this site was 63%.

Site 5.

Situated on the south-eastern edge of Hamsterley Forest at approximately 280m, this site was initially planted in 1929. Felling took place in 1983-84, and in 1985 the site was replanted with Scots pine (*Pinus sylvestris*). As with Site 1, this site had an extensive vegetation layer, which in 1992 covered 100% of the site and was dominated by grasses. In 1994 this site had the second densest vegetation layer after

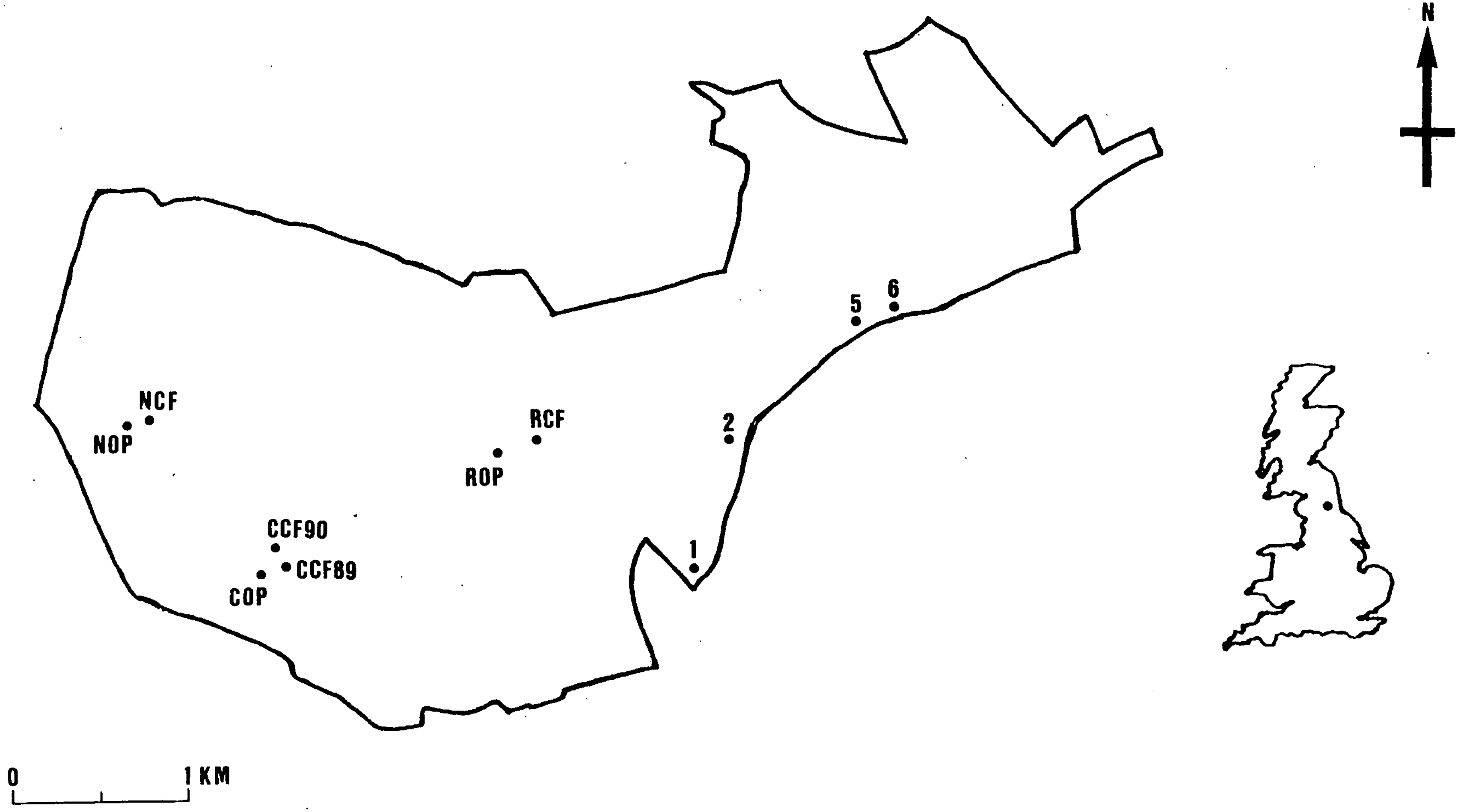


Fig. 1. Map of Hamsterley Forest showing position of study sites.

Site	First planted	Years since felling	Soil organic content (%)	Loose litter depth (mm)	Vegetation density (1994)	Vegetation cover (%) (1992)	Dominant plant species in 1992
Site 1	1928	9	63	3	609	95	grasses
Site 5	1929	9	18	14	420	100	grasses
NCF	1950	1	63	25	86	<2	*Calluna vulgaris*
CCF90	1945	2	41	21	129	10	*Chamaenerion angustifolium*
CCF89	1944	3	81	5	398	60	*Rumex acetosella,* grasses
RCF	1940	4	91	15	134	33	*Calluna vulgaris,* mosses
NOP	1950	-	90	85	68	0	-
COP	1945	-	72	95	98	0	-
ROP	1940	-	46	78	68	0	-
Site 2	1929	-	65	60	67	<2	Mosses
Site 6	1970	-	43	11	315	38	grasses

Table 1. Characteristics of the 11 Hamsterley Forest sites sampled during 1992.

Site 1 (420), the dominant plant species being *Deschampsia flexuosa* (37%), and *Pteridium aquilinum* (35%). The soil organic content at this site was 18%.

(2) Clear-felled.

Neighbour Moor Clear-felled (NCF).

Situated in the south-western part of the forest at approximately 350m, this site was initially planted in 1950, with clear-felling taking place in 1991. In 1992 the herb layer was poorly developed, covering less than 2% of the site and consisting largely of *Calluna vulgaris*. By 1994 vegetation cover had increased to 38% with a density of 86. The dominant plant species at this time were *Calluna vulgaris* (45%) and *Chamaenerion angustifolium* (10%). The soil organic content at this site was 63%.

Corner Clear-felled 1990 (CCF90).

Situated in the south-western part of the forest at approximately 380m, this site was planted in 1945, with clearance taking place in 1990. The vegetation cover at this site in 1992 was 10% and was dominated by *Chamaenerion angustifolium*. By 1994 vegetation cover had increased to 74%, with a density of 129. The dominant plant species at this site in 1994 was *Calluna vulgaris* (40%) followed by *Chamaenerion angustifolium* (18%). The soil organic content at this site was 41%.

Corner Clear-felled 1989 (CCF89).

Initial planting at this site, which was adjacent to the previous site, took place in 1944, with clear-felling occurring in 1989. In 1992 vegetation cover was 60%, the dominant plant species being *Rumex acetosella* and various grasses. By 1994, vegetation cover had increased to 82%, with a dense structure (398 touches). At this time the dominant plant species at this site was *Deschampsia flexuosa* (54%), followed by *Calluna vulgaris* (25%). The soil organic content at this site was 81%.

Rigg Clear-felled (RCF).

Situated roughly in the centre of Hamsterley Forest at approximately 320m, this site was planted in 1940, and in contrast to the previous sites was deforested not as a consequence of the normal management cycle of the site, but by windthrow in 1988/89. In 1992 this site had a vegetation cover of 33%, with the main plant species being *Calluna vulgaris* and various mosses. In 1994 vegetation cover was still only 68%, and relatively sparse (134 touches). At this time the dominant plant species was *Deschampsia flexuosa* (26%), followed by *Calluna vulgaris* (22%), and moss cover was still high (30%). This site had the highest soil organic content of any site sampled at Hamsterley (91%).

(3) Coniferous plantation.

Neighbour Moor Old Plantation (NOP).

Situated in the south-western part of the Forest at approximately 350m, this site was planted in 1950 with Norway Spruce (*Picea abies*), and as with the majority of the plantation sites at the time of this study had developed into a dense stand with a deep litter layer (85mm) and no herb layer, though a certain amount of complexity was provided by dead wood (68 touches). Soil organic content at this site was 90%.

Corner Old Plantation (COP).

This site was situated in the south-western region of Hamsterley Forest at approximately 380m. COP was planted in 1945 with Norway Spruce (*Picea abies*), and like the previous site has developed into a dense plantation, precluding the development of a herb-layer, though this site had a relatively large amount of dead wood, and therefore 'vegetation density' was the highest for any of the plantation sites at Hamsterley (98 touches). This site had the deepest litter layer of any site sampled (95mm). The soil organic content at this site was 72%.

Rigg Old Plantation (ROP).

Situated near to the clear-felled site RCF in the centre of the Forest, this site was a mature plantation of Sitka Spruce (*Picea sitchensis*), planted in 1940, and lacking a vegetation layer, though again a certain amount of complexity was provided by dead wood (68). Soil organic content at this site was 46%.

Site 2.

This site, which consisted of a mature plantation of Scots pine (*Pinus sylvestris*) at an altitude of roughly 300m, was planted in 1929 and hence constituted the site with the longest period of continuous tree cover in this study. While tree cover was still complete, Site 2 was perhaps more open than the other plantation sites, and consequently a sparse ground layer was present, consisting largely of mosses. However, the overall amount of dead wood was low, and thus density was lower at this site than at any other (67 touches). This site had the shallowest litter layer of any of the plantation sites at Hamsterley (60mm). The soil organic content at this site was 65%.

(4) Mixed-woodland.

Site 6.

At an altitude of approximately 280m this site was planted in 1970 with Sitka spruce (*Picea sitchchensis*), but suffered a partial crop failure which allowed colonisation by birch (*Betula* sp.), and also sycamore (*Acer pseudoplatanus*) at the margins. In 1992 this was an open stand (38% ground cover) containing a number of grass dominated clearings, one of which constituted the trapping site. By 1994 the canopy had become more extensive, and vegetation cover was down to less than 20%. However, the clearings that remained were fairly similar in their floral composition to the situation in 1992. Vegetation density in these clearings was high (315 touches), the dominant plant species being *Deschampsia flexuosa* (72%) and *Calluna vulgaris* (9%). The soil organic content at this site was 43%.

2.2. Wilton Moor.

Wilton Moor (NZ 5718), lies approximately 9 km south-east of Middlesbrough, Cleveland, on the Eston Hills, which are a northern outlier of the main sandstone massif of the North York Moors, and consist of an east-west lying ridge separated from the moors by a shallow vale. The ridge reaches a high point at 242m, but is mostly between 150 to 200m above sea level. The western part of the hills remains moorland, but the eastern part, on which the study area was situated, has been planted with shelter breaks and is down to arable agriculture interspersed with sheep pasture (J. Garside pers. comm.). Wilton Moor is part of a larger area of land which was purchased by ICI in 1946, the proportional land use of which at the present time is given below:

Agricultural (mainly arable and sheep pasture)	56%
Coniferous woodland	25%
Conservation areas	7%
Recreational	5%
Broad-leaved woodland	5%
Industrial	2%

(G. Cansino, pers. comm.)

The underlying geology of the area consists of both marine and freshwater mudstones, sandstones and siltstones of the middle and lower jurassic. Soils are largely sand and clay loams, with areas of deep peat.

2.2.1. Study Site.

The study site (Fig. 2) consisted of an area of grassland with a dense sward dominated by tussocks of *Dactylis glomerata* (47% of vegetation cover) and *Festuca* sp. (18%), running into a plantation of *Pinus sylvestris* planted in the early 1950's. This latter was fairly open in nature, with a vegetation cover of 6%, consisting largely of *Rubus* sp., but with grasses (mainly *Festuca* sp.) near the habitat boundary.

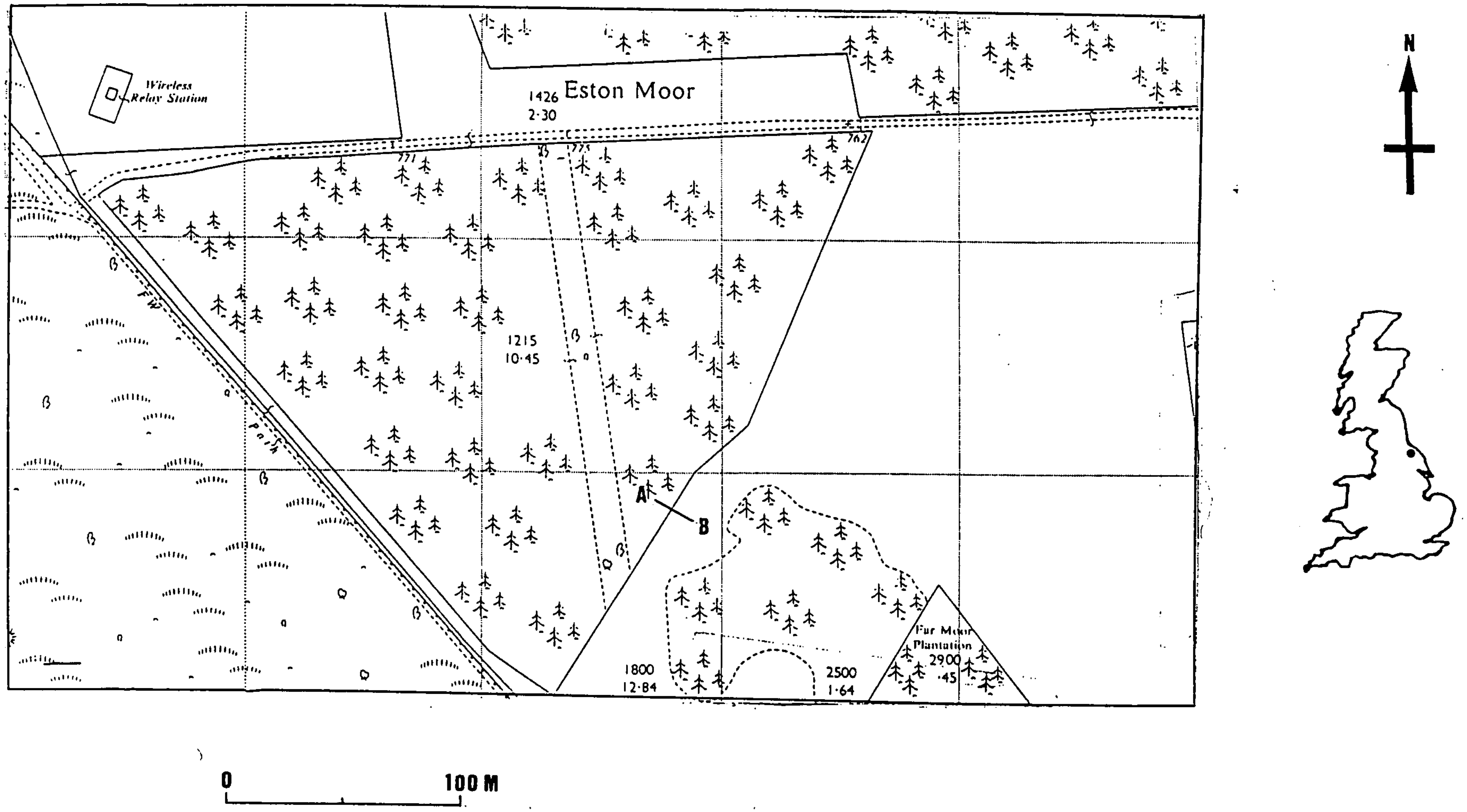


Fig. 2. Map of Wilton Moor showing study area. Line A-B marks position of pitfall transect.

During late 1994, the year before sampling took place, planting of deciduous and coniferous tree species, namely *Quercus, Betula* and *Pinus* species, had taken place within the grassland, though the height of individual plants was less than 30cm at the time sampling occurred. However, in early July 1995 the area around each plant was treated with a herbicide, and as these plantings took place in a line parallel with the boundary between grassland and plantation, this created a strip of almost bare ground running across the line of the trapping transect, between the 6m and 7.5m rows (Fig. 3). Hence while at the beginning of the sampling period, vegetation cover in the grassland was 100%, this had dropped to roughly 95% by late August.

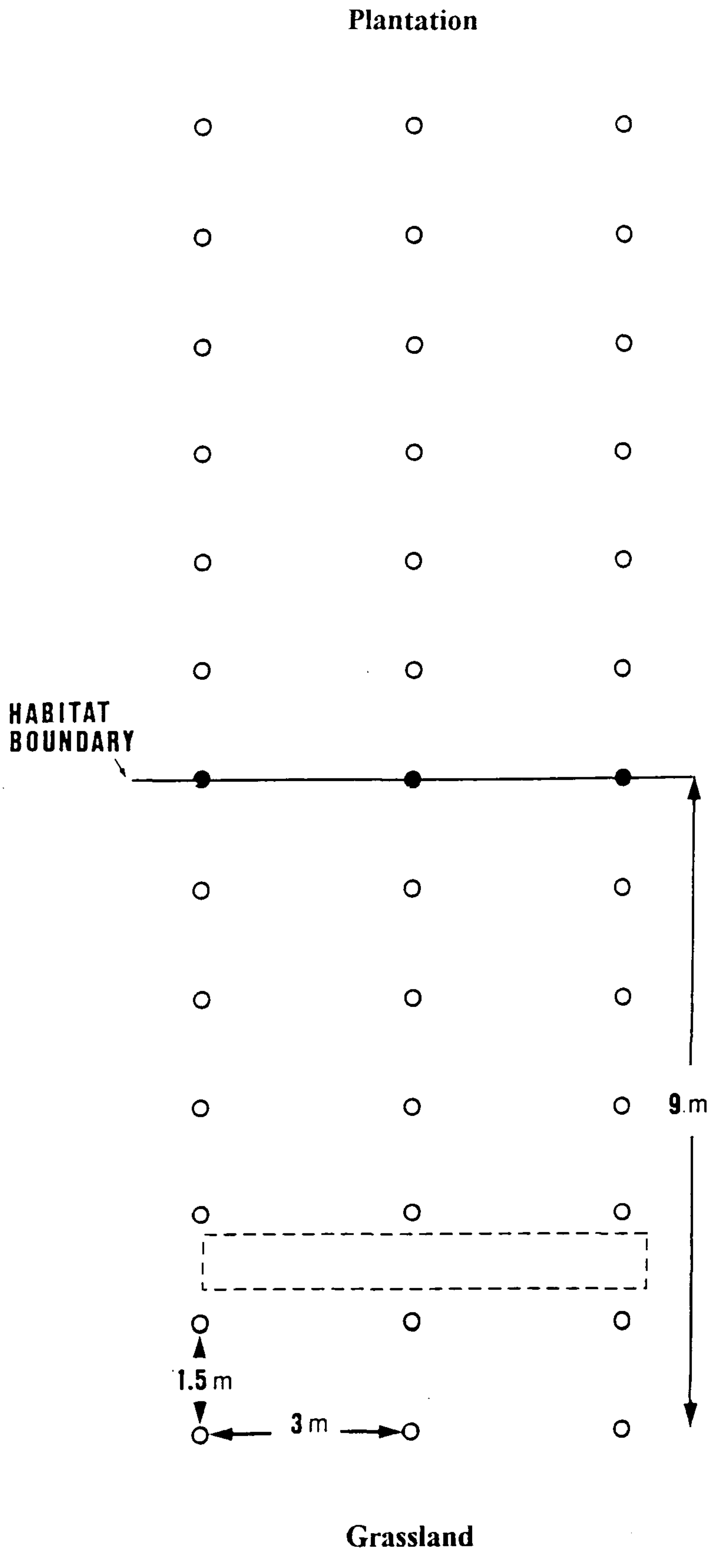


Fig. 3. Diagram showing arrangement of pitfall traps at Wilton Moor. Rectangle marks approximate extent of herbicide application during July 1995.

3. METHODS.

3.1. Pitfall Trapping.

The 11 Hamsterley Forest sites were sampled using ground-sunk pitfall-traps with a mouth diameter of 70mm, containing a 4% formalin solution with detergent. Five traps were used at each site in a 10m line, individual traps being 2m apart. Traps were emptied at roughly three-weekly intervals from May to November 1992.

The Wilton Moor site was sampled using a total of thirty-nine ground-sunk pitfall-traps, containing a 4% formalin solution. The traps were arranged in three parallel rows, 3m apart, at right-angles to the habitat boundary, with traps within each row 1.5m apart (Fig. 3). The rows extended to a distance of 9m either side of the habitat boundary into the grassland and plantation, with the central trap of each row situated on the boundary itself. Traps were emptied at roughly four-weekly intervals from June to September 1994.

Pitfall-traps have been used extensively to study various attributes of surface active arthropod populations, particularly those of the Araneae and Carabidae (Topping & Sunderland, 1992). While a number of criticisms have been levelled at this method of sampling (e.g. Luff, 1968; Southwood, 1978; Topping & Sunderland, 1992), their use has been retained in this study, as they are inexpensive, require minimum supervision, and are capable of collecting large numbers of individuals from a wide range of species at a number of habitats which can be sampled simultaneously. Particularly relevant to this study is the fact that pitfall-traps are efficient at catching small Linyphiidae (Merrett & Snazell, 1983). In addition, the number of animals caught is independent of sampling skill, and gives a reasonable estimate of species composition (Uetz & Unzicker, 1976; Merrett, 1983).

Spiders from all sites were sorted and stored in 70% alcohol. All adult spiders were identified to species using Roberts (1985, 1987, 1993) or Lockett & Millidge (1951, 1953) on the basis of their genitalia.

For each of the Hamsterley sites, monthly catches were pooled to produce eleven sets of species abundance data. Catches from the Wilton Moor study were pooled to produce six discrete sets of data, three each for grassland and plantation, with each set representing the pooled data from six traps (two rows), e.g. 9m and 7.5m, 6m and 3.5m, and so on. Data from the habitat boundary row were not used, as the number of replicates was considered insufficient to allow statistical analysis.

3.2. Vegetation Density.

Vegetation structure has been shown to have an important influence on the structure of spider communities (Rushton *et al*, 1987; Gibson *et al*, 1992; Downie *et al*, 1995) and during 1994 the density of the vegetation at each of the Hamsterley Forest sites was estimated using a point quadrat method. This entailed placing a wooden rod perpendicular to the ground surface and recording each touch by any plant structure, either living or dead up to a height of 15cm. This height represents the upper limit of the 'Open-Ground' category of the Terrestrial system (Elton 1966), and was chosen because the density of the vegetation in this layer was considered of most relevance to ground living spiders. This procedure was carried out a total of 50 times in all for each site. In addition, at each point the depth of the leaf litter was also recorded.

3.3. Data Analysis.

3.3.1. Ordination.

Ordination involves the arrangement of sites and/or species along an environmental gradient. Detrended correspondence analysis (DCA, Hill, 1979a) in common with reciprocal averaging on which it is based, is an indirect gradient analysis method, in which environmental gradients are not studied directly, but are inferred from species composition data (Palmer, 1993).

Log transformed data for all species trapped in numbers exceeding five individuals were analysed using the DCA option of the CANOCO computer program (Ter Braak, 1988), an extension of DECORANA (Hill, 1979a). DCA has several advantages over other ordination techniques. Unlike reciprocal averaging and principal components analysis, it avoids the 'arch-effect' (Gauch, 1982) which is the tendency in these techniques for higher axes to be strongly related to the first. In addition, this technique allows the analysis of large amounts of data without difficulty, and both species and sample ordinations are produced simultaneously, with axes that are rescaled in standard deviation units with a definite meaning (Hill, 1979a; Palmer, 1993).

However, DCA has come under increasing criticism. Palmer, (1993), for instance, considered the detrending algorithm inelegant and arbitrary, and pointed out that detrending will destroy any true arch that exists in the data, and both Minchin (1987), and Økland (1990), noted that this method compressed one end of the gradient into a tongue. Perhaps the most serious criticisms of DCA involve those situations where it has been shown to produce aberrant results. Oksanen (1988), investigated the performance of detrended correspondence analysis in situations where the eigenvalues of the first two axes were very similar. Under these conditions, random variation in the data can cause the order of the eigenvalues to be reversed (Mardia *et al.*, 1982), resulting in the ordinations produced by DCA being very variable. This effect, which Wilson (1981) termed inconsistency, and Greenacre (1984) called instability, seems to arise because the detrending process produces different site scores in relation to one another depending on which axis is detrended, so that the two-dimensional configuration is susceptible to changes in the first axis (Oksanen, 1988). Investigating the effect of varying the number of detrending segments on the resultant DCA ordinations, Jackson and Somers (1991) found that the choice of segmentation could substantially effect both the configuration of sites, and the magnitude of the higher dimension eigenvalues in the resultant ordinations, and suggested searching for multiple solutions with small data sets (i.e. <100-200 samples). However, in this study the initial solution was felt to be both interpretable, and presenting sufficient scope for further study, and no further solutions were attempted.

Ordination then provides an objective, if somewhat arbitrary and inelegant, method of graphically summarising multidimensional data sets. While not and end in itself, it is a useful starting point for studies of this nature, especially when used in conjunction with hierarchical methods such as TWINSPAN, suggesting affinities between sites and species which can then be investigated quantitatively at later stages of the study.

3.3.2. Classification.

Classification groups sites according to their similarities based on the relative abundance of their constituent species. Two Way Indicator Species Analysis (TWINSPAN, Hill, 1979b) achieves this in four stages;

i) An initial ordination of the data.
ii) This ordination is then split into groups of sites which are deemed similar to one another on the basis of the distribution of certain species between them.
iii) The species used to group the sites in ii) are then used as the basis for a refined ordination.
iv) This ordination is divided on the same basis as ii) to give the final classification. Species used to distinguish groups of sites at this stage are indicator species.

A problem which arises when using species abundance data of this nature is that too much emphasis is placed on the numbers of common, or in the case of pitfall-trapping, very active, species captured while downgrading the importance of less common, but equally constant species. In order to overcome this problem, the use of pseudospecies has been suggested (Hill, 1979b). In this study, pseudospecies were created for each species at six, 20, and 99 individuals. These values are arbitrary, but similar levels for terrestrial invertebrates have been used elsewhere (Butterfield & Coulson, 1983), and were used here to allow comparison with this study. As with the ordination species which were captured in numbers not exceeding five individuals were excluded from the calculation.

3.3.3. Guild Distribution.

In order to assess the interaction of the physical environment at the sites, and the lifestyle and mode of prey capture of the spiders present, species were grouped into guilds, which are 'groups of species exploiting a common resource base in a similar fashion' (Root, 1967). Six major guilds were defined (Table 2), based on Post & Riechert (1977). These guilds were defined on the basis of hunting method, period of activity and for the web building species, web structure.

3.3.4. Diversity and Species Abundance.

3.3.4.1. Diversity Indices.

The study of diversity provides a useful method of concentrating information about a community into a readily assimilable form (Morris & Lakhani, 1979), and is of theoretical interest in that it can be tied to concepts such as stability, maturity and spatial heterogeneity (Hill, 1973) which are particularly relevant to successional change. However, caution has been urged when using indices of this nature with

GUILD	INCLUSIVE FAMILIES	NUMBER OF SPECIES	MODE OF PREY CAPTURE
Diurnal running spiders	Lycosidae	8	cursorial hunters
Nocturnal running spiders	Gnaphosidae, Clubionidae	8	"
Ambushers	Thomisidae	2	ambushers
Funnel web spiders	Agelenidae	2	web-builders
Scattered line weavers	Theridiidae	3	"
Sheet web weavers	Linyphiidae	73	"

Table 2. Summary information for the six major spider guilds defined at Hamsterley Forest.

pitfall trap data (e.g. Topping & Sunderland, 1992), and in this study, four commonly used diversity indices were calculated for each site to evaluate their performance with species abundance data derived from pitfall traps.

(1) Log series α.

For each site log series α was initially estimated using William's Nomograph (Williams, 1947). The final value of the index was then rigorously extracted from the equation:

$$S_T = \alpha \log_e(1+N/\alpha)$$

where S_T = total number of species present at a site, and

N = total number of individuals at the same site.

This entailed substituting the value for α obtained from William's Nomograph, solving the equation, and continuing this process with successive values of α until the value of S obtained equalled that observed in the species abundance data in question.

(2) Margalef Index.

The Margalef index is calculated as:

$$DMg = (S-1)/\ln N$$

where S = number of species, and

N = number of individuals.

(3) Berger-Parker Index.

The Berger-Parker index is calculated as:

$$d = N_{max}/N$$

where N_{max} = the number of individuals in the commonest species, and

N = the number of individuals in all species combined.

This index is usually expressed as its reciprocal, so that an increase in the value of the index accompanies an increase in diversity (Magurran, 1988).

(4) Simpson index.

Initially the statistic C is calculated from the equation:

$$C = \sum_{1}^{S} (n_i(n_i-1)/N(N-1))$$

where n_i = number of individuals in the ith species, and

N = the total number of individuals.

The index is then:

$$D = 1/C$$

Correlation of site rankings produced by the diversity indices, along with those for species richness and number of individuals, were compared using Spearman's rank correlation coefficient (r_s, Rees, 1994). This value was then compared with tabulated values of r_s to ascertain whether there was significant correlation at the 5% level.

3.3.4.2. Species Abundance Models.

The use of species models is advocated by many workers as the only sound basis for the examination of species diversity, as a model of this nature provides the most complete description of the species abundance data of a community (Magurran, 1988). In addition, patterns of species abundance are a more sensitive measure of disturbance effects (e.g. clear-felling and subsequent succession) than species richness alone, and are less sensitive to sample bias than diversity indices (Magurran, 1988; Tokeshi, 1993; Pettersson, 1996). Initially, log abundance on rank plots were examined for each site. Species abundance data were then tested against the predicted distributions of four commonly used species abundance models.

(1) Geometric Series.

$$n_i = NC_k k(1 - k)^{i - 1}$$

where k = the proportion of the available niche space occupied by each species,

n_i = number of individuals in the ith species,

N = total number of individuals, and

$C_k = [1 - (1 - k)^s]^{-1}$, and is a constant which ensures that $\sum n_i = N$.

(2) Logarithmic Series.

$$\alpha x, \alpha x^2/2, \alpha x^3/3, \ldots. \alpha x^n/n$$

where αx = the number of species expected to have one individual,

$\alpha x^2/2$ = those with two, and so on.

x is estimated from the iterative solution of:

$$S/N = [(1-x)/x][-\ln(1-x)]$$

where S = number of species, and

N = total number of individuals.

Species are generally dealt with in terms of abundance classes, $\log_2$ being used in this case (i.e. the upper limit of each class involved a doubling of the number of species).

(3) Log normal distribution.

$$S(R)=S_0 \exp\cdot(-a^2R^2)$$

where S(R) = the number of species in the Rth octave to the right and left of the symmetrical curve,

$S_{0;}$ = the number of species in the modal octave, and

a = $(2\sigma^2)^{1/2}$ = the inverse width of the distribution.

As with the logarithmic series $\log_2$ abundance classes were used for this distribution.

(4) MacArthur's Broken Stick Model (Random Niche Boundary Hypothesis).

$$S(n) = [S(S-1)/N]\,(1-n/N)^{S-2}$$

where S(n) = the number of species in the abundance class with n individuals,

S = total number of species, and

N = total number of individuals.

As with the logarithmic series and the log normal distribution, species were dealt with in terms of $\log_2$ abundance classes.

Values obtained from these models were compared with those of the species abundance data for each site using a χ^2 goodness-of-fit test (Parker, 1983), the value obtained then being compared with tabulated values of χ^2 to ascertain whether the expected and observed values differed at the 5% level.

3.3.5. Border Transition Categories.

For all species trapped in numbers exceeding 19 individuals at Wilton Moor, significant differences in mean abundance across the transect were tested for using single factor Analysis of variance (ANOVA, Zar, 1996). For those species which showed significant differences using the initial ANOVA, differences between rows were tested using the Tukey honestly significance difference test (Zar, 1996). These procedures were also used to analyse changes in species richness, diversity and abundance across the transect. Distribution at the guild level was also analysed in a similar fashion.

Species which showed a significant difference in mean catch between rows were then assigned to one of the boundary transition categories proposed by Duelli *et al.* (1990). Studying the movement of arthropods between natural and cultivated areas in Switzerland, Duelli *et al.* (1990) defined six such categories, based on the distribution of individuals across a habitat boundary (Fig. 4). When there is no measurable result of population exchange between the two habitats, a 'hard edge' transition results (Fig. 4a), all individuals of a species being recorded in one habitat, with a sharp decline in numbers at the habitat boundary. At the other extreme is 'no edge' or 'very soft edge' (Fig. 4f), where the individuals of a species are distributed evenly between the two habitats in question. Between these two extremes lie various 'soft edge' categories. Negative influence (Fig. 4b) represents a situation where a species shows a strong

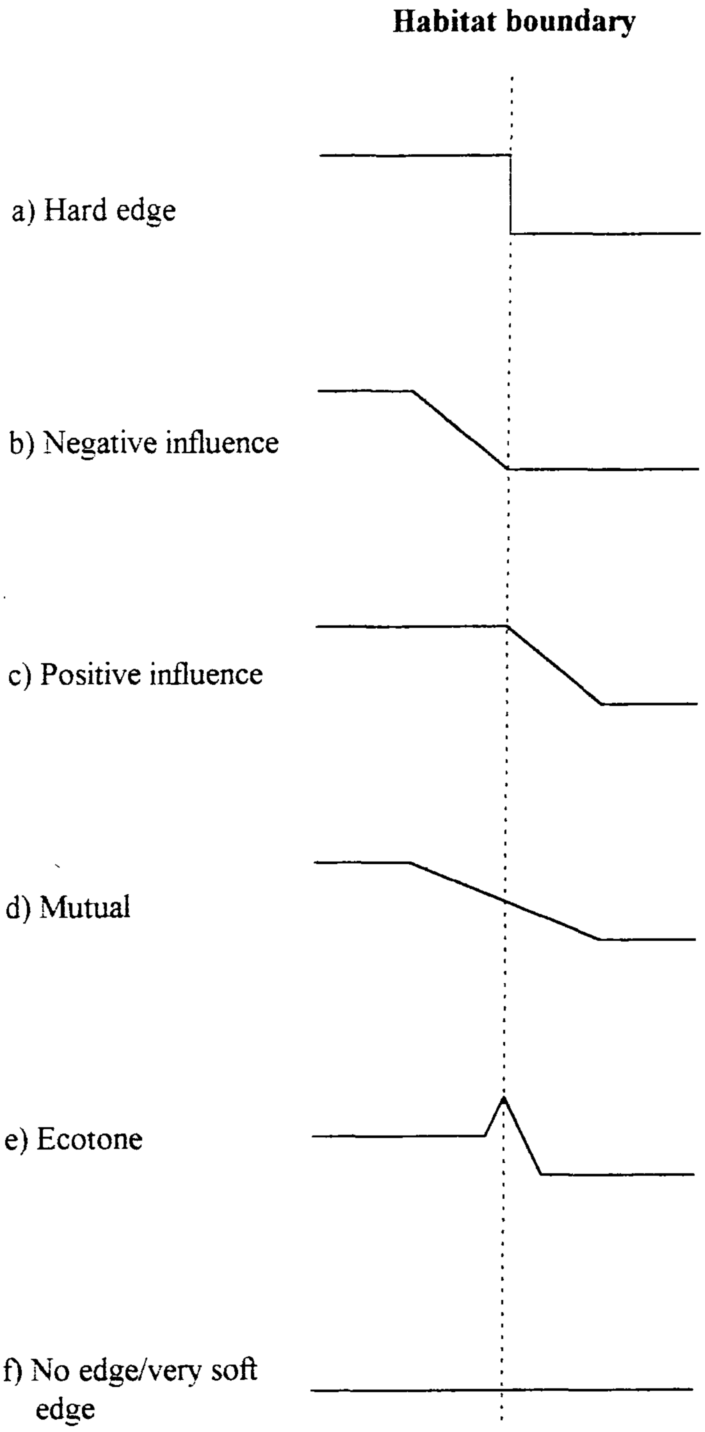


Fig. 4. Diagram showing the six types of border transition category proposed by Duelli *et al.* (1990) and based on the same.

preference for one habitat over the other, even to the extent of showing a decrease in numbers near to the habitat boundary. In the case of positive influence (Fig. 4c), while a preference for one habitat is still shown, the species invades the adjacent habitat to a greater or lesser extent. In some cases, both of these effects occur at the same time, producing a mutual influence (Fig. 4d). The final category, 'ecotone' (Fig. 4e), is found where a species occurs in the greatest numbers in and around the habitat boundary.

4. RESULTS.

The pitfall survey produced 4797 individuals from 103 species in 13 families. The number of species at individual sites ranged from 22 (NOP) to 50 (Site 1), with restocked and clear-felled sites consistently richer than sites with well established tree cover. (clear-felled/restocked mean = 42.7 ± 3.7, plantation/mixed-woodland mean = 26.6 ± 4.5, t_8=5.4 $p<0.001$). Number of individuals ranged from 149 (ROP), to 1060 (Site 5), with clear-felled/restocked sites generally with more individuals than wooded sites, though at Site 2 more individuals were trapped than at NCF, CCF89 and CCF90, and the latter two also had less individuals than NOP (clear-felled/restocked mean = 580.3 ± 273.5, plantation/mixed-woodland mean = 262.6 ± 87.3, t_6 = 2.1 p = N.S.).

4.1. Ordination.

4.1.1. Ordination of Hamsterley sites based on their spider assemblages.

Fig. 5 gives the site ordination diagram for the eleven Hamsterley sites based on the data for those species trapped in numbers exceeding five individuals. This value was chosen because five is the largest value which is not significantly different from zero (Butterfield & Coulson, 1983).

The eigenvalues associated with each of the four axes were 0.402, 0.247, 0.147 and 0.079. Axes 1 and 2 accounted for 74.17% of the variance in the data set, and

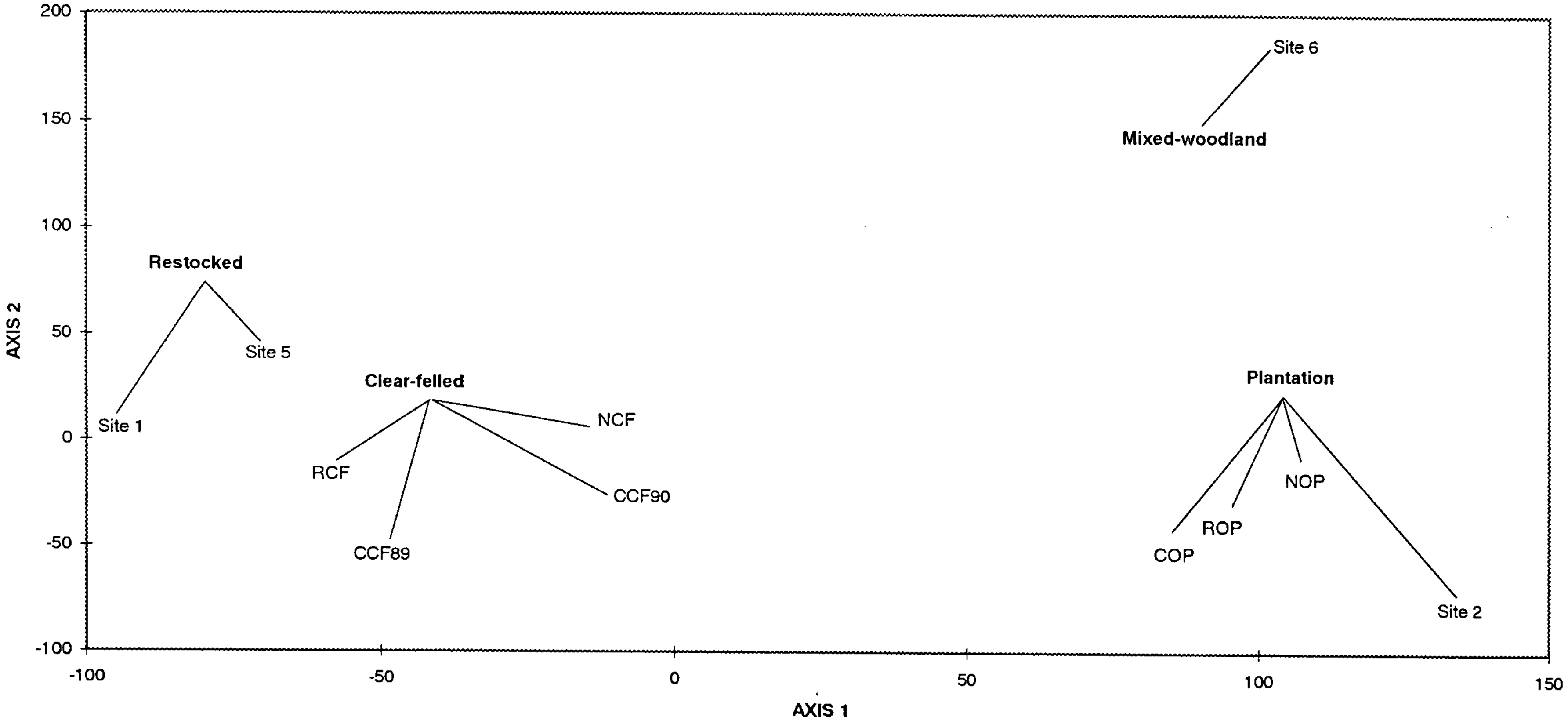


Fig. 5. CANOCO ordination diagram (Axis 1 by Axis 2) of Hamsterley sites based on the distribution of those species with numbers greater than five individuals, and showing major habitat groups.

therefore Axes 3 and 4 were not considered further. Axis 1 gives a good separation of sites. The restocked sites, Site 1 and Site 5, have the lowest scores on this axis, closely followed by the clear-felled sites, RCF, CCF89, NCF and CCF90. The plantation sites, ROP, NOP, COP and Site 2, and the mixed-woodland Site 6, have the highest scores on this axis. The restocked site, Site 1, and the plantation Site 2 have the lowest and highest scores respectively on this axis and were therefore least similar in terms of species composition, though as a typical species tends to appear, rise to its mode, and disappear in about 400 axis units in DCA ordinations (Hill, 1979a), the fact that the range of scores on Axis 1 of the current ordination is less than 250 units, suggests that these sites still had a number of species in common.

Axis 2 of the ordination gives relatively little separation of the sites, most being grouped centrally. However, Site 6 is well separated from the other sites on this axis, while the restocked sites tend to have higher scores than the plantations and clear-felled sites with the exception of NCF. Site 2 with the lowest, and Site 6 with the highest score, constitute the endpoints of the axis, and are therefore least similar in terms of their species composition.

4.1.2. Ordination of Hamsterley species based on their relative abundance at the sampled sites.

Fig. 6 shows the species ordination diagram for the Hamsterley Forest data. Only those species trapped in numbers exceeding 19 individuals have been plotted. Positive scores on Axis 1 are found among certain species of the sheet web weavers, namely *Lepthyphantes alacris, L. tenebricola, L. ericaceus, L. zimmermanni, Tapinocyba*

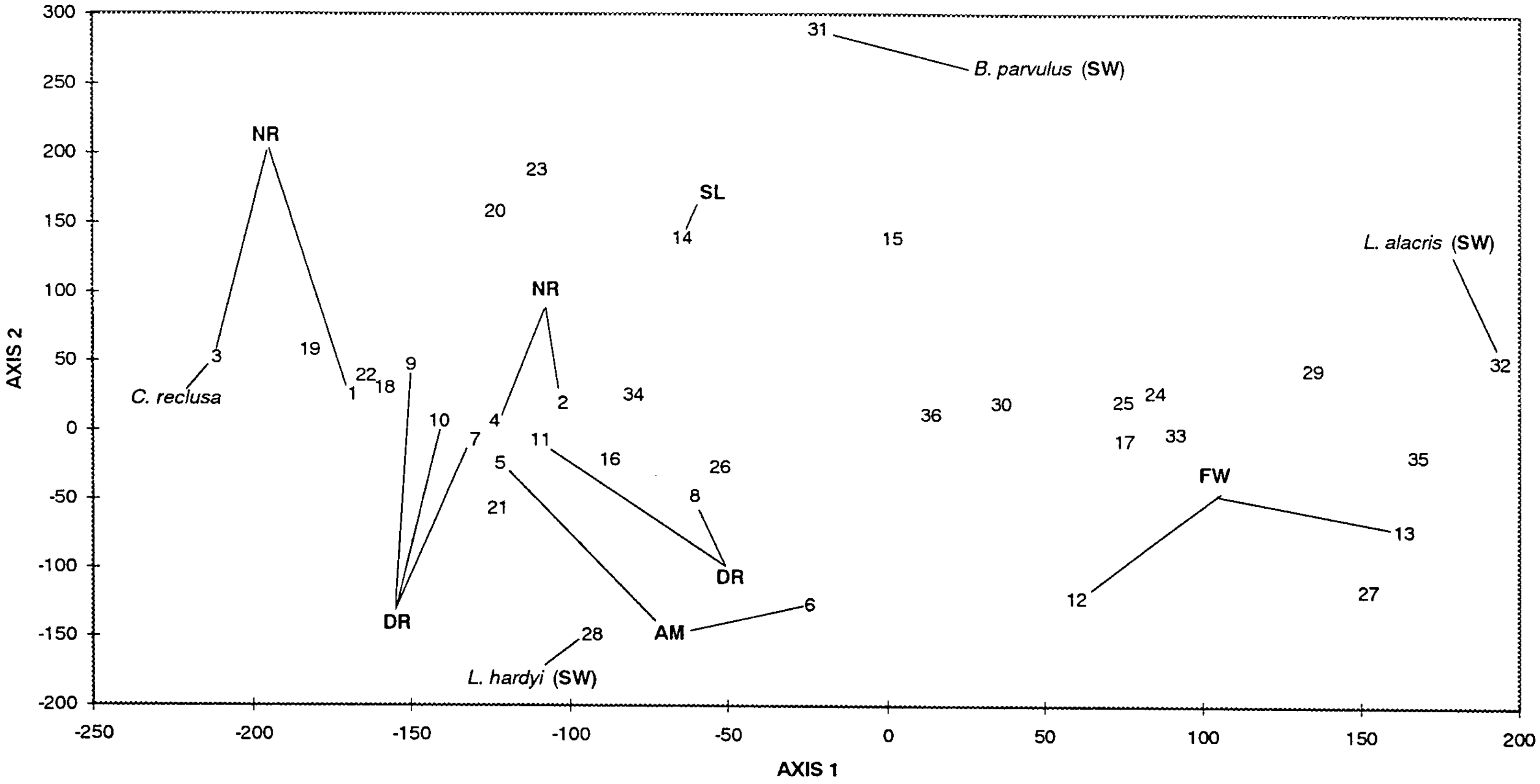


Fig. 6. CANOCO ordination diagram (Axis 1 by Axis 2) of Hamsterley species based on the distribution of those occurring in numbers greater than five individuals, and showing those with numbers greater than 19. (Key over).

1	*Drassodes cupreus*
2	*Haplodrassus signifer*
3	*Clubiona reclusa*
4	*Agroeca proxima*
5	*Xysticus cristatus*
6	*X. sabulosus*
7	*Pardosa pullata*
8	*P. amentata*
9	*P. nigriceps*
10	*Alopecosa pulverulenta*
11	*Trochosa terricola*
12	*Coelotes atropos*
13	*Cryphoeca silvicola*
14	*Robertus lividus*
15	*Ceratinella brevipes*
16	*Walckenaeria acuminata*
17	*W. cucullata*
18	*Dismodicus bifrons*
19	*Gonatium rubens*
20	*Pocadicnemis pumila*
21	*Silometopus elegans*
22	*Cnephalocotes obscurus*
23	*Minyriolus pusillus*
24	*Tapinocyba pallens*
25	*Monocephalus fuscipes*
26	*Micrargus herbigradus*
27	*Diplocephalus latifrons*
28	*Leptothrix hardyi*
29	*Centromerus dilutus*
30	*Saaristoa abnormis*
31	*Bathyphantes parvulus*
32	*Lepthyphantes alacris*
33	*L. zimmermanni*
34	*L. mengei*
35	*L. tenebricola*
36	*L. ericaceus*

DR	Diurnal running spiders
NR	Nocturnal running spiders
AM	Ambushers
FW	Funnel web spiders
SL	Scattered line weavers
SW/unlabelled	Sheet web weavers

Fig. 6. - Key to species/guilds.

pallens, Centromerus dilutus, Walckenaeria cucullata, Monocephalus fuscipes, Diplocephalus latifrons and *Saaristoa abnormis*, and the two species of funnel web spider, *Cryphoeca silvicola* and *Coelotes atropos*. The lowest scores are found among the remainder of the sheet web weavers and a number of other guilds, namely the diurnal running spiders, nocturnal running spiders, ambushers, and scattered line weavers. *Clubiona reclusa* and *Lepthyphantes alacris* have the lowest and highest scores on this axis respectively, and are therefore least similar in terms of their distribution.

The range of scores on Axis 2 is roughly the same as that of Axis 1, though the majority of species are grouped about the origin. However, there does appear to be some separation of guilds. The diurnal running spiders, with the exception of *Pardosa nigriceps,* have negative scores on this axis, as do the ambushers, *Xysticus cristatus* and *X sabulosus*, the funnel web spiders, *Coelotes atropos* and *Cryphoeca silvicola*, the nocturnal running spider *Agroeca proxima*, and the sheet web weavers *Micrargus herbigradus, Walckenaeria acuminata, Diplocephalus latifrons, Silometopus elegans, Leptothrix hardyi, Lepthyphantes zimmermanni, L. mengei, and L. ericaceus,* the latter three being particularly close to the origin. Positive scores on this axis are found in the nocturnal running spiders *Clubiona reclusa* and *Drassodes cupreus*, the scattered line weaver *Robertus lividus*, and the remainder of the common sheet web weavers, particularly *Pocadicnemis pumila, Minyriolus pusillus* and *Bathyphantes parvulus*. The members of the sheet web weavers have widely differing scores on this axis, both the species with the lowest (*Leptothrix hardyi*), and highest (*Bathyphantes parvulus*) scores being of this family.

4.1.3. Derivation of ordination axes.

The first axis of the ordination appears to be most closely related to vegetation density, as there is a significant negative correlation between this variable and Axis 1 site scores (r_9 = -0.65, $p<0.05$). However, the fact that the relationship is not exact suggests that other factors play a more important part at certain sites, and it is likely that the main factor in the separation of the clear-felled and restocked sites on the one hand, and the plantation sites and the mixed-woodland on the other, was the presence of tree cover at the latter, hence the relatively high score of Site 6 on this axis despite its dense vegetation. In addition, as few of the common species at the plantation sites utilise above ground structures, its seems likely that the apparent link between axis score and vegetation density at these sites is spurious, and the relative scores of these sites may be linked to some other factor, perhaps litter depth.

The derivation of Axis 2 of the ordination is more difficult to assess. The lowest scoring species on this axis, *Leptothrix hardyi* and *Xysticus sabulosus* are typical of sites with a high percentage of bare ground (Merrett, 1976), while among the highest scoring species, those such as *Robertus lividus* and *Pocadicnemis pumila*, are associated with woodland or upland sites, or sites with a well developed vegetation layer (Lockett & Millidge, 1953; Coulson & Butterfield, 1986; Rushton *et al.*, 1987). This axis may therefore be related to the amount of bare ground or some aspect mediated by this, perhaps humidity. Again the relationship between axis score and environmental variable is not exact, indicating the influence of other factors at particular sites, and the relative scores of the plantation sites on this axis appear to be due to some other factor, perhaps age.

While a more detailed analysis of species disposition is carried out below, an initial consideration of species and site ordination diagrams suggests that, while there is a degree of overlap between the sites in terms of their species composition, there were clear differences between the communities of the restocked and clear-felled sites on the one hand, and the plantations and mixed-woodland on the other. The former were characterised by a range of species with negative scores on Axis 1 of the ordination, including members of the diurnal and nocturnal running spiders, the ambushers, and the scattered line weaver *Robertus lividus*, and also including a number of sheet web weavers, such as *Gonatium rubens, Cnephalocotes obscurus* and *Dismodicus bifrons.* The plantation and mixed-woodland sites were characterised by a more limited range of species, consisting largely of sheet web weavers, such as *Lepthyphantes alacris* and *L. tenebricola*, and the funnel web spider *Cryphoeca silvicola*, with positive scores on Axis 1 of the ordination. While the position of the mixed-woodland, Site 6, on Axis 1 of the ordination implies a close similarity between the community of this site and those of the plantations, the high score of this site on Axis 2 suggests that the community of Site 6 contains an element more typical of the clear-felled/restocked sites, namely the sheet web weavers *Pocadicnemis pumila, Minyriolus pusillus* and *Bathyphantes parvulus*, and the scattered line weaver *Roberts lividus*, which have high scores on this axis. In addition a number of species, the sheet web weavers *Ceratinella brevipes*, *Lepthyphantes ericaceus* and *Saaristoa abnormis*, and perhaps the funnel web spider *Coelotes atropos*, appear to show no preference for either the clear-felled and restocked sites on the one hand, or the plantations and mixed-woodland on the other. It is apparent from the above description that the sheet web weavers show three discrete types of distribution, namely, confined to clear-felled/restocked sites, showing no preference for either clear-felled/restocked or plantation/mixed-woodland sites, and occurring in greater abundance at the plantation/mixed-woodland sites.

4.2. Classification.

4.2.1. Grouping of Hamsterley sites based on their spider assemblages.

TWINSPAN was used to group sites, and to allow mean catches of individual species to be compared between these groups. TWINSPAN classified the 11 sites into four Endgroups representing different spider communities. Fig. 7 shows a dendrogram based on the results, showing the indicator species at each division, while Fig. 8 superimposes the TWINSPAN divisions on the ordination diagram (Fig. 6).

Initially TWINSPAN divided the sites into two groups, one consisting of the restocked and clear-felled sites, the other of the plantation sites and the mixed-woodland Site 6. The indicator species for this division is the diurnal running spider *Pardosa pullata*, which occurred in large numbers at both restocked and clear-felled sites. This parallels the configuration of the sites on Axis 1 of the ordination diagram (Fig. 8).

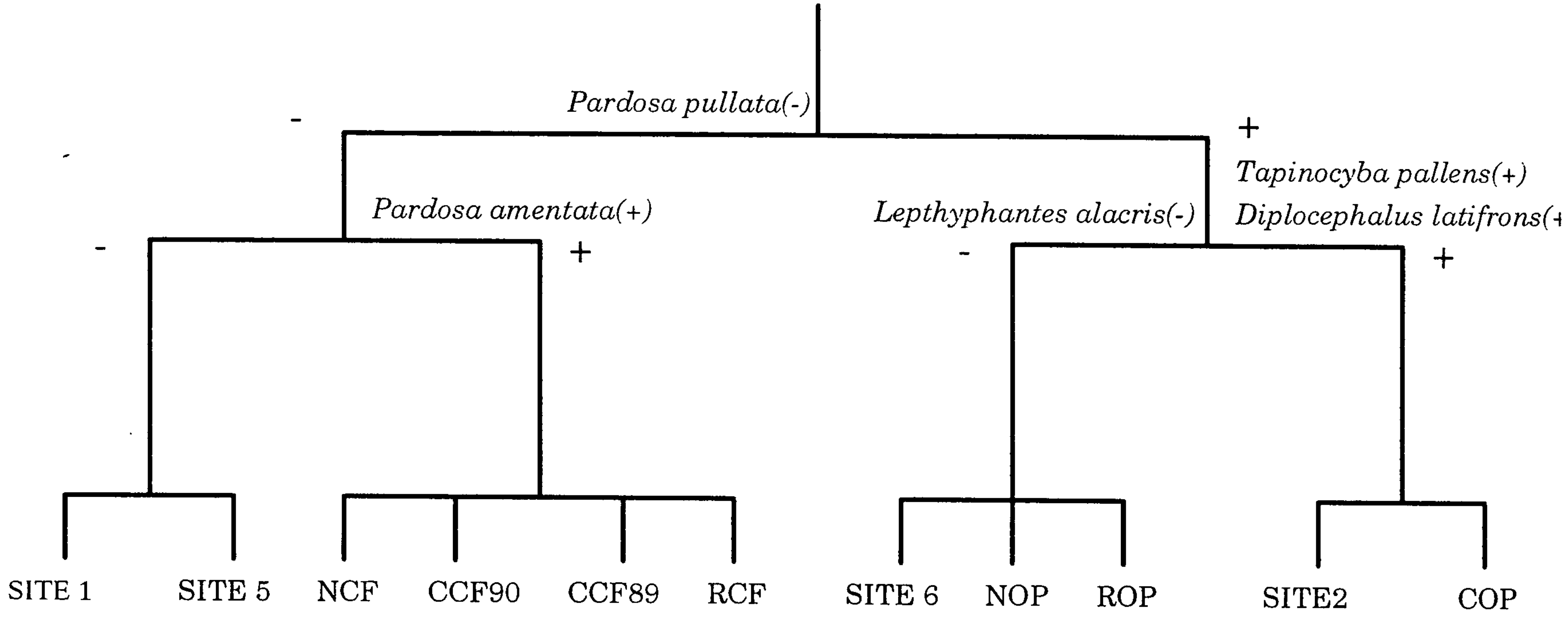


Fig. 7. Dendrogram derived from TWINSPAN analysis of Hamsterley spider data for those species present in numbers exceeding five individuals, and showing indicator species for each division.

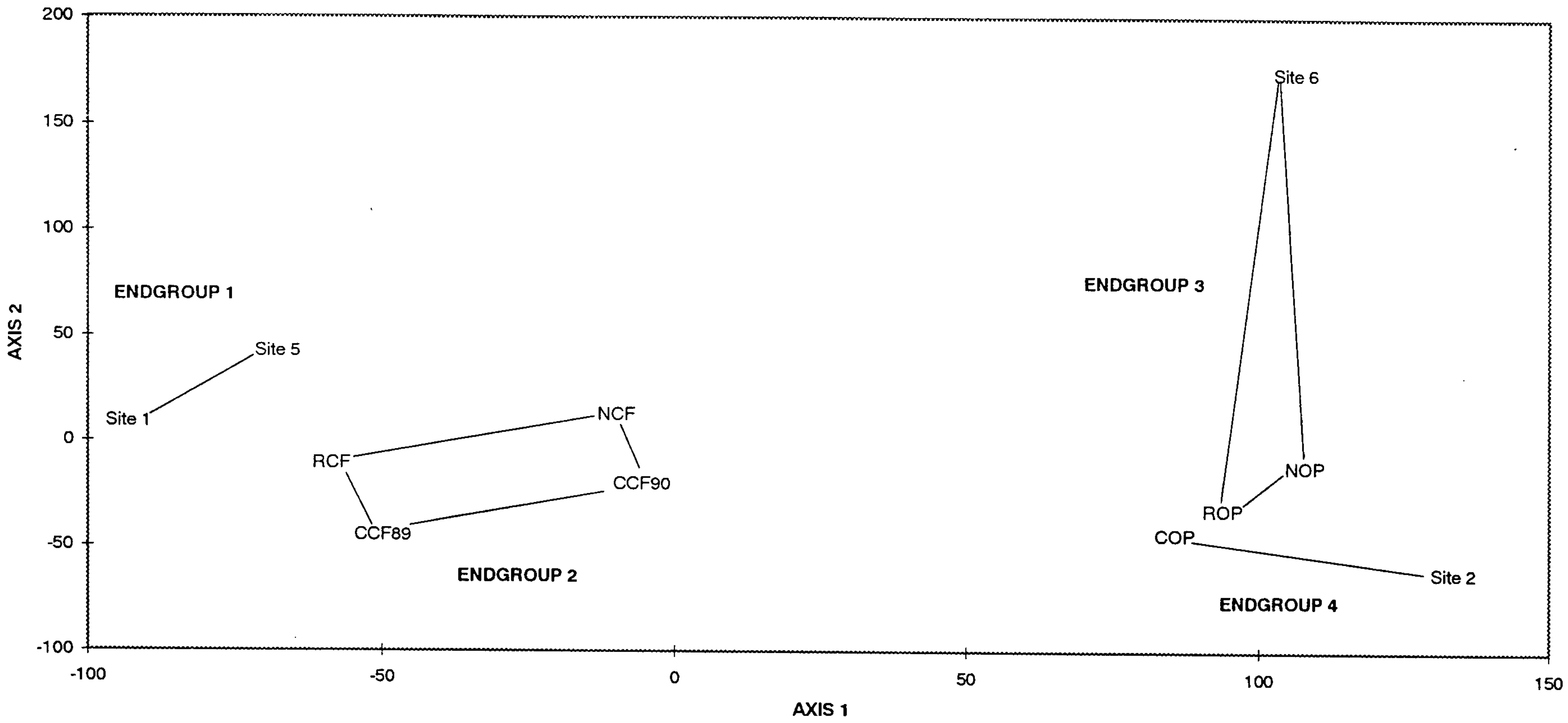


Fig. 8. CANOCO ordination diagram (Axis 1 by Axis 2) of Hamsterley sites based on their spider assemblages, and showing TWINSPAN Endgroups.

In dividing the restocked from the clear-felled sites, TWINSPAN identified *Pardosa amentata* as a positive indicator. This species occurred at all sites in both Endgroups, but was consistently more abundant at Endgroup 2.

Endgroup 1 consists of the restocked sites, Site 1 and Site 5, and is clearly separated from the Endgroup 2 sites (NCF, CCF89, CCF90 and RFC) on the ordination diagram, the former having the lowest scores on Axis 1, and generally higher scores on Axis 2 of the ordination (Fig. 8), though there is some overlap.

The third division made by TWINSPAN separates the mixed-woodland Site 6 and the plantation sites NOP and ROP (Endgroup 3), from the remaining plantation sites, COP and Site 2 (Endgroup 4). Both Endgroups have high scores on Axis 1 of the ordination diagram (Fig. 8), while Endgroup 3 sites have consistently higher scores on Axis 2. However, the arrangement of sites on the ordination diagram implies that the Endgroup 3 sites ROP and NOP, and the Endgroup 4 site COP have communities which were more similar to each other than they were to those of the other members of their Endgroups. ROP and COP in particular have similar scores on both axes, while COP is also closer to NOP on both axes than to Site 2, which lies at the extreme lower right of the ordination diagram. Site 6 is close to NOP on Axis 1, while being well separated on Axis 2.

4.2.2. Distribution of Common species across Hamsterley sites.

Table 3 gives the distribution of the 32 commonest species based on the TWINSPAN output. Only species trapped in numbers exceeding 19 individuals were included, as

		ENDGROUP										
		1		2				3			4	
	SPECIES	SITE 1	SITE 5	NCF	CCF90	CCF89	RCF	SITE 6	NOP	ROP	SITE 2	COP
A	*Clubiona reclusa*	18	2				1				1	
	Cnephalocotes obscurus	65	11				7					
	Drassodes cupreus	6	4		1		10					
	Pocadicnemis pumila	51	128	3			2	4				
	Minyriolus pusillus	7	20	1				2				
	Walckenaeria acuminata	19	22		2	6						10
B	*Pardosa pullata*	252	439	67	40	46	60		1			
	Alopecosa pulverulenta	231	173	37	21	20	178					
	Gonatium rubens	19	26	1		1	1					
	Micrargus herbigradus	4	8		3	1	1				1	3
	Haplodrassus signifer	44	8		2	4	10	1			2	
	Pardosa nigriceps	56	32	10	2		8					
	Agroeca proxima	9	6		3	1	19			1		
	Dismodicus bifrons	14	4	2	1		9					
C	*Lepthyphantes mengei*	4	4	8		4	13	1			1	
	Xysticus cristatus	9	1	19	2	6	11					
D	*Pardosa amentata*	19	5	42	78	102	89					
	Silometopus elegans	3	1	1	4	12	1					
	Trochosa terricola	3	3	7		3	17			1		

Table 3. Distribution of species trapped in numbers exceeding 19 individuals across Hamsterley sites, based on TWINSPAN output. Letters A to J indicate associations of species.

		ENDGROUP										
		1		2				3			4	
	SPECIES	SITE 1	SITE 5	NCF	CCF90	CCF89	RCF	SITE 6	NOP	ROP	SITE 2	COP
E	*Xysticus sabulosus*			1	2	17						
	Leptothrix hardyi				3	28						
F	*Robertus lividus*	29	6			1	1	5		2		
	Bathyphantes parvulus	1	37		1			12				
G	*Lepthyphantes ericaceus*	1	5	4	7	1	2	1	2			8
	Saaristoa abnormis	7	4	4	1	2	2	3	2	1	4	3
	Walckenaeria cucullata	6	7	22	6	1	17	8	27	12	14	9
	Coelotes atropos		1			4	17			2	9	3
H	*Ceratinella brevipes*	5	4		1	2	1	8	1		1	
	Centromerus dilutus		1	1		2	2	6	2	6	5	
	Lepthyphantes alacris		2	10				20	25	7	9	14
I	*Lepthyphantes zimmermanni*	10	5	25	24	10	9	26	39	25	52	21
J	*Cryphoeca silvicola*	2	1		2		1	2		13	74	4
	Monocephalus fuscipes	23	43	36	21	9	12	49	54	29	101	61
	Tapinocyba pallens	6	18	21	10		15	14	32	16	51	26
	Diplocephalus latifrons			3	18	3	2		70	7	25	24
	Lepthyphantes tenebricola		2	4	5		2	6	42	9	23	22

Table 3. (continued).

these contributed most significantly to the resulting classification, and were the most amenable to statistical analysis. Table 4 gives a summary of the data in Table 3, showing mean catch per site with standard errors, of each species in each of the four Endgroups identified by TWINSPAN.

The letters A to J indicate groups of species which formed associations (i.e. tended to occur together), based on the list of preferentials produced by TWINSPAN at each division.

Associations A to F include those species which TWINSPAN considered more closely associated with Endgroups 1 and 2 as a whole, constituting those species on the ordination diagram, (Fig. 6) with scores less than zero on Axis 1. These species were more consistent, and reached their highest mean catches, at at least one of these Endgroups. Of the 23 species in these associations, 11 did not occur at either Endgroup 3 or 4, and of the remaining species, only *Micrargus herbigradus, Haplodrassus signifer, Lepthyphantes mengei* and *Robertus lividus* occurred at more than one site in either Endgroup 3 or 4. In addition, only two species, *Walckenaeria acuminata* and *Bathyphantes parvulus*, occurred at any Endgroup 3 or 4 site in numbers exceeding five individuals.

However, due to the variation in total catch between Endgroups 1 and 2, and the relatively low numbers involved in some cases, only two of these species, *Xysticus cristatus* (Endgroup 1/Endgroup 2 mean = 8±2.7, Endgroup 3/Endgroup 4 mean = 0, $t_9= 2.7$, $p<0.4$), and *Lepthyphantes mengei* (Endgroup 1/Endgroup 2 mean = 5.5±0.8, Endgroup 3/Endgroup 4 mean = 0.4±0.3, $t_9= 2.5$, $p<0.04$) occurred in significantly

		ENDGROUP			
	SPECIES	1	2	3	4
A	*Clubiona reclusa*	10.8±8	0.25±0.3	0	0.5±0.5
	Cnephalocotes obscurus	38±27	1.8±1.8	0	0
	Drassodes cupreus	5±1	2.8±2.4	0	0
	Pocadicnemis pumila	89.5±38.5	1.3±0.8	1.3±1.3	0
	Minyriolus pusillus	13.5±6.5	0.3±0.3	0.7±0.7	0
	Walckenaeria acuminata	20.5±1.5	2±1.4	0	5±5
B	*Pardosa pullata*	345.5±93.5	53.3±6.2	0.3±0.3	0
	Alopecosa pulverulenta	202±29	64±38.2	0	0
	Gonatium rubens	22.5±3.5	0.8±0.3	0	0
	Micrargus herbigradus	6±2	1.3±0.6	0	2±1
	Haplodrassus signifer	26±18	4±2.2	0.3±0.3	1±1
	Pardosa nigriceps	44±12	5±2.4	0	0
	Agroeca proxima	7.5±1.5	5.8±4.5	0.3±0.3	0
	Dismodicus bifrons	9±5	3±2	0	0
C	*Lepthyphantes mengei*	4±0	6.3±2.8	0.3±0.3	0.5±0.5
	Xysticus cristatus	5±4	9.5±3.7	0	0
D	*Pardosa amentata*	12±7	77.8±12.9	0	0
	Silometopus elegans	2±1	4.5±6	0	0
	Trochosa terricola	3±0	6.8±3.7	0.3±0.3	0
E	*Xysticus sabulosus*	0	8±4	0	0
	Leptothrix hardyi	0	7.8±6.8	0	0
F	*Robertus lividus*	17.5±11.5	0.5±0.3	2.3±1.5	0
	Bathyphantes parvulus	19±18	0.3±0.3	4±4	0
G	*Lepthyphantes ericaceus*	3±2	3.5±1.3	1±0.6	4±4
	Saaristoa abnormis	5.5±1.5	2.3±0.6	2±0.6	3.5±0.5
	Walckenaeria cucullata	6.5±0.5	11.5±4.8	15.7±5.8	11.5±2.5
	Coelotes atropos	0.5±0.5	5.3±4	0.7±0.7	6±3
H	*Ceratinella brevipes*	4.5±0.5	1±0.4	3±2.5	0.5±0.5
	Centromerus dilutus	0.5±0.5	1.3±0.5	4.7±1.3	2.5±2.5
	Lepthyphantes alacris	1±1	2.5±2.5	17.3±5.3	11.5±2.5
I	*Lepthyphantes zimmermanni*	7.5±2.5	17±4.3	30±4.5	36.5±15.5
J	*Cryphoeca silvicola*	1.5±0.5	0.8±0.5	5±4	39±35
	Monocephalus fuscipes	33±10	19.5±6.1	44±7.6	81±20
	Tapinocyba pallens	12±6	11.5±4.4	20.7±5.7	38.5±12.5
	Diplocephalus latifrons	0	6.5±3.8	25.7±22.2	11.5±2.5
	Lepthyphantes tenebricola	1±1	2.8±1.1	19±11.5	22.5±0.5

Table 4. Means (± SE) at each TWINSPAN Endgroup for the 36 species trapped in numbers exceeding 19 individuals, based on Table 3.

greater numbers at Endgroups 1 and 2. This is in addition to the diurnal running spiders *Pardosa amentata, P. pullata* and *Alopecosa pulverulenta*, which were not tested due to their abundance at Endgroup 1 and 2 sites, and their virtual absence from those of Endgroups 3 and 4.

Associations A and B characterised the Endgroup 1 sites, which represented the situation nine years after clear-felling, with their dense and extensive vegetation cover. Association A includes those species which reached their highest mean abundance at this Endgroup, and were trapped at all sites within it. While no species was completely confined to Endgroup 1, *Cnephalocotes obscurus, Clubiona reclusa* and *Minyriolus pusillus* occurred at only one site in Endgroup 2, though the last two species also occurred at one site in either Endgroup 3 or 4, and no species occurred at more than half of the sites in Endgroup 2, though again two species, *Pocadicnemis pumila* and *Walckenaeria acuminata* were trapped at one site each in Endgroups 3 and 4. In the case of the latter, the abundance of this species at COP in Endgroup 4 was the third highest at any site. In addition, *Drassodes cupreus* was most abundant at RCF in Endgroup 2, but was consistent, and had a higher mean catch at Endgroup 1.

Species in association B were again consistent, and had their highest mean catch at Endgroup 1. However, unlike the species in association A, these species tended to be consistent, or virtually so, at Endgroup 2. The diurnal running spiders *Pardosa pullata*, the negative indicator for the first TWINSPAN division, and *Alopecosa pulverulenta*, for instance, occurred at all sites in Endgroups 1 and 2, while all of the remaining species occurred at at least three Endgroup 2 sites. In all but two cases, *Gonatium rubens* and *Micrargus herbigradus*, at least one site involved numbers in excess of five individuals, generally RCF, though *Pardosa nigriceps* also occurred in significant numbers at NCF. In addition, *Agroeca proxima* was most abundant at the Endgroup 2 site RCF.

Association C includes those species which did not show any preference for either Endgroup 1 or 2. *Xysticus cristatus* occurred at all sites within both Endgroups, while reaching its highest mean catch per site at Endgroup 2. *Lepthyphantes mengei* was consistent within Endgroup 1, though the numbers involved were relatively small, and reached its highest mean catch per site at Endgroup 2.

Associations D and E include those species which were more closely linked with the relatively sparsely vegetated Endgroup 2 sites, which represented the period between one and four years after clear-felling. Of the species in association D, two, the positive indicator for the second TWINSPAN division, *Pardosa amentata*, and *Silometopus elegans*, occurred at all sites within both Endgroups 1 and 2, while *Trochosa terricola* was not trapped at CCF90. However, all three species were most abundant at an Endgroup 2 site, and had their highest mean catch here. *Pardosa amentata* in particular was consistently more abundant at Endgroup 2 sites, while *Silometopus elegans* and *Trochosa terricola* were trapped in numbers exceeding five individuals only at Endgroup 2.

Association E includes those species most characteristic of Endgroup 2. *Xysticus sabulosus* and *Leptothrix hardyi* were the only common species confined to a single

Endgroup, though neither species was trapped at all sites in Endgroup 2. *X. sabulosus* was trapped at NCF, CCF90 and CCF89, and *L. hardyi* at CCF90 and CCF89, though both occurred in numbers exceeding five individuals only at CCF89.

Association F consists of species which were weakly associated with the clear-felled and restocked sites as a whole. Both *Robertus lividus* and *Bathyphantes parvulus* were trapped at both Endgroup 1 sites, and had their highest mean catch at this Endgroup. However, both were virtually absent from Endgroup 2, and had a higher mean catch at Endgroup 3, largely due to their occurrence at Site 6. *Bathyphantes parvulus* was trapped in significant numbers only at Site 5 in Endgroup 1, and Site 6 in Endgroup 3.

Association G contains those species which showed no clear preference for either Endgroup 1/Endgroup 2 sites, or Endgroup 3/Endgroup 4 sites, and t-tests on the distribution of these species showed no significant differences between these two groups of sites. Of these species, two, *Saaristoa abnormis* and *Walckenaeria cucullata*, were trapped at all 11 sites, showing the highest mean catches in Endgroups 1 and 3 respectively. *Lepthyphantes ericaceus* occurred at all sites in Endgroups 1 and 2, while reaching its highest mean catch at Endgroup 4, while *Coelotes atropos* was most abundant at the Endgroup 2 site RCF, but was consistently trapped only at Endgroup 4, where it also reached its highest mean catch.

Associations H to J contain those species more closely associated with the plantation/mixed-woodland sites of Endgroups 3 and 4. These sites represented mature habitats, from approximately 20 to 50 years after clear-felling, and were generally characterised by a poorly developed, or absent, vegetation layer, though at the mixed-woodland, Site 6, vegetation density was the fourth highest overall. What is clear is that, while many of these species reach their highest abundance at one of these sites, and/or their highest mean catch at one of these Endgroups, only the positive indicator for the third TWINSPAN division, *Diplocephalus latifrons*, did not occur at all four Endgroups, being absent from Endgroup 1, and only *Ceratinella brevipes, Centromerus dilutus, Cryphoeca silvicola* and *Lepthyphantes tenebricola* did not occur at any Endgroup 1 or 2 site in numbers exceeding five individuals.

Significant differences between mean catch per site for Endgroup 1/Endgroup 2 and Endgroup 3/Endgroup 4 were obtained for *Monocephalus fuscipes* (Endgroup 1/Endgroup 2 mean = 24±5.4, Endgroup 3/Endgroup 4 mean = 58.8±11.8, t_9 = 2.8, $p<0.02$), *Lepthyphantes zimmermanni* (Endgroup 1/Endgroup 2 mean = 13.8±3.5, Endgroup 3/Endgroup 4 mean = 32.6±5.7, t_9 = 2.9, $p<0.02$), *Tapinocyba pallens* (Endgroup 1/Endgroup 2 mean = 11.7±3.2, Endgroup 3/Endgroup 4 mean = 27.8± 6.7, t_9 = 2.3, $p<0.02$), *Lepthyphantes alacris* (Endgroup 1/Endgroup 2 mean = 2±1.6, Endgroup 3/Endgroup 4 mean = 15±3.4, t_9 = 3.7, $p<0.01$) and *L. tenebricola* (Endgroup 1/Endgroup 2 mean = 2.2±0.8, Endgroup 3/Endgroup 4 mean = 20.4±6.3, t_9 = 3.1, $p<0.02$).

Association H includes those species which were most characteristic of Endgroup 3. The negative indicator for the third TWINSPAN division, *Lepthyphantes alacris*, is included in this association for convenience, despite the fact that TWINSPAN considered this species more strongly associated with the wooded sites as a whole than any other. This species was trapped at all Endgroup 3 and 4 sites, but reached its highest mean catch at Endgroup 3. In addition, this species was trapped at one site in each of Endgroups 1 and 2, but only exceeded five individuals at NCF in the latter. *Centromerus dilutus* occurred consistently at only Endgroup 3, where it also reached its highest mean catch, and indeed, was not trapped in numbers exceeding five individuals outside this Endgroup. *Ceratinella brevipes* was consistent at only Endgroup 1, and reached its highest mean catch here, though it occurred in the greatest numbers at Site 6, the only site at which it exceeded five individuals.

Association I contains a single species, *Lepthyphantes zimmermanni*, which showed no preference for either Endgroup 3 or 4. This species was trapped at all sites sampled, and occurred in numbers exceeding five individuals at every site with the exception of Site 5 in Endgroup 1, though it was trapped in the greatest numbers at Site 2 in Endgroup 4, also reaching its highest mean catch at this Endgroup.

Association J contains those species which TWINSPAN considered most characteristic of Endgroup 4. All five species occurred consistently at the sites of this Endgroup, though in the case of *Cryphoeca silvicola* numbers were low at COP. *Lepthyphantes tenebricola*, *Cryphoeca silvicola*, *Tapinocyba pallens* and *Monocephalus fuscipes* all reached their highest mean catch at this Endgroup. *Diplocephalus latifrons* was trapped in the greatest numbers at NOP in Endgroup 3, where it also reached its highest mean catch, though it was not consistent at this Endgroup.

4.2.3. The relationship between the classification of Hamsterley sites and their position on the successional gradient.

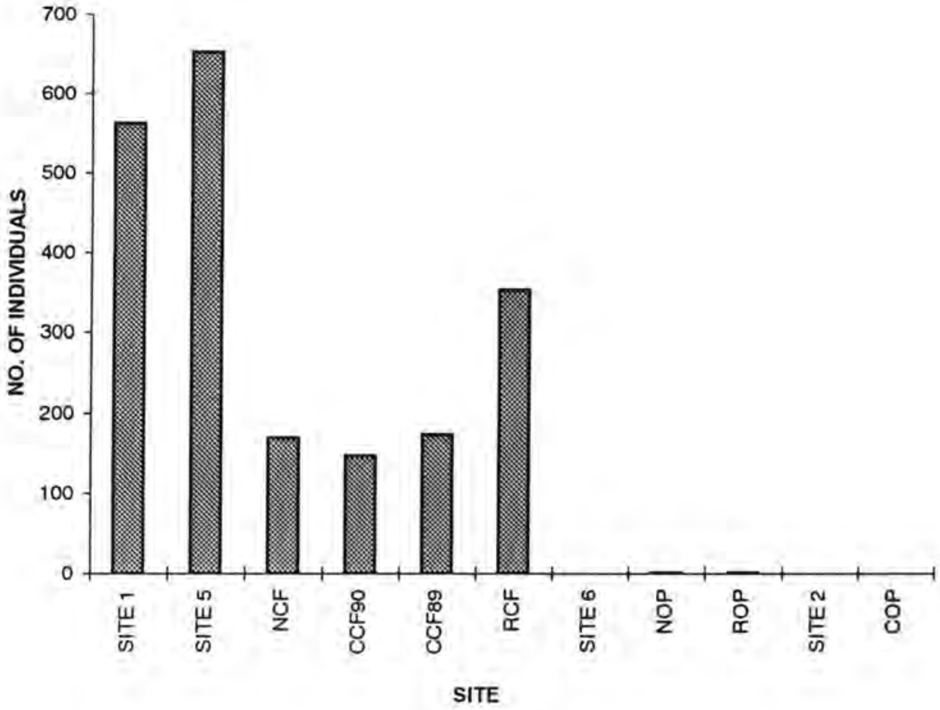
The classification of the Hamsterley sites by TWINSPAN reflected to some extent their relative positions on the successional gradient. Hence the relatively sparsely vegetated clear-felled sites, representing years one to four of succession, were grouped in Endgroup 2, while the restocked sites, which represented the ninth year and had a dense and extensive vegetation layer, were grouped in Endgroup 1. However, while the plantations and the mixed-woodland, representing years 21 to 52 of succession, were separated from Endgroups 1 and 2 in the first TWINSPAN division, paralleling their separation on the ordination diagram (Fig. 5), the separation of these sites into Endgroups 3 and 4 did not conform to their position on the successional gradient, though a consideration of the data shows that there was very little difference between them in terms of their common species. In addition the inclusion of Site 6 in Endgroup 3 highlights the similarity of its fauna to those of the plantation sites. This is despite the fact that, in contrast to these sites, it had a shallow litter layer and dense vegetation, again suggesting that tree cover was an important factor influencing the structure of spider communities at Hamsterley. However, the occurrence at Site 6 of species such as *Pocadicnemis pumila, Minyriolus pusillus, Robertus lividus*, and particularly *Bathyphantes parvulus*, which were most abundant at Endgroup 1, confirms the implication of the ordination that Site 6 had some species in common with the more open sites.

4.3. Distribution of the six major spider guilds across Hamsterley sites.

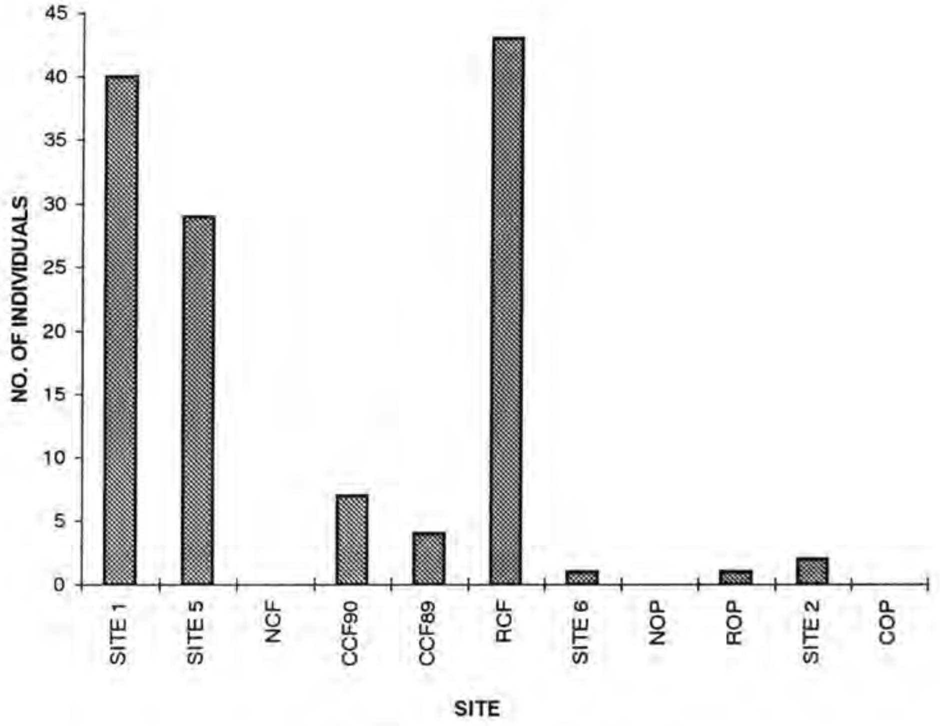
Fig. 9 shows the distribution of individuals across the 11 sites for each of the six major guilds. A major guild in this case was defined as one which contained at least one of the common species included in Table 3.

(a) Diurnal running spiders.

The diurnal running spiders (Fig. 9a), were trapped in significantly greater numbers at the clear-felled/restocked sites of Endgroups 1 and 2 (Endgroup 1/Endgroup 2 mean = 343±89.5, Endgroup 3/Endgroup 4 mean = 0.4±0.2, $t_9 = 3.5$, $p<0.01$), with the greatest numbers caught at the Endgroup 1 sites, particularly Site 5 (652), and RCF in Endgroup 2 (353). Table 5 shows the contribution of each major guild to the catch at each site. At the clear-felled sites. the diurnal running spiders were caught in greater numbers than any other single guild, and at all of these sites, with the exception of NCF (46.8%), accounted for over half of all individuals trapped. The highest percentage was that at RCF (65.1%), followed by the Endgroup 1 sites, Site 5 and Site 1 (61.5% and 58.1% respectively). Values at the remaining sites were 56.1% (CCF89), 50.2% (CCF90) and 46.8% (NCF). Table 6 shows the contribution of each family to the total number of species at each site, while Table 7 gives the mean numbers of species for the major guilds in each of the TWINSPAN Endgroups based on Table 6. It is apparent that, though the diurnal running spiders were trapped in large numbers at the above sites, the number of species involved was relatively small.

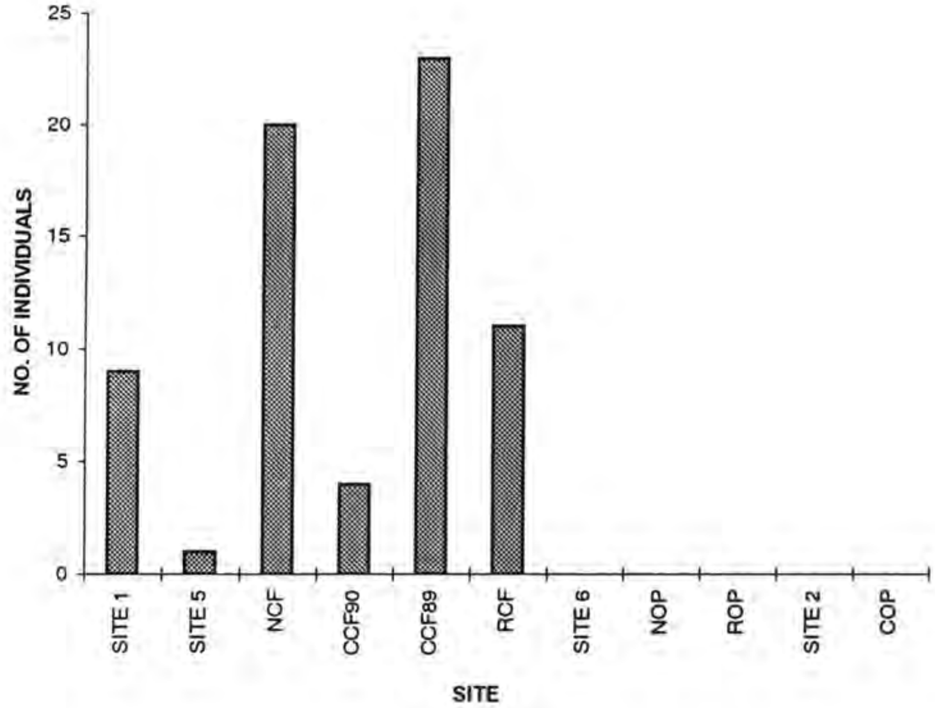


a) Diurnal running spiders.

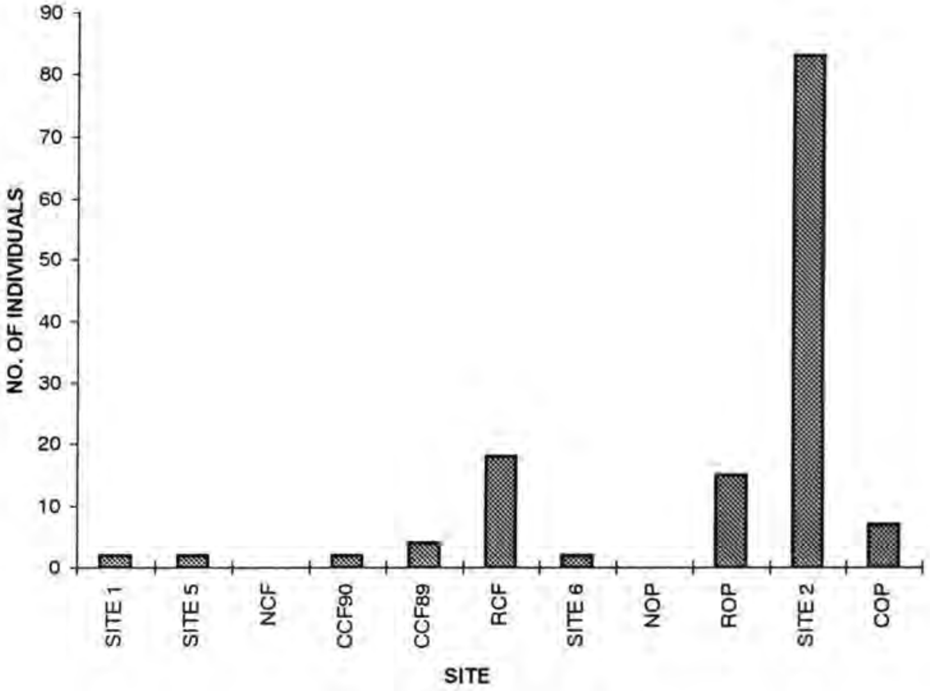


b) Nocturnal running spiders.

Fig. 9. Distribution of individuals between sites for the six major spider guilds identified at Hamsterley.

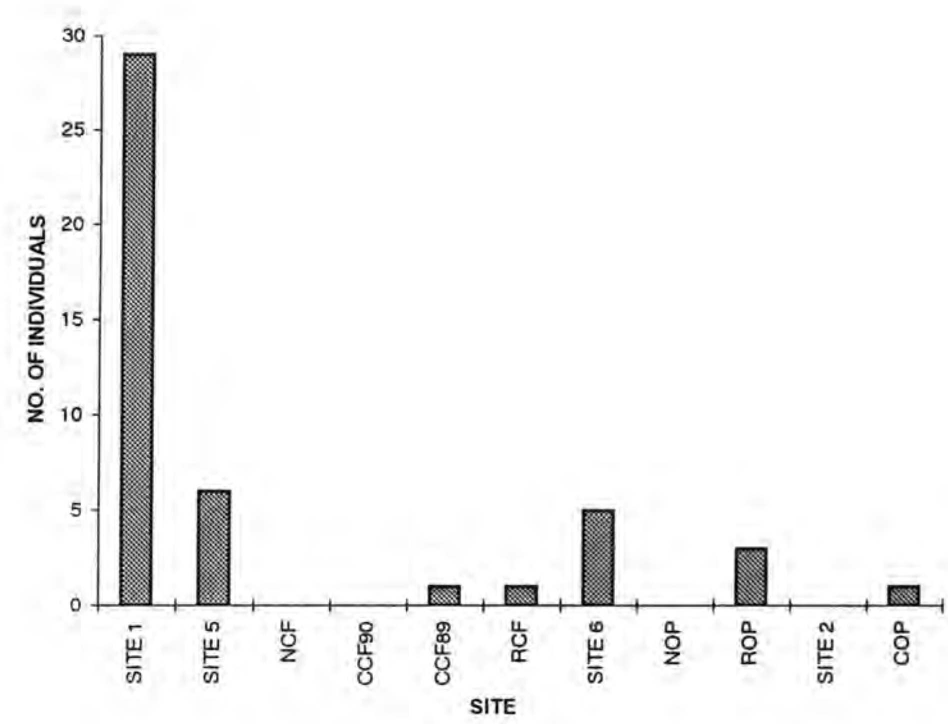


c) Ambushers.

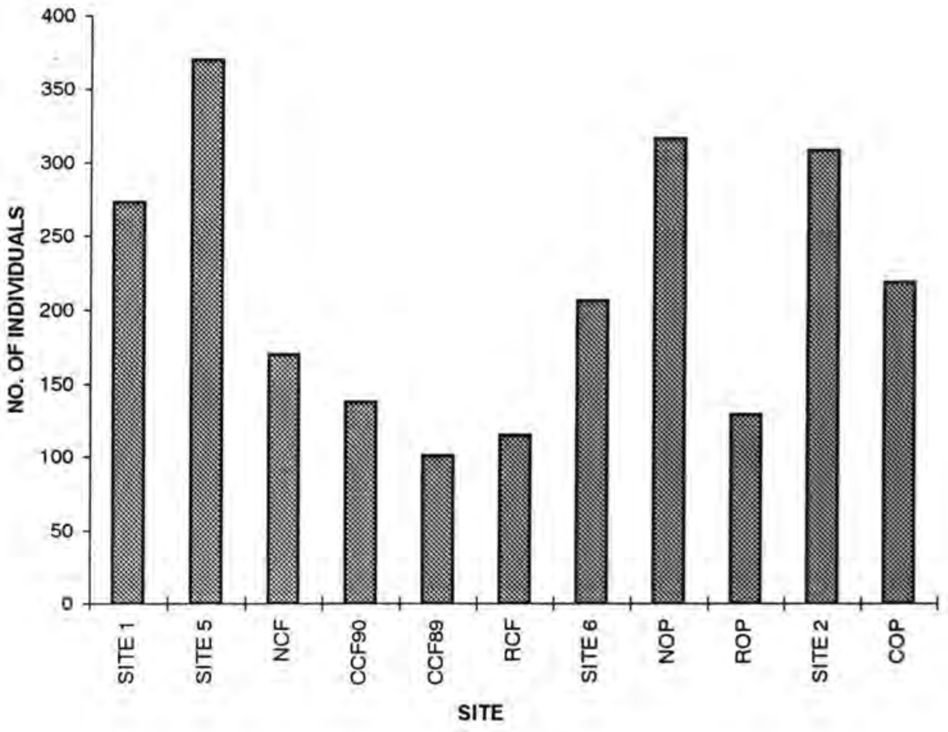


d) Funnel web spiders.

Fig. 9. Distribution of individuals between sites for the six major spider guilds identified at Hamsterley.



e) Scattered line weavers.



f) Sheet web weavers.

Fig. 9. Distribution of individuals between sites for the six major spider guilds identified at Hamsterley.

	ENDGROUP										
	1		2				3			4	
GUILD	Site 1	Site 5	NCF	CCF90	CCF89	RCF	Site 6	NOP	ROP	Site 2	COP
Diurnal running spiders	58.1	61.5	46.8	50.2	56.1	65.1	0	0.3	0.7	0	0
Nocturnal running spiders	9.3	2.7	0	2.4	1.6	7.9	0.5	0	0.7	0.5	0
Ambushers	0.9	0.1	5.5	1.4	7.4	2.0	0	0	0	0	0
Funnel web spiders	0.2	0.2	0	0.7	1.3	3.3	0.9	0	10.1	20.5	3.1
Scattered line weavers	3.0	0.6	0	0	0.3	0.2	2.3	0	2.0	0	0.4
Sheet web spinners	28.2	34.9	46.8	45.4	32.6	21.2	95.8	99.7	86.6	76.1	96.0

Table 5. Percentage contribution of each major guild to the catch at each site, showing TWINSPAN Endgroups.

	ENDGROUP										
	1		2				3			4	
GUILD	Site 1	Site 5	NCF	CCF90	CCF89	RCF	Site 6	NOP	ROP	Site 2	COP
Diurnal Running Spiders	6	5	6	5	5	6	0	1	1	0	0
Nocturnal Running Spiders	7	7	0	4	2	6	1	0	1	1	0
Ambushers	1	1	2	2	2	1	0	0	0	0	0
Funnel web spiders	1	1	0	1	1	2	1	0	2	2	2
Scattered line weavers	1	1	0	0	1	1	1	0	2	0	1
Sheet web weavers	32	30	26	29	27	27	30	21	18	24	19

Table 6. Contribution of each guild to the total number of species at each site, showing TWINSPAN Endgroups.

	ENDGROUP			
GUILD	1	2	3	4
Diurnal Running Spiders	5.5±0.5	5.5±0.3	0.7±0.3	0
Nocturnal Running Spiders	7±0	3±1.3	0.7±0.3	0.5±0.5
Ambushers	1±0	1.75±0.3	0	0
Funnel web spiders	1±0	1±0.4	1±0.6	2±0
Scattered line weavers	1±0	0.5±0.3	1±0.6	0.5±0.5
Sheet web weavers	31±1	27.3±0.6	23±3.6	21.5±2.5

Table 7. Mean number of species (± SE) for the major guilds at each TWINSPAN Endgroup.

Despite their dominance at the Endgroup 1 sites in terms of abundance, in terms of mean number of species (Table 7) the diurnal running spiders were only the third most important guild after the sheet web weavers and nocturnal running at this Endgroup, while at Endgroup 2, only the sheet web weavers were more important in this respect.

(b) Nocturnal running spiders.

Like the diurnal running spiders, the nocturnal running spiders (Fig. 9b) were trapped in significantly greater numbers at the Endgroup 1/Endgroup 2 sites than at the Endgroup 3/Endgroup 4 sites (Endgroup 1/Endgroup 2 mean = 20.5±7.8, Endgroup 3/Endgroup 4 mean = 0.8±0.4, $t_9 = 2.9$, $p<0.05$), with peaks at Site 1 (40), Site 5 (29), and particularly RCF (43). On the sites where they occurred, members of this guild were often the third most numerous group in terms of number of individuals trapped (Table 5), though never approaching the sheet web weavers or diurnal running spiders in this respect. The highest contribution of this guild to the total catch occurred at Site 1 (9.3%), followed by RCF (7.9%), Site 5 (2.7%), CCF90 (2.4%), CCF89 (1.6%), ROP (0.7%), Site 2 (0.5%) and Site 6 (0.5%), again emphasising the preference for clear-felled/restocked sites. The number of species of this guild trapped at each site (Table 6), closely reflects the above sequence, with the highest numbers found at Site 1 (7), Site 5 (7) and RCF (6), followed by CCF90 (4), CCF89 (2), ROP, Site 2 and Site 6 (all with 1). At the first three of these sites, this guild represented the second most abundant guild in terms of numbers of species. In terms of mean number of species (Table 7), this guild was most abundant at Endgroup 1, where it was the second most important guild in this respect.

(c) Ambushers.

Fig. 9c shows the distribution of individuals belonging to the ambushers. As with the previous guild, the ambushers showed a preference for the Endgroup 1/Endgroup 2 sites (Endgroup 1/Endgroup 2 mean = 11.3±7.8, Endgroup 3/Endgroup 4 mean = 0, t_9 = 2.9, $p<0.02$), and were trapped in the greatest numbers at CCF89 (23), NCF (20) and RCF (11) in Endgroup 2. In general the contribution of this guild to the total catch was low (Table 5). However, at CCF89 (7.4% of all individuals at this site) and NCF (5.5%), this was the third most abundant guild after the sheet web weavers and diurnal running spiders. Values at the remaining sites were; RCF (2.0%), CCF90 (1.4%), Site 1 (0.9%) and Site 5 (0.1%). As with number of individuals, number of species (Table 6) was low, though at NCF and CCF89 this guild was the third most important in this respect due to the presence of *X. sabulosus*. The generally low number of species involved is reflected in the low mean species per Endgroup (Table 7), and even at Endgroups 1 and 2, this guild was only the fourth most important overall in this respect.

(d) Funnel web spiders.

Fig. 9d shows the distribution of the funnel web spiders. Peaks occur at Site 2 (83), RCF (18) and ROP (15), though overall the numbers involved are small. Of these, that at Site 2 is largely due to the presence of *Cryphoeca silvicola* (Table 3), while at RCF *Coelotes atropos* is the main species. Overall the distribution shows a preference for the wooded sites, though this difference is not significant (Endgroup 1/Endgroup 2 mean = 4.7±2.7, Endgroup 3/Endgroup 4 mean = 21.4±15.6, t_9 = 0.84, $p > 0.4$). This largely reflects the distribution of *C. silvicola,* which accounted for 73.3% of all individuals of this guild trapped, and at Site 2, COP and ROP, this was the second most abundant guild after the sheet-line weavers (Table 5), largely due to the abundance of this species at these sites. In terms of number of species (Table 6) the contribution of this guild was low, with the highest mean number of species (Table 7) at Endgroup 4. Despite this, at all sites in Endgroups 3 and 4, with the exception of NOP, this was the second most important guild after the sheet web weavers in this respect.

(e) Scattered line weavers.

Fig. 9e shows the distribution of the scattered line weavers. *Robertus lividus* was the only species of this guild trapped in significant numbers during this study, and hence the data largely reflects the distribution of this species between sites (Table 3), with 63.0% of all guild members trapped at Site 1 (29) and the remainder being sparsely distributed over both open and wooded sites. The contribution of the scattered line weavers to the catch at each site was generally low (Table 5), though at the two sites with the lowest catch in terms of numbers of individuals, Site 6 (2.3%) and ROP (2.0%), this guild was second and third respectively in terms of abundance. The greatest contribution of this guild to overall number of individuals was at Site 1 (3.0%), due to the abundance of *R. lividus*. In terms of numbers of species (Table 6), the contribution of this guild to the community was generally low, and mean number of species (Table 7) never exceeded one. However, at Site 6 and ROP, this was the second most important guild in this respect.

(f) Sheet web weavers.

Taken as a guild, the sheet web weavers show little in the way of preference for either open or wooded sites (Endgroup 1/Endgroup 2 mean = 194.5±43.1, Endgroup 3/Endgroup 4 mean = 235.4±34.8, t_9 = 0.7, p>0.2). Fig. 9f shows that significant numbers of this guild occurred at all sites, but with peaks at Site 5 (370), NOP (316), Site 2 (308) and Site 1 (273). Table 5 shows that the contribution of this guild to the total number of individuals caught was consistently high, and at Endgroups 3 and 4 the sheet web weavers were the most abundant guild, with values ranging from 76.1% (Site 2) to 99.7% (NOP). At Endgroup 1 and 2 sites, this was generally the second most abundant guild, with values ranging from 21.2% (RCF) to 46.8% (NCF). In this latter case, this was the dominant guild in this respect along with the diurnal running spiders. In terms of number of species (Table 6), this guild was the most abundant at all sites, with values ranging from 18 (ROP) to 32 (Site 1). Number of species was generally higher at Endgroups 1 and 2, particularly the former, and this is reflected in the higher means for these Endgroups (Table 7), though the mixed-woodland, Site 6, had the second highest value overall.

It is apparent that not all of the guilds defined in this study were equally sensitive in responding to changes in the environment along the successional gradient. At one extreme, the scattered line weavers were largely represented by one species, *Robertus* *lividus*, and the observed pattern was therefore likely due to its particular habitat requirements. At the other end of the spectrum, the sheet web weavers were represented by more than 70 species, and this guild as a whole appeared to be relatively insensitive to changes along the successional gradient, as the large number of different lifestyles and habitat requirements involved obscured any picture which may have been gained using a smaller and/or more heterogeneous group of species. However, subsets of this guild did show patterns of distribution which could be linked to successional change, particularly those species most typical of Endgroups 3 and 4. The most useful guilds in identifying broad changes along the gradient were the diurnal and nocturnal running spiders. The absence of the former from Endgroups 3 and 4, and their ubiquity at Endgroups 1 and 2, suggests some link with the closing of the canopy, while the increased evidence of the latter at Endgroup 1 implies that the increased vegetation complexity at these sites may be important to this guild.

4.4. Diversity and species abundance.

4.4.1. Diversity indices.

4.4.1.1. Ranking of sites.

Table 8 gives the values for species richness and abundance at each of the 11 Hamsterley sites, with the values of the four indices calculated.

Site	No. of Individuals	No. of Species	Log Series α	Margalef Index	Reciprocal Berger-parker	Reciprocal Simpson
Site 1	968	50	11.18	7.13	3.85	7.12
Site 5	1060	45	9.53	6.32	2.42	4.59
NCF	363	37	10.31	6.28	5.42	11.95
CCF90	293	41	12.97	7.04	3.76	8.94
CCF89	310	39	11.80	6.62	3.04	6.73
RCF	542	44	11.31	6.83	3.05	6.50
Site 6	215	34	11.37	6.15	4.39	11.19
NOP	317	22	5.37	3.65	4.53	7.57
ROP	149	24	8.09	4.60	5.13	10.19
Site 2	405	30	7.48	4.83	4.02	7.34
COP	227	23	6.70	4.23	3.72	8.23

Table 8. Species richness and abundance data for each of the 11 Hamsterley sites, with the values of the four diversity indices calculated.

(1) Log series α.

Values for the log series α ranged from 5.37 (NOP), to 12.97 (CCF90). Endgroup 1 and 2 sites had higher α values (i.e. were more diverse) than plantation sites, though Site 6, the mixed-woodland, had the third highest α value overall (11.37). Within Endgroups 1 and 2, the highest α values were attained by CCF90, CCF89 (11.80) and RCF (11.31). Index values for Site 1 and Site 5 were 11.18 and 9.53 respectively, straddling that of the Endgroup 2 site NCF (10.31). The most diverse of the plantation sites with this index was ROP (8.09) followed by Site 2 (7.48), COP (6.70) and NOP (5.37).

(2) Margalef index.

Overall values of this index ranged from 3.65 (NOP) to 7.13 (Site 1), and as with the log series α, Endgroup 1 and 2 sites were more diverse than the plantations. In the case of Site 6, however, the value obtained using the Margalef index (6.15) was lower than those of the clear-felled and restocked sites. After Site 1 the most diverse site using this index was CCF90 (7.04), followed by RCF (6.83), CCF89 (6.62), Site 5 (6.32) and NCF (6.28). Of the Endgroup 3 and 4 sites, Site 6 (6.15) had the highest index value, followed by Site 2 (4.83) and ROP (4.60). Again, the lowest index values were those of the plantation sites COP (4.23) and NOP (3.65).

(3) Berger-Parker Dominance index

Reflecting as it does the dominance/eveness component of the species abundance data, the ranking of Hamsterley sites based on this index differed markedly from those obtained using the log series α and Margalef indices. Values of the reciprocal of this index ranged from 5.42 (NCF) to 2.42 (Site 5), higher values indicating a higher eveness, and therefore diversity. Generally Endgroup 3 and 4 sites had higher rankings using this index, though NCF had the highest value and COP (3.72) the fourth lowest.

(4) Simpson index.

Values of the reciprocal of this index ranged from 11.95 (NCF) to 4.59 (Site 5). In general, Endgroup 3 and 4 sites were more diverse using this index, though NCF and CCF90, representing the earliest stages of succession, were ranked first and fourth respectively. Of the Endgroup 3 and 4 sites, the most diverse with this index was the mixed-woodland, Site 6, while the least diverse was the oldest of the plantations, Site 2.

4.4.1.2. Correlation between indices.

Table 9 gives the results of comparisons between the site rankings produced by each of the variables in Table 8 using Spearman's rank correlation coefficient. Species richness was significantly correlated with all other variables with the exception of the reciprocal Simpson index, the strongest correlation being with the Margalef index ($p<0.01$). In contrast, number of individuals showed significant correlation only with

Variable	Abundance	Log series α	Margalef index	Berger-Parker index	Simpson index
Species richness	+	+	++	-	N.S.
Abundance		N.S.	N.S.	N.S.	-
log series α			++	N.S.	N.S.
Margalef index				N.S.	N.S.
Berger-Parker index					--

Table 9. Probabilities and direction of correlation obtained from comparisons between species richness, abundance and four diversity indices using Spearman's Rank Correlation Coefficient. +,- p <0.05, ++,-- p <0.01, N.S. = not significant.

the reciprocal Simpson index ($p<0.05$). Amongst the diversity indices, the species richness indices showed a strong positive correlation with each other ($p<0.01$), as did the dominance/eveness indices at the same level. However, indices from one group did not show any significant correlation with indices from the other.

Previous studies have shown that diversity indices are often correlated (Magurran, 1988). Goodman (1975), studying the behaviour of a range of diversity indices, found that rankings produced by species richness indices were closely correlated, while the same was true for eveness/dominance indices, though the rankings produced by the two groups of indices were different. Magurran (1981) observed a similar relationship between indices derived from light trap data in Irish woodlands. In general, this study is in agreement with these results, the two groups of indices producing different rankings, but with the indices within each group closely correlated. However, where the results differ from those of Goodman (1975) and Magurran (1981) is in the significant negative correlation between the ranking produced by the reciprocal of the Berger-Parker index, and that produced by species richness.

4.4.1.3. The use of pitfall trap data in relation to the calculation of diversity indices.

While pitfall trapping has been shown to be a useful method for surveying invertebrate populations, caution must be observed when using data derived from this method of sampling to calculate diversity indices. The assumption when calculating indices of this nature from species abundance data is that the resulting value is a representation of some aspect of the diversity of the physical habitat, manifested in the sampled fauna

(Bullock, 1971). However, Topping & Sunderland (1992) have shown that pitfall trap catches do not give a true representation of the relative abundance of species in the sampled community, due to the fact that the catch size of individual species is influenced by a range of factors which are independent of the actual abundance of the species (e.g. Tretzel, 1954; Duffey, 1956; Baars, 1979; Chiverton, 1984). However, in the current study the use of diversity indices with pitfall data has been retained, as it is the opinion of the author that, as long as the factors which affect the catch are appreciated, useful comparisons may still be made using indices of this nature.

4.4.1.4. The performance of individual diversity indices with the Hamsterley data.

One of the factors which can effect the catch of a species in pitfall traps is activity rate (Tretzel, 1954; Heydemann, 1961). Relatively active species are more likely to encounter a trap than sedentary forms, and hence the numbers of the former are likely to be overestimated, and the latter underestimated, relative to each other. Bearing this in mind, it would seem logical to assume that those indices based on species richness would be more satisfactory than those based on the dominance/eveness component of diversity when used in conjunction with species abundance data derived from pitfall traps, as both the Berger-Parker and Simpson indices are heavily influence by the abundance of the commonest species (Southwood, 1978; Magurran, 1988). In this study both of these indices tended to give low values for Endgroup 1 and 2 sites, such as CCF89, RCF and Site 5, which were each dominated by one species of diurnal running spider, which are active hunters and overestimated by pitfall trapping (Delchev & Kajak, 1974). This is particularly pronounced in the case of the Berger-Parker index, which is reliant only on the ratio of the abundance of the commonest species to total abundance, and as the Endgroup 1 and 2 sites were also the most species rich, this accounts for the significant negative correlation between the ranking produced by this index and that produced by species richness. While the Simpson index is not so dependent on the abundance of the commonest species for its calculation, this effect is still apparent in the ranking produced using this method, though it is not as pronounced as with the Berger-Parker index. Hence the three lowest ranked sites with the Simpson index were Site 5, RCF and CCF90 which were three of the most species rich sites in this study.

The log series α is one of the most widely used diversity measures, and Southwood (1978) considered it an excellent candidate for a universal diversity statistic. It is relatively easy to calculate, has good discriminant ability, and is less affected by the abundance of the commonest species than other popular indices (Magurran, 1988). However, Butterfield & Coulson (1983) found that the log series α underestimated the diversity of large samples, and overestimated that of small samples, and in the current study, while the ranking produced by this index was not significantly correlated with number of individuals, the relatively low ranking of Site 5, and relatively high ranking of Site 6, did seem to be manifestations of this problem. In the case of Site 6, the low catch at this site may well have been due to the sedentary nature of the species making up its community, coupled with the high vegetation density. The high catch at Site 5 was largely due to the abundance of the diurnal running spider *Pardosa pullata*, which made up over 40% of the catch at this site. This species occurred at all Endgroup 1 and 2 sites, but was most closely associated with Endgroup 1. As this species was likely already abundant at this site, the low vegetation density in relation to Site 1 may have resulted in a higher catch, and hence the relatively low diversity of this site may be attributable, at least in part, to the trapping method.

The Margalef index was the most satisfactory of the four diversity measures evaluated in this study. Based as it is on the species richness component of the data, this index did not suffer to the same extent as the Berger-Parker and Simpson indices from the problems caused by the effect of differential activity rates on the catches of individual species. Neither did it appear as prone to the effects of both large and small N values which influenced the log series α, though the relatively low ranking for Site 5 using this index was perhaps attributable to this effect.

4.4.2. Species abundance models.

4.4.2.1. Log abundance on rank plots.

Fig. 10 shows log abundance on rank plots for the 11 Hamsterley Forest sites. The shallowest curves, and hence the most equitable distributions, are those of the Endgroup 1 sites (Sites 1 and 5), while the steepest curve is that of the plantation site NOP, and it is clear from this figure that, in general, the Endgroup 1 and 2 sites had a more even distribution of abundance than Endgroups 3 and 4. However, it is difficult to discern trends in eveness within each of these groups from this figure. Figs. 11 and 12 show plots for these sites based on the first TWINSPAN division. Fig. 11 suggests that there was a general increase in eveness throughout the period represented by

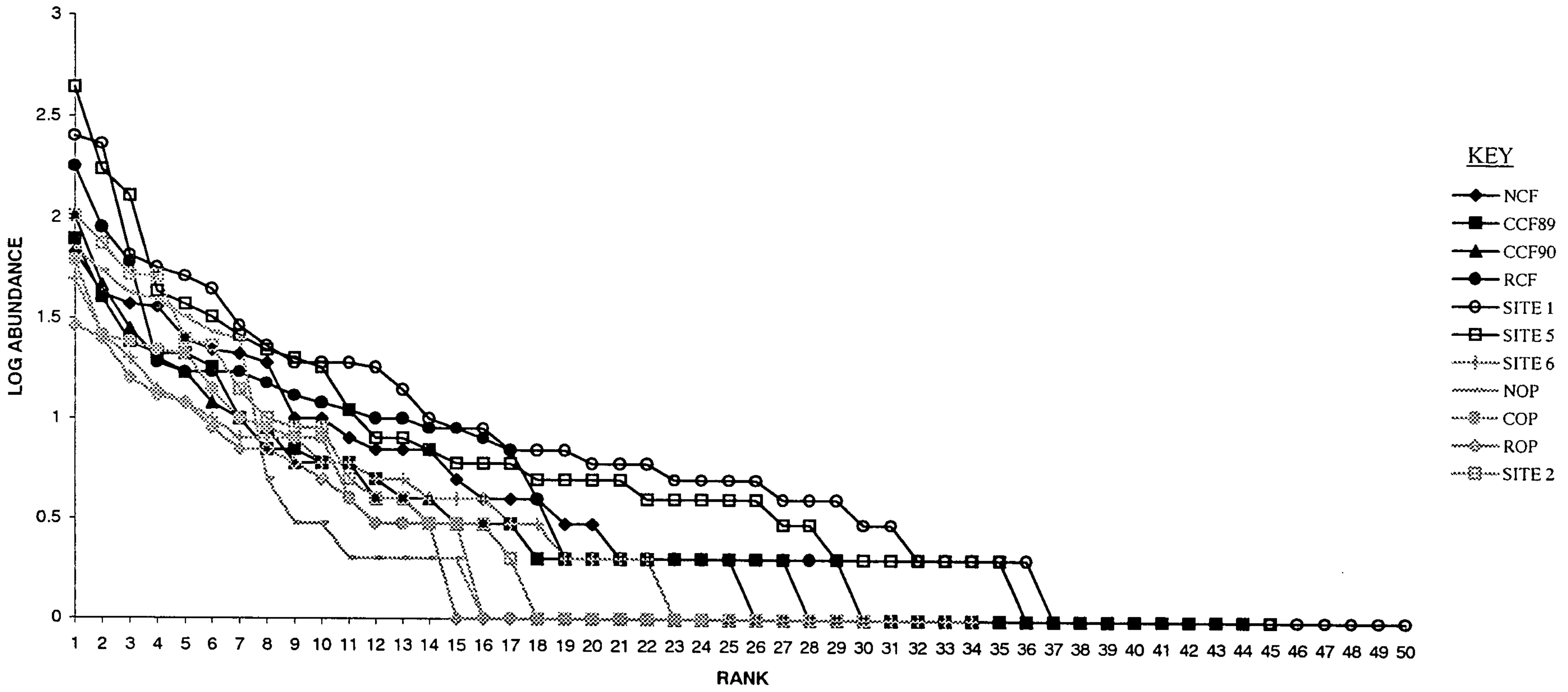


Fig. 10. Plot of log abundance against rank for the 11 Hamsterley Forest sites.

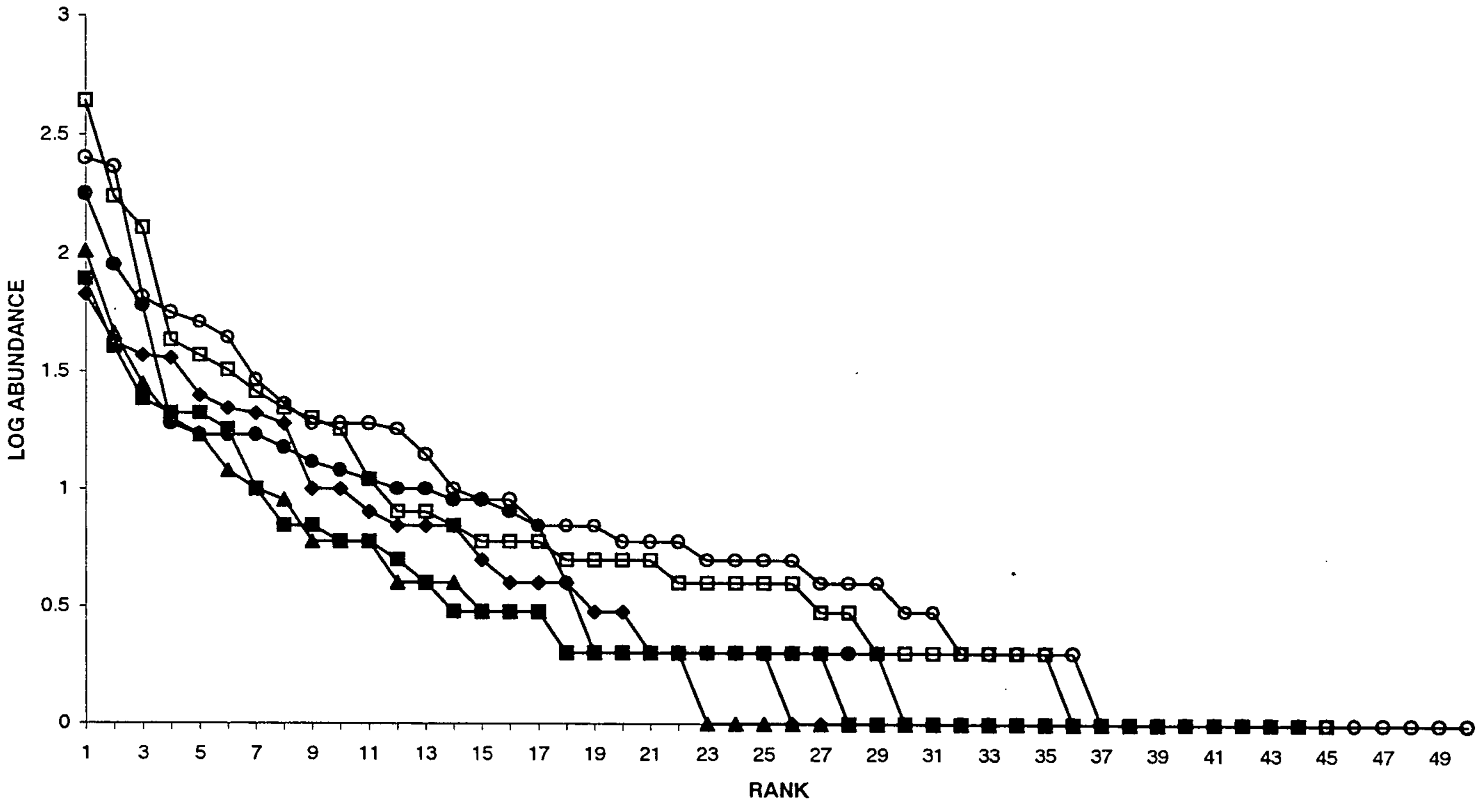


Fig. 11. Plot of log abundance against rank for Endgroup 1 and 2 sites. Symbols as for Fig. 10.

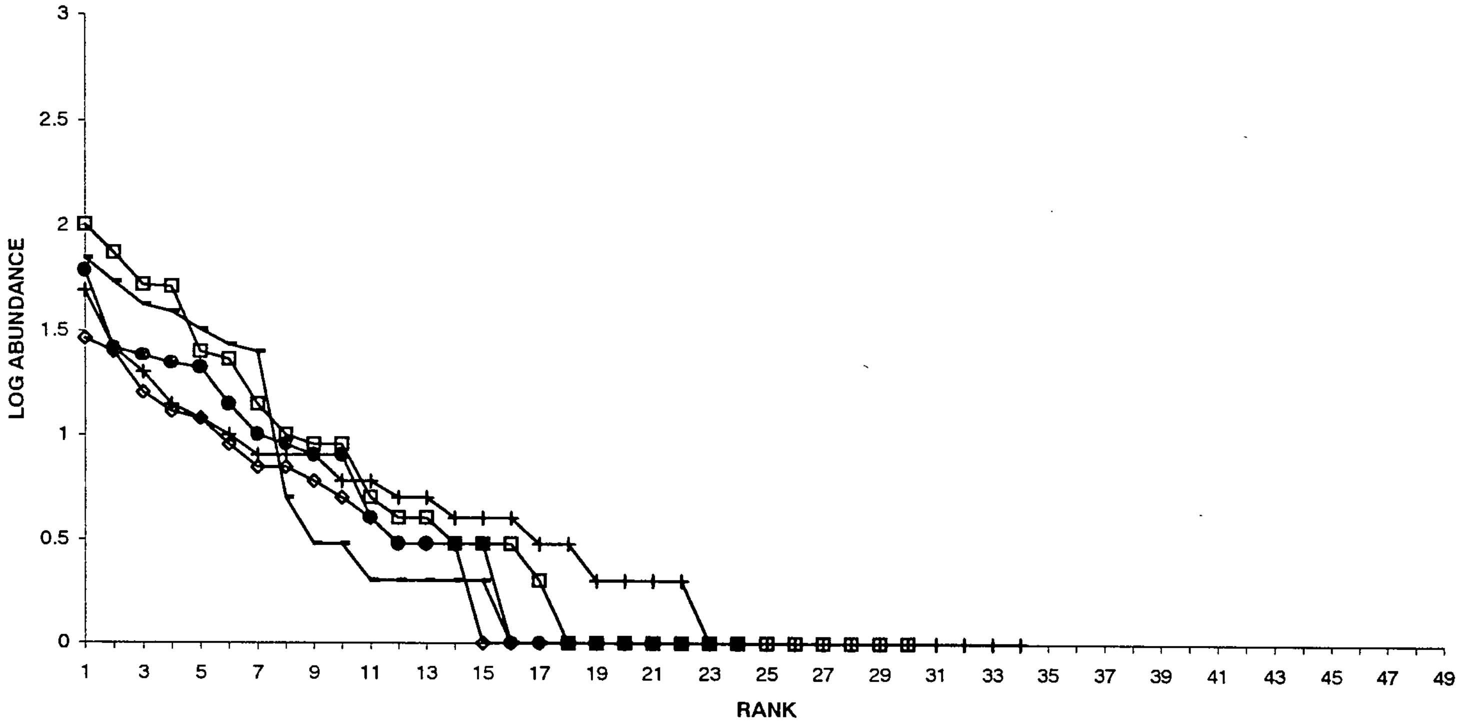


Fig. 12. Plot of log abundance against rank for Endgroup 3 and 4 sites. Symbols as for Fig. 10. Scaling is the same as that for Fig. 11 to allow comparison.

Endgroups 1 and 2, though NCF appears to be slightly more even than CCF89 and CCF90. Fig. 12 shows that, while Endgroup 3 and 4 sites were generally less even than Endgroup 2 sites with the exception of RCF, in terms of the plantation sites, there appears to be no pattern in eveness related to successional age, as after NOP, the site with the least even distribution of abundance appears to be Site 2.

4.4.2.2. Performance of individual species abundance models with the Hamsterley data.

Table 10 gives χ^2 values, degrees-of-freedom and probabilities for the fit of each of the four models to the observed species abundance data at the 11 Hamsterley sites. Graphical representations of these results can be found in Appendix 3. The null hypothesis for χ^2 in each case was that there was no difference between the values predicted by these models, and those observed in the species abundance data.

The least satisfactory of the four models tested was MacArthur's broken stick, which did not adequately describe the observed species abundance data at any of the 11 sites, and at all sites with the exception of Site 6 provided the poorest description. The geometric series performed marginally better, providing an adequate description of the data at COP, and the best description at ROP along with the log series. However, at the remaining sites it furnished the poorest description of the observed data, and overall its performance was inadequate. The two remaining models, the log series and truncated log normal, performed fairly well with the data. However, of the two, the

SITE	GEOMETRIC SERIES			LOG SERIES			TRUNCATED LOG NORMAL			MACARTHUR'S BROKEN STICK		
	χ^2	d.f.	p	χ^2	d.f.	p	χ^2	d.f.	p	χ^2	d.f.	p
SITE 1	791.2	49	<0.001	7.3	8	<0.9>0.5	5.8	6	<0.5>0.1	132.8	8	<0.001
SITE 5	1365.8	44	<0.001	12.1	8	<0.5>0.1	6.2	5	<0.5>0.1	76.5	7	<0.001
NCF	67.4	36	<0.001	4.4	6	<0.9>0.5	3.5	4	<0.5>0.1	127.6	7	<0.001
CCF90	195.9	40	<0.001	8.5	6	<0.5>0.1	5.5	4	<0.5>0.1	43.3	6	<0.001
CCF89	290.1	38	<0.001	5.4	6	<0.5>0.1	1.5	4	<0.9>0.5	38.3	6	<0.001
RCF	517.8	43	<0.001	17.6	7	<0.0.5>0.01	12.4	5	<0.05>0.01	81.8	7	<0.001
SITE 6	63.6	33	<0.001	1.0	5	>0.9	0.8	3	<0.9>0.5	16.6	6	<0.05>0.01
NOP	47.0	21	<0.001	7.9	6	<0.5>0.1	9.0	4	<0.1>0.05	41.6	6	<0.001
ROP	18.7	23	<0.9>0.5	3.6	5	<0.9>0.5	4.8	3	<0.5>0.1	13.6	6	<0.05>0.01
SITE 2	129.6	29	<0.001	6.3	7	<0.9>0.5	2.7	4	<0.9>0.5	52.7	7	<0.001
COP	30.4	22	<0.5>0.1	3.2	6	<0.9>0.5	4.2	4	<0.5>0.1	11.8	6	<0.1>0.05

Table 10. Chi-square values, degrees-of-freedom and probabilities for the fit of four species abundance models to the data at each site. Underlined p values indicate the best fit to the observed data at each site.

log series was more satisfactory, as it performed more consistently, providing the best fit to the observed data at 10 of the 11 sites, and at all sites with the exception of CCF89 furnished a fit to the observed data at least as good as that of the truncated log normal.

4.4.2.3. The suitability of goodness-of-fit tests for assessing the fit of species abundance models.

The inability of goodness-of-fit tests to give a clear distinction between different species abundance models has lead to criticism of this method, and some authors, (e.g. Lambshead & Platt, 1985; Hughes, 1986), have recommended inspection of the graphical data alone (Magurran, 1988). However, the use of this method is retained here, as Magurran (1988) considered that interpretation of results in terms of both goodness-of-fit tests and the shape of the species abundance data would in virtually all cases provide the best solution to the problem.

4.4.2.4. The relative merits of the four species abundance models in relation to their performance with the Hamsterley data.

Though species abundance data can be described by one or more of a family of distributions (Pielou, 1975), it is usually examined in relation to the four models used in this study (Magurran, 1988). These four distributions represent a sequence from the geometric series, with a few dominant species, to MacArthur's broken stick, where the abundance of the species making up the community is more or less equal (Magurran, 1988).

In terms of theoretical derivation, the geometric series, log series and broken stick distributions arise mainly from consideration of relatively simple systems with only a single factor considered to be involved in determining the organisation of the community, whereas the log normal would be expected to occur in situations in which many factors play a part (May, 1975; Magurran, 1988; Putman, 1994), though Pielou (1975) suggested a single resource model for the occurrence of this model in natural communities. However, Magurran (1988) considered that it was more useful to consider these models as a statistical fit to empirical data, as the hypotheses behind them are either unproved or discredited.

The geometric series is usually found in communities which are species poor or in the early stages of succession, where environmental conditions may be harsh (Magurran, 1988). In this study successional stage and species richness were more or less mutually exclusive, the early successional sites being more species rich than those later in succession. Overall, the fit of the geometric series to the data was poor, with probabilities generally less than 0.001. However, at the plantation sites COP (χ^2 = 30.4, d.f. = 22, $p<0.5>0.1$) and ROP (χ^2 = 18.7, d.f. = 23, $p<0.9>0.5$), which were two of the least species rich sites, this model gave a better fit to the observed data, and indeed at the latter provided the best fit along with the log series. At the remaining sites, this model had a tendency to underestimate the numbers of the commonest species, and overestimate those of the less common, though at NCF, which represented the first year after clear-felling, this model gave a relatively good description of the observed data for all species with the exception of the commonest, *Pardosa pullata*, the numbers of which were underestimated. At the site with the lowest species richness, NOP, this model gave a good description of the abundance of the common and rare species, but overestimated the numbers of the moderately common species *Agyneta conigera, Porrhomma pallidum, Centromerus dilutus* and *C. prudens,* perhaps because the period when they were most abundant lay outside the trapping period, or perhaps because, these species were less susceptible to capture using pitfall traps. The latter highlights the fact that, as the fit of this model is based on the abundance of individual species, it too is susceptible to trapping bias, particularly in the case of the commonest species where large differences between the expected and observed values for individual species can result in high χ^2 values, and rejection of the fit of this model. With the remaining models, where the fit is based on the number of species in particular abundance classes, this effect is likely to be less important, as the χ^2 values of only one or two abundance classes will be affected

The log series was first suggested as a suitable descriptor for species abundance data by Fisher *et al.* (1943). Magurran (1988) considered that the geometric series would grade into the log series as conditions became less harsh, or as succession proceeds, and the two distributions are closely related (May, 1975; Magurran, 1988). In this study there was little evidence that the fit of this model improved with site age, though the overall fit appeared marginally better at the Endgroup 3 and 4 sites. Bullock (1971), studying avian communities in south-east Asia, considered that, while the log series and log normal were equally effective in terms of actual fit to the data, the log series was more satisfactory due to the relative ease of its calculation, its more consistent performance, and the overly flexible nature of the log normal, making it prone to spurious fits. Taylor (1978) and Kempton & Wedderburn (1978) considered that the log series was a more suitable descriptor of natural communities than the log normal, because of its poor fit at the rare end of the spectrum, hence ensuring only resident species were considered (Magurran, 1988), and in this study this model was generally a poorer fit to the observed data than the log normal for those species with between one and four individuals (octaves I and II), though the differences involved were relatively small. In general the log series was the most satisfactory of the four models tested, providing the best fit to the observed data at all sites with the exception of CCF89, though at RCF the fit was still poor ($\chi^2 = 17.6$, d.f. = 7, $p<0.05>0.01$).

First applied to species abundance data by Preston (1948), the log normal is the most common distribution met with by ecologists in relation to natural communities, and May (1975) considered this the most appropriate model for use with species abundance data, as it reflects the many processes at work in a community. In addition, Magurran (1988) considered that the fact that this model describes more data sets than the log series makes it a more suitable means to compare communities. In this study the log normal generally gave a good description of the observed species abundance data. Probabilities obtained when comparing the expected values from the truncated log normal with the observed species abundance data were the highest found at Site 5, CCF90, CCF89, RCF and Site 2, though only at CCF89 was the fit of this model better than that of the log series. However as both Bullock (1971) and Magurran (1988) have pointed out, the flexibility of this model allows it to be fitted to a wide range of species abundance data. This is due to the fact that the rarer species in a community are generally not sampled, and as such, a log normal curve fitted to such data will be truncated at the left hand side, this point being termed the 'veil-line' (Preston, 1948). As the sample size increases, this moves to the left, revealing more of the curve, but in relatively small samples, it is difficult to tell whether an observed log normal truly represents this situation. The species abundance data at all sites in this study have the first term (i.e. the value in the first octave) greatest, so that the 'veil-line' must lie at, or to the right of the mode, and in these circumstances it is difficult to differentiate between the log series and log normal (Bullock, 1971), and many sets of species abundance data are described by both of these models (Magurran, 1988).

Proposed by MacArthur (1957) this model is usually found in rather limited communities of closely related species (Magurran, 1988). In this study, despite the limited nature of the communities studied, this was the least satisfactory of the four models tested, with probabilities generally less than 0.001, and never greater than 0.1. In nearly all cases this model greatly underestimated the number of species with one or two individuals (octave I), with expected values between roughly two and five times smaller than observed, though at NCF and CCF89 the underestimation of number of species with between 65 and 128 individuals (octave VII) was greater, and at Site 1 the same was true for species with between 129 and 256 individuals (octave VIII). This model came closest to the observed data at COP (χ^2 = 11.8, d.f. = 6, $p<0.1>0.05$), but was still less successful than the other three models in this respect, and at all sites, with the exception of Site 6 where this model was a better fit to the data than the geometric series, the broken stick provided the least satisfactory description of the observed data.

4.4.3. Changes in diversity and species abundance in relation to successional age.

It is apparent that there are clear trends in the attributes of the species abundance data along the successional gradient at Hamsterley. In general, species richness, abundance, diversity and eveness showed an increase in the first nine years of succession, as represented by the sites of Endgroups 1 and 2, in tandem with the increasing vegetation density. After this, these attributes tended to show a decline into the late successional period as represented by Endgroups 3 and 4, though the pattern was less clear in the case of abundance. The plantation sites, which represent the latest stages of succession, were less diverse, species rich and even than NCF, which represents the situation immediately after clear-felling. However, except for the mixed-woodland, Site 6, which was intermediate in terms of richness, diversity and eveness between the Endgroup 1 sites and the plantations, the relative values of these attributes in late succession did not seem to show any consistent pattern related to age. At the plantation sites NOP, COP and ROP, with ages of 41, 46 and 51 years respectively, overall abundance of individuals did show a decrease from 317 to 149 in tandem with age. However, the magnitude of this increase, and the fact that the communities of these sites were very similar in other respects, suggests that some factor other than successional stage, perhaps site wetness, is responsible.

4.5. Border transition categories.

The Wilton Moor study produced 2274 individuals from 65 species in 9 families. Both mean number of species and mean number of individuals per trap were greater in the grassland than the plantation, though only in the case of the latter was this difference significant (S - grassland mean = 17.7±1.6, plantation mean = 14.7±1.3, $t_{34} = 1.5$, p = N.S.; N - grassland mean = 67.9±12.1, plantation mean = 39.8±5.1, $t_{34} = 2.1$, $p<0.05$).

4.5.1. Distribution of species richness, diversity and number of individuals across the habitat boundary at Wilton Moor.

Fig. 13 gives a graphical representation of the mean number of species, individuals, and species diversity per trap for each row, with standard errors, at each of the six rows across the habitat boundary.

Table 11 gives mean number of species, individuals and species diversity per trap at each of the six rows, and shows the results of testing these value with one-way analysis of variance (ANOVA). The values obtained indicate that there was no significant difference between the largest and smallest mean values per trap for any of these variables, and thus the null hypothesis, that all row means were not significantly different at the 0.05 significance level, is accepted for all three.

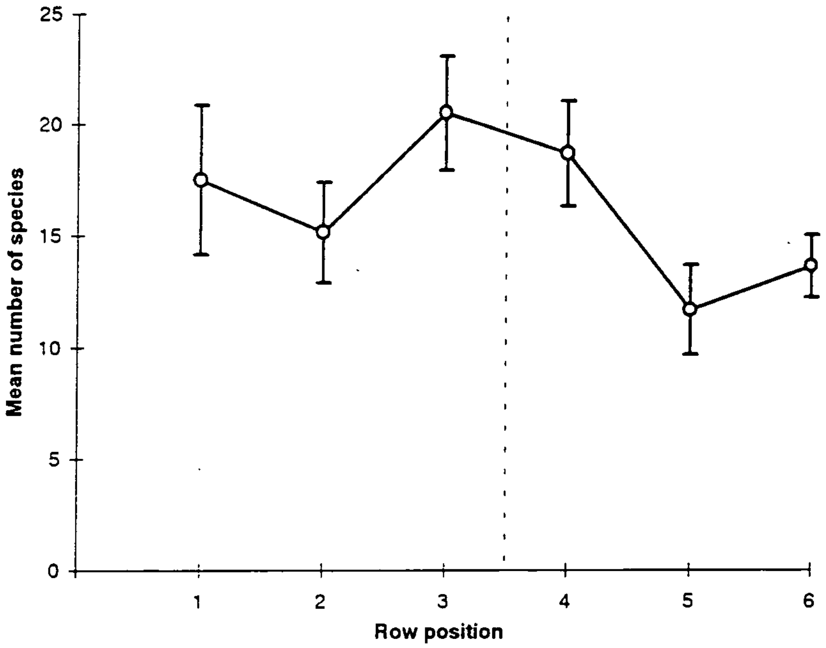


Fig. 13a). Mean number of species at each point on the Wilton Moor transect, with standard errors (n = 6). Position of boundary shown. Grassland rows 1-3, plantation rows 4-6.

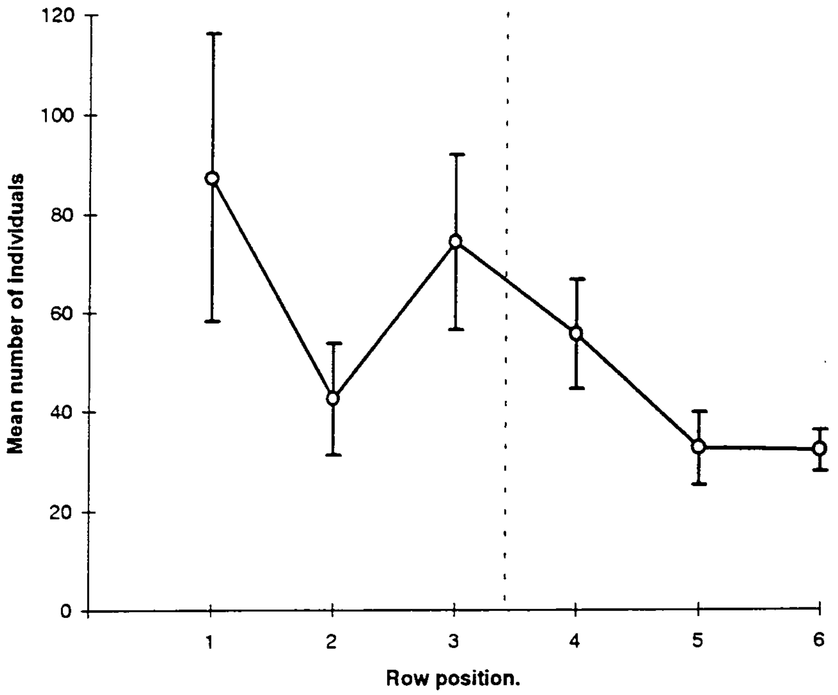


Fig. 13b). Mean number of individuals at each point on the Wilton Moor transect, with standard errors (n = 6). Position of boundary shown. Grassland rows 1-3, plantation rows 4-6.

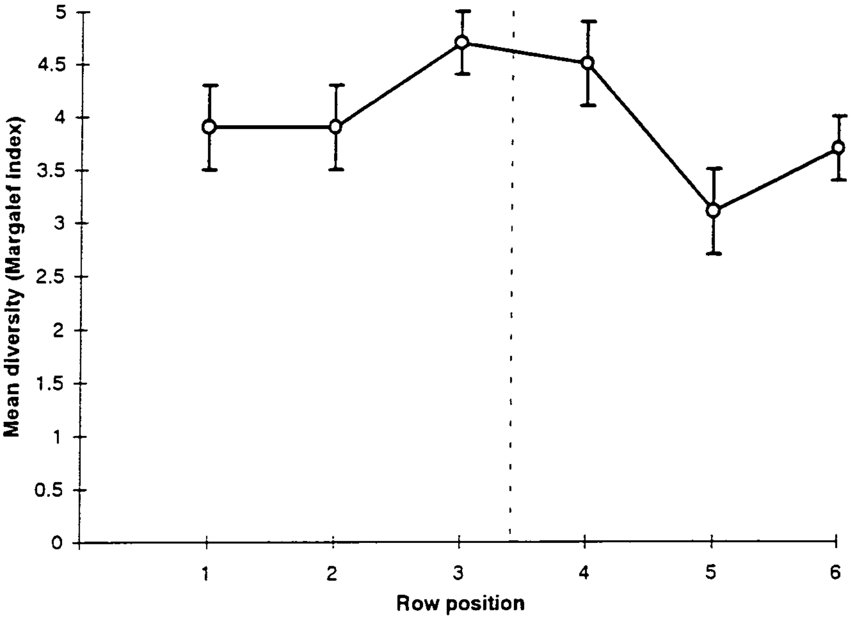


Fig 13c). Mean species diversity at each point on the Wilton Moor transect, with standard errors (n=6). Position of boundary shown. Grassland rows 1-3, plantation rows 4-6.

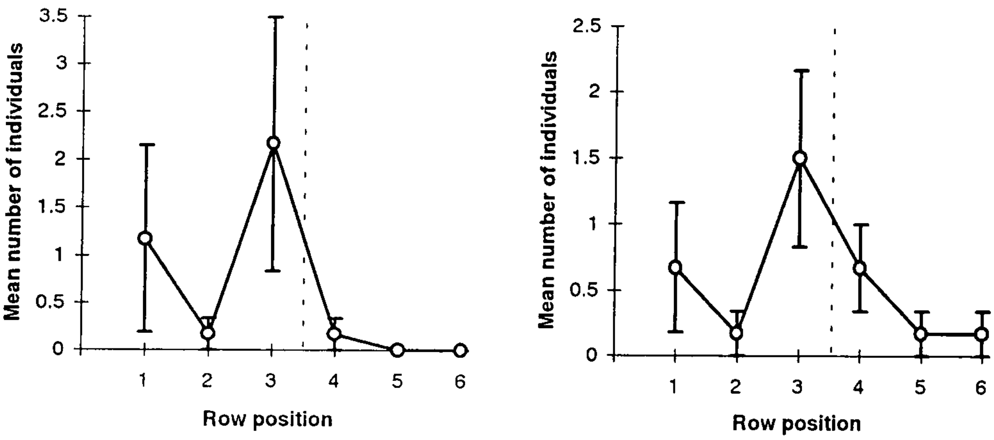
Row	Mean number of individuals	SE	Mean number of species	SE	Mean diversity Margalef Index	SE
1	87.2	29.0	17.5	3.4	3.9	0.4
2	42.3	11.4	15.2	2.3	3.9	0.4
3	74.2	17.8	20.5	2.6	4.7	0.3
4	55.0	11.0	18.7	2.4	4.5	0.4
5	32.5	7.3	11.7	2.0	3.1	0.4
6	32.0	4.2	13.7	1.4	3.7	0.3
ANOVA	F = 2.1		F = 1.9		F = 2.3	
d.f.	35		35		35	
p	N.S.		N.S.		N.S.	

Table 11. Mean number of individuals, species richness, and species diversity per trap for each row position at Wilton Moor, with results of ANOVA.

4.5.2. Distribution of individual species.

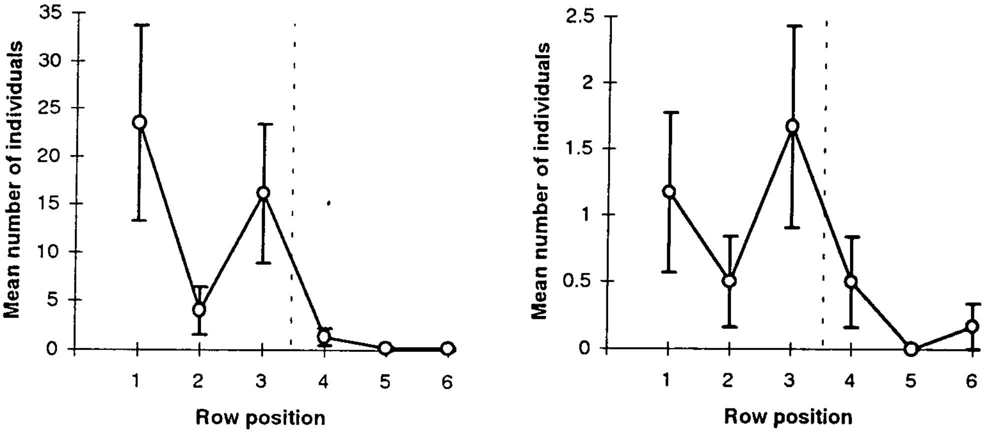
Fig. 14 shows the distribution of the 25 species trapped in numbers exceeding 19 individuals at Wilton Moor. This value was carried over from the first part of the study largely because using a value which constituted 5% of the total number of individuals here would have meant including species containing as few as nine individuals, and these were not considered amenable to statistical analysis using ANOVA. Table 12 shows the results of testing the significance of the differences between mean number of individuals per trap for grassland and plantation using student's t-test for each of the species shown in Fig. 14. Of the 25 species nine, *Pacygnatha degeeri, Oedothorax retusus, Lepthyphantes tenuis, Bathyphantes gracilis, Pardosa pullata, Erigone dentipalpis, Tiso vagans, Alopecosa pulverulenta* and *Gongylidiellum vivum*, were trapped in significantly greater numbers in the grassland, while seven species, *Lepthyphantes zimmermanni, Ceratinella brevipes, C. brevis, Diplocephalus latifrons, Cryphoeca silvicola, Robertus lividus*, and *Pelecopsis mengei*, were significantly more abundant in the plantation. The remaining species showed no significant difference in numbers trapped between the grassland and plantation.

Tables 13, 14 and 15 give the mean number of individuals per trap at each of the six rows for grassland species, plantation species, and those species showing no significant difference between the two habitats, and the results of the initial ANOVA analyses. As in the case of species richness, diversity, and number of individuals, the null hypothesis for the one-way ANOVA in this case was that all row means were not significantly different at the 0.05 significance level.



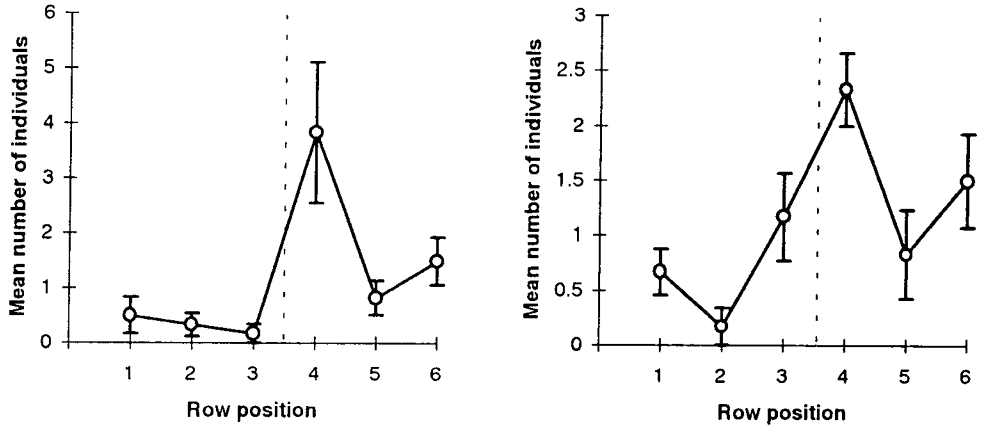
a) *Drassodes cupreus*

b) *Haplodrassus signifer*



c) *Pardosa pullata*

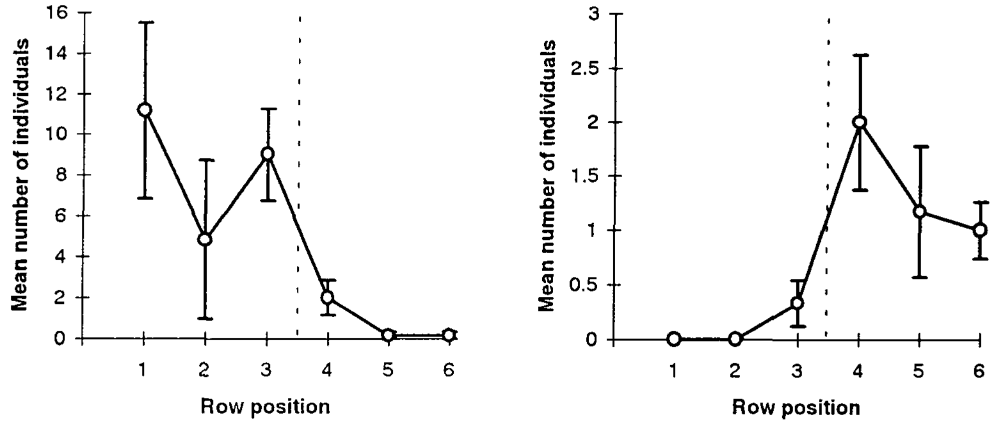
d) *Alopecosa pulverulenta*



e) *Cryphoeca silvicola*

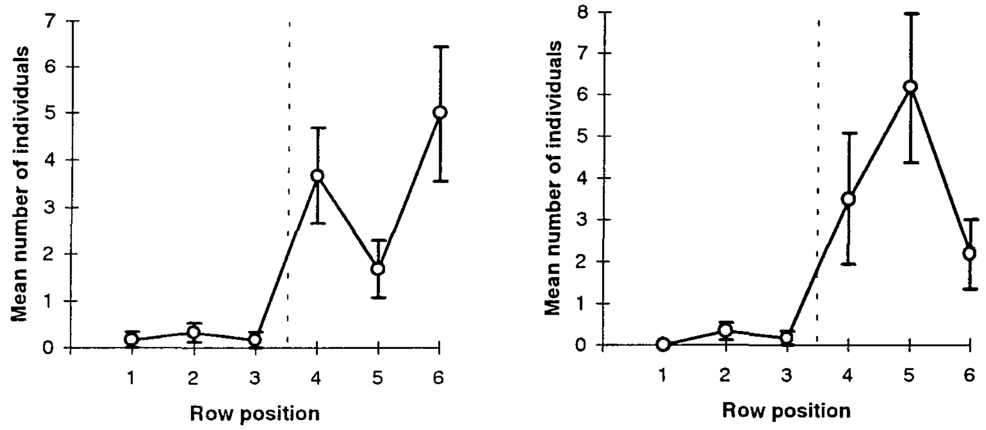
f) *Robertus lividus*

Fig. 14. Distribution of the common species across the Wilton Moor transect, with standard errors (n = 6). Position of boundary shown. Grassland rows 1-3, plantation rows 4-6.



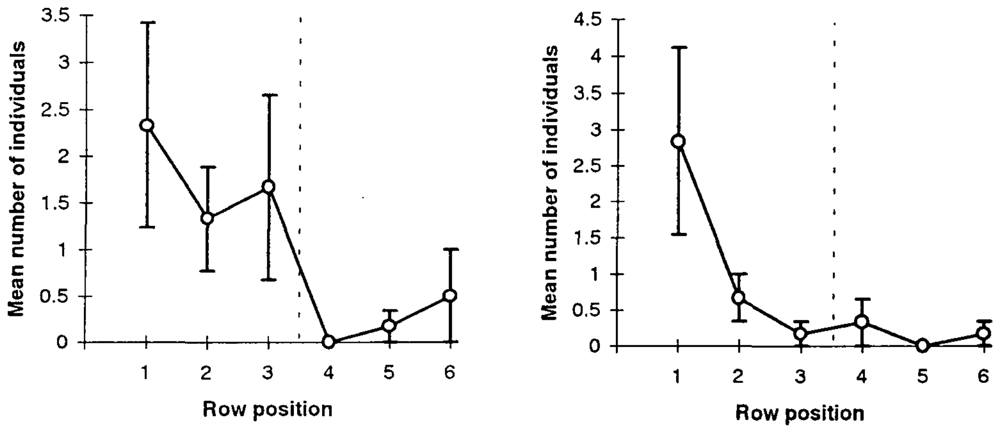
g) *Pacygnatha degeeri*

h) *Ceratinella brevipes*



i) *Ceratinella brevis*

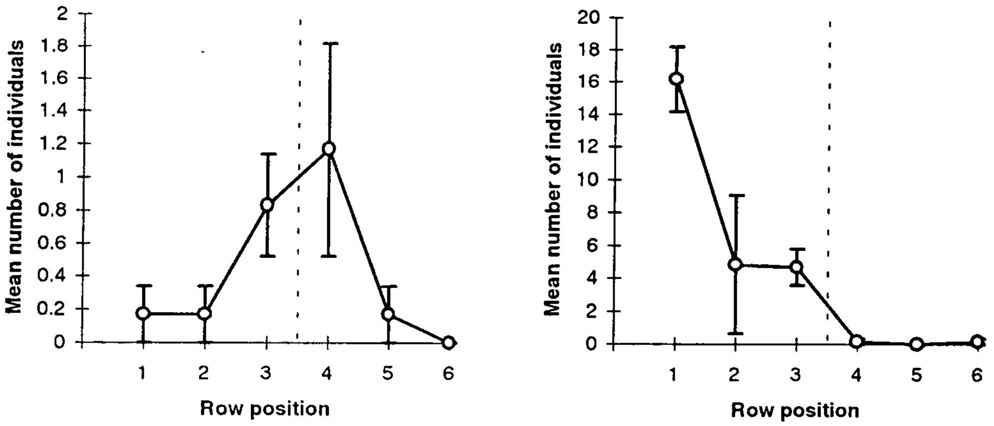
j) *Lepthyphantes zimmermanni*



k) *Bathyphantes gracilis*

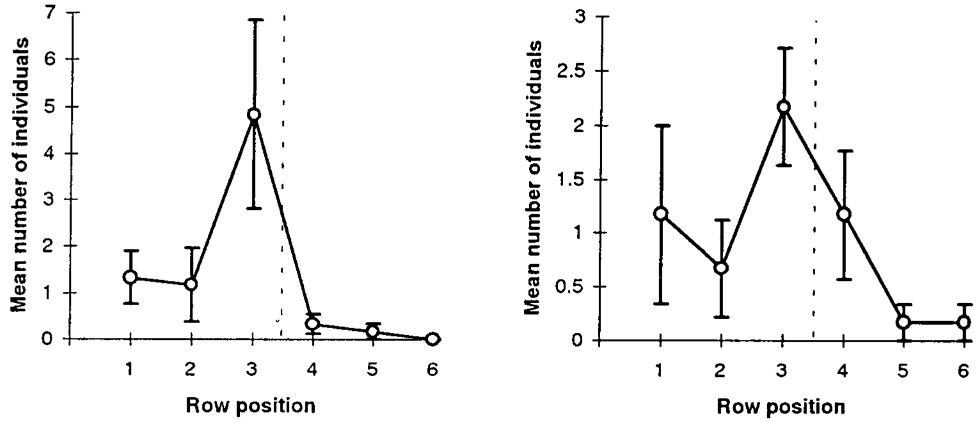
l) *Silometopus elegans*

Fig. 14. Distribution of the common species across the Wilton Moor transect, with standard errors (n = 6). Position of boundary shown. Grassland rows 1-3, plantation rows 4-6.



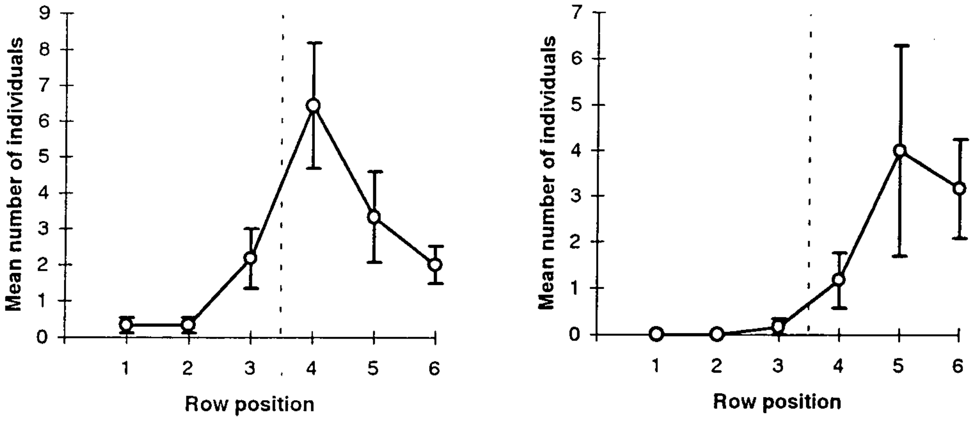
m) *Pocadicnemis pumila*

n) *Oedothorax retusus*



o) *Tiso vagans*

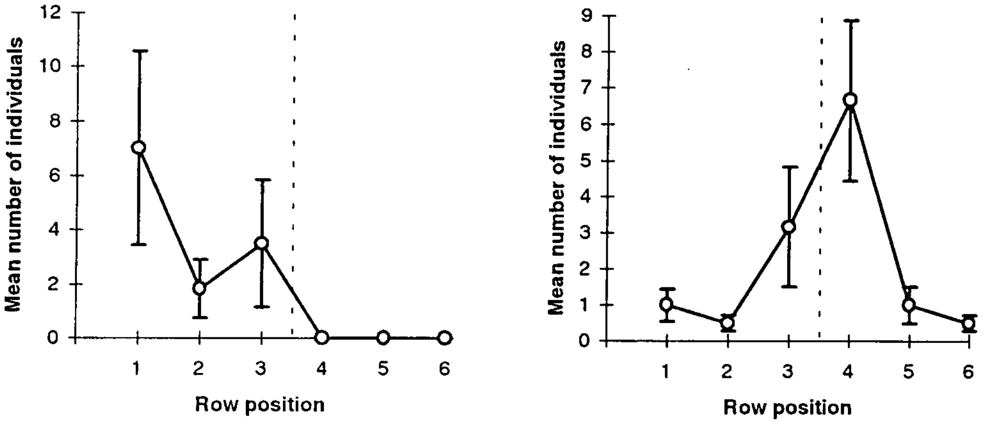
p) *Gongylidiellum vivum*



q) *Micrargus herbigradus*

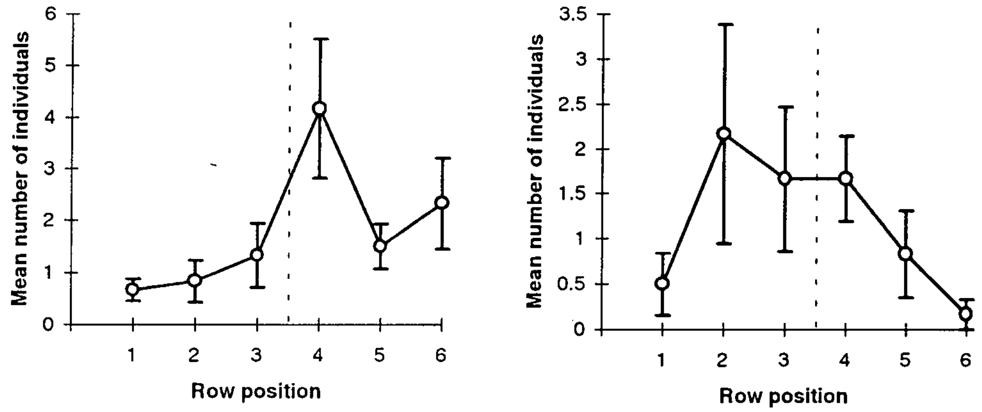
r) *Diplocephalus latifrons*

Fig. 14. Distribution of the common species across the Wilton Moor transect, with standard errors (n = 6). Position of boundary shown. Grassland rows 1-3, plantation rows 4-6.



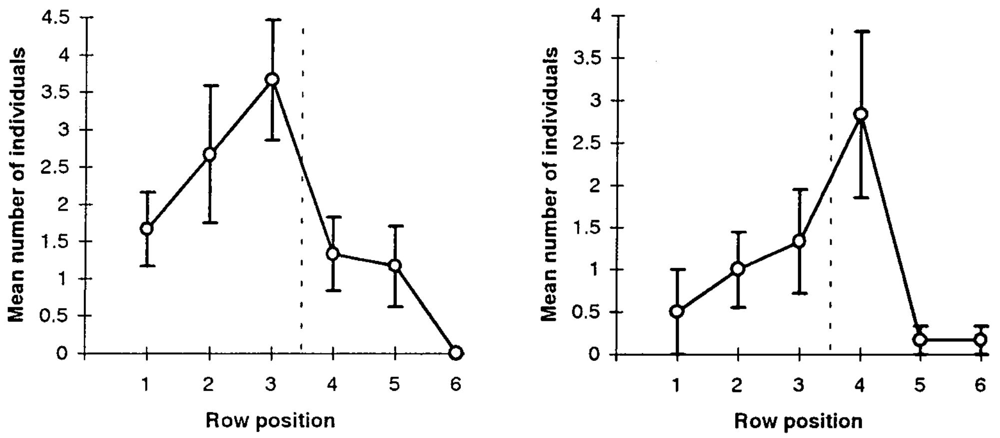
s) *Erigone dentipalpis*

t) *Meioneta saxatilis*



u) *Pelecopsis mengei*

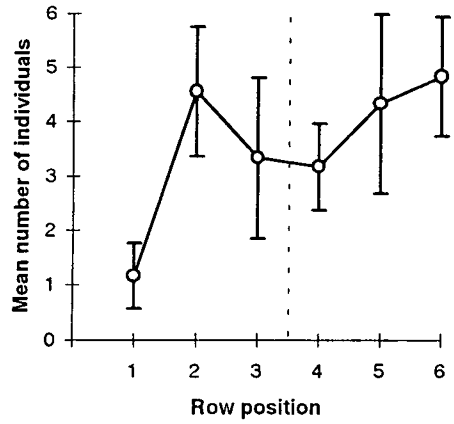
v) *Bathyphantes parvulus*



w) Lepthyphantes tenuis

x) *Lepthyphantes mengei*

Fig. 14. Distribution of the common species across the Wilton Moor transect, with standard errors (n = 6). Position of boundary shown. Grassland rows 1-3, plantation rows 4-6.



y) *Lepthyphantes ericaceus*

Fig. 14. Distribution of the common species across the Wilton Moor transect, with standard errors (n = 6). Position of boundary shown. Grassland rows 1-3, plantation rows 4-6.

Species	Grassland mean	Plantation mean	t	d.f.	p
Pacygnatha degeeri	9.3±2.0	0.8±0.3	+4.3	17.9	0.00
Oedothorax retusus	9.4±2.2	0.2±0.1	+4.2	17.1	0.001
Lepthyphantes tenuis	2.7±0.5	0.8±0.3	+3.5	27.6	0.002
Bathyphantes gracilis	1.9±0.5	0.2±0.2	+3.3	21.0	0.004
Pardosa pullata	15.4±4.6	0.6±0.3	+3.2	17.2	0.003
Erigone dentipalpis	4.2±1.4	0	+2.9	17.0	0.009
Tiso vagans	2.4±0.8	0.2±0.1	+2.7	17.4	0.01
Alopecosa pulverulenta	1.2±0.3	0.2±0.1	+2.6	21.9	0.01
Gongylidiellum vivum	1.6±0.4	0.5±0.2	+2.4	28.5	0.02
Drassodes cupreus	1.2±0.6	0.1±0.1	+2.0	17.3	N.S.
Silometopus elegans	1.2±0.5	0.2±0.1	+2.0	19.0	N.S.
Bathyphantes parvulus	1.5±0.5	0.6±0.2	+1.7	22.5	N.S.
Haplodrassus signifer	0.8±0.3	0.5±0.2	+0.8	34.0	N.S.
Pocadicnemis pumila	0.4±0.1	0.4±0.2	+0.2	34.0	N.S.

Table 12. Mean number of individuals per trap (± SE) from grassland and plantation for the 25 spider species trapped in numbers exceeding 19 individuals at Wilton Moor, and showing the results of significance testing using student's t-test. Positive t values indicate greater abundance in the grassland, while negative values indicate greater abundance in the plantation.

Species	Grassland mean	Plantation mean	t	d.f.	p
Lepthyphantes zimmermanni	0.2±0.1	3.9±0.9	-4.2	17.4	0.001
Ceratinella brevipes	0.1±0.1	1.4±0.3	-4.1	19.1	0.001
C. brevis	0.8±0.4	3.4±0.7	-3.4	25.8	0.002
Diplocephalus latifrons	0.1±0.1	2.8±0.9	-3.1	17.1	0.006
Micrargus herbigradus	1.1±0.3	3.9±0.9	-3.1	22.2	N.S.
Cryphoeca silvicola	0.3±0.1	2.1±0.5	-3.1	19.3	0.005
Robertus lividus	0.7±0.2	1.6±0.3	-2.7	29.6	0.01
Pelecopsis mengei	1±0.3	2.6±0.6	-2.5	23.1	0.02
Lepthyphantes ericaceus	3.1±0.7	4.2±0.7	-1.1	34.0	N.S.
Meioneta saxatilis	1.6±0.6	2.7±1	-1.0	34.0	N.S.
Lepthyphantes mengei	0.9±0.3	1.1±0.4	-0.2	34.0	N.S.

Table 12. (continued).

	Row						ANOVA		
Species	1	2	3	4	5	6	F	d.f.	p
Pacygnatha degeeri	11.7±4.5	6.8±3.5	9.3±2.1	2±0.7	0.2±0.2	0.2±0.2	4.0	35	0.007
Oedothorax retusus	16.7±5.4	6.8±1.8	4.7±1	0.3±0.2	0	0.2±0.2	7.6	35	0.00
Lepthyphantes tenuis	1.7±0.5	2.7±0.9	3.7±0.8	1.3±0.5	1.17±0.54	0	4.3	35	0.005
Bathyphantes gracilis	2.3±1.1	1.8±0.6	1.7±1.0	0	0.17±0.17	0.5±0.5	2.1	35	N.S.
Pardosa pullata	24.2±10.9	4.7±2.3	6.2±7.2	1.3±0.9	0.2±0.2	0.2±0.2	3.4	35	0.02
Erigone dentipalpis	7.2±3.3	1.8±1.1	3.5±2.4	0	0	0	2.8	35	0.04
Tiso vagans	1.3±0.8	1.27±0.8	4.8±2.0	0.3±0.2	0.2±0.2	0	3.7	35	0.01
Alopecosa pulverulenta	1.3±0.6	0.5±0.3	1.7±0.8	0.5±0.3	0	0.2±0.2	2.3	35	N.S.
Gongylidiellum vivum	1.2±0.8	1.2±0.6	2.3±0.4	1.2±0.6	0.2±0.2	0.2±0.2	2.4	35	N.S.

Table 13. Mean number of individuals per trap (± SE) at each row for each of the nine species trapped in significantly greater numbers in the grassland at Wilton Moor, with results of ANOVA analysis.

Species	Row						ANOVA		
	1	2	3	4	5	6	F	d.f.	p
Ceratinella brevipes	0	0	0.3±0.2	2±0.6	1.2±0.6	1±0.3	4.3	35	0.005
C. brevis	0.2±0.2	0.3±0.2	2±0.9	3.7±1.0	1.7±0.6	5±1.4	4.9	35	0.002
Diplocephalus latifrons	0	0	0.2±0.2	1.2±0.6	4±2.3	3.17±1.1	2.7	35	0.04
Cryphoeca silvicola	0.5±0.3	0.3±0.2	0.2±0.2	3.8±1.3	0.8±0.3	1.5±0.4	5.2	35	0.001
Robertus lividus	0.7±0.2	0.2±0.2	1.2±0.4	2.3±0.3	0.8±0.4	1.5±0.5	4.5	35	0.004
Pelecopsis mengei	0.8±0.3	0.8±0.4	1.3±0.6	4.2±1.4	1.5±0.43	2.2±0.9	2.7	35	0.04
Lepthyphantes zimmermanni	0.2±0.2	0.3±0.2	0.2±0.2	3.5±1.6	6.17±1.8	2.2±0.8	5.4	35	0.001

Table 14. Mean number of individuals per trap (± SE) at each row for each of the seven species trapped in significantly greater numbers in the plantation at Wilton Moor, with results of ANOVA analysis.

	Row						ANOVA		
Species	1	2	3	4	5	6	F	d.f.	p
Drassodes cupreus	1.2±1	0.2±0.2	2.2±1.3	0.2±0.2	0	0	1.7	35	N.S.
Silometopus elegans	2.8±1.3	0.7±0.3	0.2±0.2	0.3±0.3	0	0.2±0.2	3.6	35	0.01
Bathyphantes parvulus	0.7±0.3	2.2±1.2	1.7±0.8	1.2±0.5	0.5±0.22	0.2±0.2	1.4	35	N.S.
Haplodrassus signifer	0.7±0.5	0.2±0.2	1.5±0.7	0.7±0.3	0.2±0.2	0.7±0.3	1.5	35	N.S.
Pocadicnemis pumila	0.2±0.2	0.2±0.2	0.8±0.3	1.2±0.7	0.17±0.17	0	2.2	35	N.S.
Micrargus herbigradus	0.3±0.2	0.5±0.2	2.3±0.8	6.3±1.9	3.3±1.3	2±0.5	4.7	35	0.003
Meioneta saxatilis	1±0.5	0.5±0.2	3.2±1.7	6.7±2.2	1±0.5	0.5±0.2	4.3	35	0.005
Lepthyphantes ericaceus	1.2±0.6	4.7±1.2	3.3±1.5	3.2±0.8	4.33±1.65	5±1.2	1.4	35	N.S.
L. mengei	0.5±0.5	1±0.5	1.3±0.6	2.8±1	0.17±0.17	0.2±0.2	3.3	35	0.02

Table 15. Mean number of individuals per trap (± SE) at each row for each of the nine species which showed no significant difference in mean catch between grassland and plantation at Wilton Moor, with results of ANOVA analysis.

Of the 25 species distributions analysed, eight gave non-significant F values using one-way ANOVA. Five of these, namely *Bathyphantes parvulus*, *Drassodes cupreus*, *Haplodrassus signifer*, *Pocadicnemis pumila* and *Lepthyphantes ericaceus*, showed no significant difference in mean catch per trap between the grassland and plantation using a t-test, while the remaining species, *Alopecosa pulverulenta, Gongylidiellum vivum* and *Bathyphantes gracilis* were more abundant in the grassland. All of the plantation species gave significant F values with ANOVA.

Table 16 represents the results of Tukey multiple comparison tests on the data for the 17 species which gave significant F values for the initial ANOVA. The null hypothesis in this case was that there was no significant difference at the 0.05 level between the means of each pair of rows compared.

Of these species, seven, *Pardosa pullata, Pacygnatha degeeri, Erigone dentipalpis, Tiso vagans, Oedothorax retusus. Silometopus elegans* and *Lepthyphantes tenuis* reached their highest mean catch per trap in one of the grassland rows, and in all cases, with the exception of *S. elegans*, row means were consistently higher in the grassland than in the plantation. However, in no case were all grassland means significantly higher than those in the plantation, and surprisingly in two cases, *P. pullata* and *Erigone dentipalpis*, none of the grassland means were significantly greater than those in the plantation. Indeed these two species showed no differences between any means, despite the significant result in the initial ANOVA. Five of these species, *P. pullata, P. degeeri, E. dentipalpis, O. retusus* and *S. elegans*, reached their highest row mean at

Species	Row ranking (ascending order)
Pacygnatha degeeri	5 6 **4 2 3** 1
Oedothorax retusus	5 6 4 3 **2** 1
Lepthyphantes tenuis	6 **5 4** 1 2 3
Pardosa pullata	5 6 4 2 3 1
Erigone dentipalpis	4 5 6 2 3 1
Tiso vagans	6 5 4 **2 1** 3
Silometopus elegans	5 3 6 4 **2** 1
Lepthyphantes zimmermanni	1 3 2 **6 4** 5
Ceratinella brevipes	1 2 3 **6 5** 4
C. brevis	1 2 **5 3 4** 6
Diplocephalus latifrons	1 2 3 4 6 5
Micrargus herbigradus	1 2 **6 3 5** 4
Cryphoeca silvicola	3 2 1 5 **6** 4
Robertus lividus	2 1 **5 3 6** 4
Pelecopsis mengei	1 2 **3 5 6** 4
Meioneta saxatilis	2 6 1 5 **3** 4
Lepthyphantes mengei	5 6 **1 2 3** 4

Table 16. Representation of the results of the Tukey multiple comparison tests on the species in Table 12 which gave significant F values in the initial ANOVA. Underlined values showed no significant difference to those values above and below them, while values in normal type separated by these values were shown to be significantly different.

row 1, while *T. vagans* and *L. tenuis* reached their highest mean at row 3. No species reached their highest mean number of individuals per trap at row 2.

The remaining species reached their highest mean catch per trap in the plantation, though only five of these, *Cryphoeca silvicola, Ceratinella brevipes, Diplocephalus latifrons, Pelecopsis mengei* and *Lepthyphantes zimmermanni* had consistently higher row means in the plantation as opposed to the grassland. Again none of these species had plantation means which were all significantly higher than those in the grassland, and in the case of *D. latifrons*, none were significantly higher. Of these species, seven, *C. silvicola, R. lividus, C. brevipes, M. herbigradus, M. saxatilis, P. mengei* and *L. mengei* reached their highest means per trap at row 4, two, *D latifrons* and *L. zimmermanni*, at row 5, and one, *C. brevis*, at row 6.

4.5.3. Distribution of major guilds.

As in the ordination/classification section, six major guilds were defined in this part of the study, based on the occurrence of one of the 25 species included in Table 13. For the most part these guilds were the same as those defined earlier. However, at Wilton the ambushers were represented by only five individuals of *Xysticus cristatus*, and thus in this part of the study this guild is replaced by the orb weavers as represented by a single species, *Pacygnatha degeeri.* Members of this guild generally build complex radial webs with sticky threads, and are specialised to catch aerial prey (Lockett & Millidge, 1953; Roberts, 1985), though members of this genus only build webs of this nature when immature, reverting to a ground living habit as adults (Foelix, 1982).

Table 17 gives the results of testing for significant differences between grassland and plantation means for each of the six major guilds. In addition to the orb weavers, two other guilds were also represented by only one individual, the funnel web spiders (*Cryphoeca silvicola*) and the scattered line weavers (*Robertus lividus*). The results for these two guilds are included in Table 17 for completeness, though the distribution of the individual species has been dealt with above. Two guilds, the diurnal running spiders and orb weavers, were trapped in significantly greater numbers in the grassland, while the funnel web spiders and scattered line weavers were significantly more abundant in the plantation. The remaining guilds, the nocturnal running spiders and sheet web weavers, showed no significant difference between grassland and plantation means.

Table 18 gives the mean number of individuals per trap at each row position for each major guild, as well as the results of an initial one-way ANOVA. Discounting those guilds containing only one species, only one of the major guilds, the diurnal running spiders, gave a significant F value in the initial ANOVA, though the resulting Tukey test only found significant differences between row 1 in the grassland and rows 5 and 6 in the plantation.

4.5.4. A discussion of the results of the Wilton Moor study.

The limited size of this study, and hence the small numbers involved, has limited the conclusions that can be drawn from the data. While plots of the variables against row position may suggest certain patterns of distribution, these values tend to show little in the way of consistent variation when subjected to statistical analysis using

Guild	Grassland mean	Plantation mean	t	d.f.	p
Orb weavers	9.3±2.0	0.8±3.0	+4.3	17.9	0.00
Diurnal running spiders	16.8±5.0	1.1±0.4	+3.2	17.3	0.006
Sheet web weavers	39.6±5.3	33.7±4.0	+0.9	34.0	N.S.
Nocturnal running spiders	0.9±0.5	0.7±0.2	+0.4	34.0	N.S.
Funnel web spiders	0.3±0.1	2.1±0.5	-3.1	19.3	0.005
Scattered line weavers	0.7±0.2	1.6±0.3	-2.7	29.6	0.01

Table 17. Mean number of individuals per trap (± SE) from grassland and plantation for each of the six major spider guilds identified at Wilton Moor, and showing results of significance testing using student's t-test. Positive t values indicate a greater abundance in the grassland, while negative values indicate greater abundance in the plantation.

	Row						ANOVA		
Guild	1	2	3	4	5	6	F	d.f.	p
Diurnal running spiders	26.7±11.7	5.2±2.6	18.7±8	2.2±1.2	0.2±0.2	0.8±0.3	3.5	35	0.01
Nocturnal running spiders	2.0±1.4	0.3±0.2	0.3±0.3	1.2±0.6	0.2±0.2	0.7±0.3	1.1	35	N.S.
Funnel web spiders	0.5±0.3	0.3±0.2	0.2±0.2	3.8±1.3	0.8±0.3	1.5±0.4	5.2	35	0.001
Orb weavers	11.7±4.5	6.8±3.5	9.3±2.1	2.0±0.7	0.2±0.2	0.2±0.2	4.0	35	0.007
Scattered line weavers	0.7±0.2	0.2±0.2	1.2±0.4	2.3±0.3	0.8±0.4	1.5±0.5	4.5	35	0.004
Sheet web weavers	45.2±12.7	29.3±6.1	44.2±8.1	43.5±8.4	30.3±6.7	27.3±4.3	1.1	35	N.S.

Table 18. Mean number of individuals per trap (± SE) at each row for each of the six major guilds at Wilton Moor, with results of ANOVA analysis.

ANOVA. Hence in terms of the distribution of species richness, diversity and abundance of individuals, the only statistically significant difference found was that mean abundance per trap in the grassland was higher than that in the plantation. This is in general agreement with Downie *et al.* (1996), who found a similar result studying the effect of a habitat boundary on spider communities in northern England. At Wilton, a large part of the catch in the grassland traps was made up of species such as the diurnal running spider *Pardosa pullata*, the orb weaver *Pacygnatha degeeri*, and the sheet web weavers *Oedothorax retusus* and *Erigone dentipalpis*, which have been shown to be particularly susceptible to capture by pitfall trapping (Topping & Sunderland, 1992), and thus it seems that the presence of species such as these in the grassland has resulted in higher catches here.

In terms of the disposition of the major spider guilds at Wilton, the distribution of the diurnal running spiders, nocturnal running spiders, and sheet web weavers between grassland and plantation is comparable to that observed at Hamsterley between open and wooded sites. The diurnal running spiders were more abundant at the open sites in both parts of the study, likely due to the relatively high temperatures required for egg development (Humphreys, 1987). The nocturnal running spiders showed no significant difference in their mean abundance between the open and wooded sites at Hamsterley, or the grassland/plantation sites at Wilton. In the case of the former this was largely due to the uneven distribution of members of this guild between clear-felled and restocked sites, while at Wilton, this may have merely been due to the small number of individuals involved. In contrast to the other guilds defined in this study, which tended to consist of one, or a few closely related species with similar life styles, the sheet web weavers constituted a large guild in terms of numbers of species, with a correspondingly large range of microhabitat requirements and life styles. Hence the lack of a clear preference in this guild for either open or forested sites is not surprising.

In contrast to these guilds, both the funnel web spiders and the scattered line weaver *Robertus lividus* showed a distribution between grassland and plantation at Wilton which was at odds with that observed between open and wooded sites at Hamsterley. At Hamsterley the funnel web spiders showed no significant difference in abundance between open and wooded sites, largely due to their uneven occurrence within the latter, while at Wilton this guild was trapped in significantly greater numbers in the plantation. Similarly, *R. lividus*, which was also significantly more abundant in the plantation at Wilton, was unevenly distributed between the Hamsterley sites, being virtually confined to the restocked sites, and the mixed-woodland Site 6, and showed no significant difference in mean catch between Endgroup 1 and 2 on the one hand, and Endgroups 3 and 4 on the other. The remaining major guild, the orb weavers, was most abundant in the grassland at Wilton, while members were absent from the Hamsterley sites in significant numbers.

In terms of the distribution of individual species at Wilton, the lack of statistical significance in the data made it impossible to carry out the main purpose of this part of the study, i.e. to assign species to border transition categories as defined by Duelli *et al.* (1990). However, the data has been sufficient to allow meaningful statistical comparisons to be made between the abundance of individual species in grassland and plantation, and hence to compare these distributions with those found at Hamsterley.

Of the 25 common species at Wilton, 15 were also among the commonest species at Hamsterley. In terms of those species showing a preference for the grassland at Wilton, only two of these, the diurnal running spiders *Pardosa pullata* and *Alopecosa pulverulenta*, were also common at Hamsterley, where both species were significantly more abundant at Endgroups 1 and 2, which is in agreement with the requirement of members of this guild for relatively high daytime temperature for optimum egg development (Nørgaard, 1951; Humphreys, 1987). Of the remaining Wilton grassland species, *Pacygnatha degeeri, Erigone dentipalpis, Tiso vagans* and *Oedothorax retusus* have been recorded as showing an association with grassland (Luff & Rushton, 1989; Gibson *et al.*, 1992; Rushton & Eyre, 1992), and as such might be expected to shows a preference for habitats with relatively greater solar insolation. The more complex vegetation structure in the grassland may be important for *Lepthyphantes tenuis* and *Bathyphantes gracilis*, as the former has been observed to build webs in tall grasses (Duffey, 1968), while *Bathyphantes parvulus*, which is closely related to *B. gracilis*, builds small webs low down in the vegetation (Duffey, 1956). The remaining grassland species at Wilton, *Gongylidiellum vivum*, is recorded as being associated with moss, grass and leaf litter in damp places (Roberts, 1987), and there may also be a structural requirement in this species.

Five of the seven species at Wilton which showed a preference for the plantation were also among the commonest species at Hamsterley. Of these species, four, *Lepthyphantes zimmermanni, Ceratinella brevipes, Cryphoeca silvicola* and *Diplocephalus latifrons* were considered more typical of the wooded sites at

Hamsterley by TWINSPAN, though the last three species did not show significant difference between open and wooded sites due to their rather uneven distribution. The distribution of these species, is generally consistent with what is known of their ecology, as they are associated with woodlands and/or damp or sheltered habitats, and are therefore likely adapted to the relatively low temperature and high humidity in the plantation as compared to the grassland. *Diplocephalus latifrons*, for instance, is a species closely associated with woodlands (Lockett & Millidge, 1953; Roberts, 1987), while *Cryphoeca silvicola,* and *Lepthyphantes zimmermanni* also occur in upland habitats (Lockett & Millidge, 1951, 1953; Roberts, 1985, 1987). Similarly *Pelecopsis mengei* and *Ceratinella brevis,* which were not among the commonest species at Hamsterley, occur in situations where saturation deficits are also low, the former in damp habitats, and the latter in moss or leaf litter (Lockett & Millidge, 1953; Roberts, 1987). *Robertus lividus*, which again is a species associated with both woodlands and uplands (Lockett & Millidge, 1953; Roberts, 1985), while more abundant at the plantation at Wilton, was considered by TWINSPAN to be marginally more typical of Endgroups 1 and 2 at Hamsterley. This may well reflect a requirement for both humid conditions and structural features of the vegetation, hence accounting for its absence from the majority of the wooded sites at Hamsterley.

The eight remaining species which were common at both Wilton and Hamsterley showed no preference for either grassland or plantation at the former site. Of these, only one, the sheet web weaver *Lepthyphantes ericaceus*, showed a similar distribution at Hamsterley, occurring in the centre of Axis 1 of the ordination, and being considered by TWINSPAN to show no preference for either open or wooded sites. The remaining species in common, *Bathyphantes parvulus*, *Lepthyphantes mengei*, *Silometopus elegans*, *Pocadicnemis pumila*, *Micrargus herbigradus*, *Drassodes cupreus* and *Haplodrassus signifer*, occurred to the left of the Hamsterley ordination, and were considered by TWINSPAN to be more indicative of the clear-felled and restocked sites. The lack of a preference at Wilton may merely be due to the small number of individuals involved in this case. Alternatively, it may be that at least some of these species have some requirement for structural features of vegetation which were generally not provided by the wooded sites at Hamsterley, but were present in the plantation at Wilton, which had a relatively well developed herb layer, at least near the habitat boundary. Of these species, *B. parvulus* has been observed to build small webs low down in the vegetation (Duffey, 1956), while certain members of the genus *Lepthyphantes* have been shown to use vegetation in a similar manner (Duffey, 1968). The remaining species which showed no preference at Wilton, *Meioneta saxatilis*, did not occur at Hamsterley. This species is generally found in low vegetation, grass, moss or leaf litter (Roberts, 1987), and was relatively abundant at rows 3 and 4, either side of the habitat boundary. However, the lack of significant differences using both t-test, and to a large extent ANOVA, makes it difficult to draw any meaningful conclusions concerning the distribution of this species.

5. DISCUSSION.

5.1. The use of pitfall traps in community studies.

While pitfall traps provide a useful method for sampling invertebrate populations, the view they give of the relative abundance of the constituent species is somewhat distorted due to the selective nature of the trapping method. Topping & Sunderland (1992), for instance, sampled spiders in a field of winter wheat using both pitfall trapping and absolute density sampling. They found that the relative abundance of the species in pitfall catches was different from that indicated by density sampling. They considered that these differences could be due to a number of factors. The most important of these was differential activity rates, resulting in a greater chance of capture for individuals of more active species, the activity/abundance concept of Tretzel (1954) and Heydemann (1961), which itself can be affected by life-cycle stage (Tretzel, 1954; Merrett, 1967; Duffey, 1956), availability of food (Grüm, 1971; Muller, 1984; Chiverton, 1984) or vegetation density (Baars, 1979). In addition they considered it conceivable that individual species may be more able to avoid capture than others, as has been observed in carabids (Halsall & Wratten, 1988). The importance of this in relation to the present study is that the sites representing the first nine years of succession, i.e. those grouped in Endgroups 1 and 2 by TWINSPAN, were dominated by large numbers of lycosids which are highly active species, and hence likely to be overestimated by this method of trapping.

5.2. Changes in spider communities during succession.

Vegetation structure has been cited as the main factor influencing the structure of spider communities in a number of studies. Hence Downie *et al.* (1995), studying the spider communities on three summit plateaux in the northern Pennines, found that vegetation density was the major factor influencing spider distribution, while a number of studies investigating the effect of different management regimes on grassland spider communities (Rushton *et al.*, 1987; Luff & Rushton, 1989; Rushton *et al.*, 1989; Gibson *et al.*, 1992; Rushton & Eyre, 1992;) have found that the change in spider communities under different regimes was largely due to the effect of management on vegetation structure.

Previous studies have found that both the abundance, and diversity of spider communities are positively correlated with vegetation density (Duffey, 1962a; Cherrett, 1964). However, in this current study the site with the denser vegetation cover did not necessarily support the most diverse or abundant fauna. In the case of abundance, lower catches at sites with higher vegetation density can probably be attributed to the decreased efficiency of the trapping method at such sites. Hence Site 2, which had the lowest vegetation density of any site, had the fourth highest abundance, and discounting the presence of the highly active diurnal running spiders, which accounted for over 50 percent of the catch at Site 1, Site 5 and RCF, the total number of individuals trapped was virtually the same as that of the Endgroup 1 sites which had the highest vegetation density of all.

In terms of diversity, the most striking discrepancy between diversity and vegetation density was at Site 6. This site had the fourth highest vegetation density overall after the Endgroup 1 sites and CCF89, but had a lower diversity than any site in either Endgroup 1 or 2. The reason for this discrepancy may be related to the different microclimate at Site 6 due to the presence of tree cover. Huhta (1971), studying the effect of clear-cutting and burning on ground living spider communities in Finland, found that clear-felled habitats were characterised by increased solar radiation levels in comparison with wooded sites and had correspondingly higher temperatures and reduced air moisture content during the day in summer. Hence, of the guilds typical of Endgroups 1 and 2 as a whole at Hamsterley, the ambushers are diurnal hunters typical of open habitats, and it seems likely that members of this guild are adapted to the relatively high temperature and low humidity found in these situations. In the case of the diurnal running spiders their occurrence at these sites is likely to be related to the fact that the lycosids require a temperature of around 30 °C for optimum egg development (Norgaard, 1951; Humphreys, 1987). While Site 6 was quite open and contained a number of clearings, the surrounding trees would tend to cast shade into these clearings, and overall the presence of tree cover, with the associated reduction in solar radiation levels, would tend to result in a relatively lower temperature and higher humidity during the day at this site, and as a consequence, those species more typical of Endgroups 1 and 2 were absent.

Some comment must be made at this point concerning the relatively low scores of NCF and RCF on Axis 1 of the ordination in relation to their vegetation density.

These sites were ranked eighth and fifth respectively in terms of their vegetation density, but had the fifth and second lowest scores on this axis, and in terms of their spider communities showed a similarity to Endgroup 1 sites, mainly in the occurrence of certain species of diurnal and nocturnal running spiders. While this may in part may have been due to the increased efficiency of the trapping method in catching these active species in habitats with sparse vegetation cover, in the case of RCF the similarity was particularly pronounced. Coulson & Butterfield (1986) considered that soil wetness was a more important consideration than habitat structure for some species, while McIver *et al.*, (1992) found that site wetness effected the rate of succession in spider communities after clear-cutting, with the communities of wetter sites coming to resemble those of the preceding woodland more rapidly than those of relatively dry sites. As soil organic content is high at RCF, and as this factor has been shown to be closely correlated with soil wetness (Downie *et al.*, 1995), it may be that the increased suitability of this site for certain Endgroup 1 species, where humidity was relatively high due to the dense vegetation cover, allowed them to occur in relatively high numbers here.

In addition to diversity and abundance, a number of studies have found that the equitability of the species abundance data rises along the successional gradient. Hence both Bazzaz (1975) studying plant succession, and Southwood *et al.*, (1979) studying the same in Coleoptera and Heteroptera, found that the eveness of the species abundance data increased throughout succession. In this study, the slopes of the rank abundance plots for the Endgroup 2 sites, representing the first four years of succession, were steeper than those of the nine year old Endgroup 1 sites. However, the slopes of the plots for the late successional sites of Endgroups 3 and 4 were in general steeper than those of Endgroups 1 and 2, and indeed the plantation sites ROP and COP were the only sites at which the species abundance data was described by the geometric series. Butterfield (1992) found a similar decrease in eveness in carabids from replanted to plantation sites, while Coyle (1981) found that the spider communities of clear-cut areas were more equitable than those of the forest habitats which preceded them. To some extent this probably reflects the limited element of the spider community studied, i.e. ground living species, but also the homogeneous nature of the habitat at these sites. The fit of the species abundance data for ROP and COP implies that one factor played an important part in the structure of the communities at these sites (Magurran, 1988), perhaps litter depth.

The importance of tree cover has been discussed above in relation to the relatively low diversity of Site 6, and the major distinction between spider communities at Hamsterley was between those typical of the wooded sites of Endgroups 3 and 4, containing the plantations and mixed-woodland, and the open Endgroup 1 and 2 sites. The former were largely characterised by the species in associations H, I and J, particularly species such as *Lepthyphantes alacris*, *L. tenebricola* and *Diplocephalus latifrons*, while the diurnal and nocturnal running spiders, ambushers and a small number of sheet web weavers in associations A to F typified the latter. However, while the spider communities of the wooded sites were very similar and showed little in the way of consistent differences associated with successional age, there were clear differences between the communities of the sparsely vegetated Endgroup 2 sites (NCF, CCF90, CCF89 and RCF with vegetation cover between 1 and 60%), representing the first four years of succession, and those of the more extensively and densely vegetated Endgroup 1 sites (Site 1 and Site 5 with 95 to 100% cover), which represent the situation after nine years. The former were characterised by a relatively small group of species in associations D and E, a number of which (i.e. *Leptothrix hardyi* and *Xysticus sabulosus*) were confined to the sites of this Endgroup. Endgroup 1 was distinguished by a relatively larger number of species such as *Clubiona reclusa*, *Cnephalocotes obscurus* and *Pardosa pullata*, in associations A and B which, while they also occurred at Endgroup 2, were more consistent and/or abundant at Sites 1 and 5.

This separation of sites based on their ground cover is in agreement with the findings of Merrett (1976), who considered that the amount of bare ground was the most useful factor when assessing the change in spider communities on a heathland in southern England after burning,. At the Endgroup 2 sites, with their generally sparse vegetation cover, the microclimate created appears to be the most important factor in the distribution of the species in association E, *Xysticus sabulosus* and *Leptothrix hardyi*, which were the species most characteristic of this Endgroup. *X sabulosus* is typical of heathland, particularly where the amount of bare ground is high (Lockett & Millidge, 1951; Merrett, 1976; Roberts, 1985), and is presumably adapted to tolerate conditions of extreme temperature and humidity, while *L. hardyi* is a stenochronous winter mature species (i.e. occurring as an adult and reproducing during this season) in the terminology of Schaefer (1987), occurring in the uplands, and on heaths in southern Britain (Lockett & Millidge, 1953; Merrett, 1976; Roberts, 1987), and presumably requiring the low temperature during winter which these habitats provide to optimise reproductive success (Schaefer, 1976, 1987). This species occurs at a number of grazed grassland sites in the northern Pennines, such as Cow Green and Grass Common in County Durham and Dun Fell and Moor House in Cumbria (Coulson *et al.*, 1984), and as such its adaptation to these habitats makes it pre-adapted to the conditions found at the early successional sites with their poorly developed vegetation layer.

Despite the extreme conditions of temperature and humidity which undoubtedly occur at the Endgroup 2 sites, a significant element of the fauna consisted of species in associations H, I and J which were more typical of Endgroups 3 and 4. This appears to be due to the fact that, while a large proportion of the litter volume at these sites is damaged or removed completely during felling and extraction of the crop, sufficient remains to provide continuity of habitat for the species inhabiting it. As succession proceeds, this litter layer further degrades as illustrated by the reduction in litter depth from 25mm at NCF, to 5mm at CCF89, and a corresponding reduction can be seen in the numbers of species such as *Monocephalus fuscipes* and *Tapinocyba pallens*. A similar decrease in litter living species was found by both Huhta (1971), and Coyle (1981) after clear-felling. While this decrease in numbers could be attributed to the effect of increasing vegetation density from NCF to CCF89 on trap efficiency, a similar pattern has been observed using absolute density measurements (J. Butterfield, pers. comm.). At RCF the process is modified by the fact that this site was created by wind action, and hence spared the effects of extraction on the litter-layer. Hence the litter-layer at this site was relatively deep (15mm as opposed to 5mm at CCF89) with a correspondingly higher abundance of the litter living species. In addition, a number of studies (e.g. Usher *et al.*, 1993; Mader, 1984) have shown that the communities of small areas of habitat are often heavily influenced by those of surrounding habitats due to their large edge to interior ratio (Downie *et al.*, 1996), and as this site was relatively small, and closely bounded on three sides by plantations, it may be that this also played a part in the relative abundance of the litter living species here.

The higher humidity at Endgroup 1 (Sites 1 and 5 with 95-100% ground cover) has already been mentioned above in relation to RCF, and the increased shading and humidity offered by the denser vegetation may be of general benefit to the nocturnal running spiders, the species of which all showed an increase in abundance and/or consistency at Endgroup 1, and particularly *Drassodes cupreus* and *Haplodrassus signifer* which do not appear to have specialised requirements for vegetation structure. As members of this guild are active during the night, when humidity is relatively high and temperature relatively low, it is likely they are not adapted to the reverse conditions during the day, as there is a close link between habit, and ability to withstand extremes of temperature and humidity (Cloudsley-Thompson, 1957; Pulz, 1987). While they are able to buffer themselves to some extent by spending the day in silken shelters which provide relatively stable conditions compared to those outside (Humphreys, 1987; Nentwig & Heimer, 1987), this may not be sufficient to protect them from the relatively extreme conditions of temperature and humidity they are likely to encounter at the Endgroup 2 sites. An exception is RCF, the similarity of which to the Endgroup 1 sites in terms of certain species has been mentioned above. This site was both wetter than the other sites in its Endgroup, and subjected to more shading from the surrounding trees due to its small size, and all of the common species of nocturnal running spiders, with the exception of *Clubiona reclusa* with its specific structural requirements, were relatively abundant here.

In addition to the more favourable microclimate provided by the vegetation cover at Endgroup 1, the increased abundance and/or consistency of certain species at this Endgroup appears to be due to the structure of the vegetation itself. Hence the diurnal running spider *Pardosa nigriceps*, which was most abundant at Sites 1 and 5, has been found to prefer taller vegetation than other members of the genus, regardless of its type (Duffey, 1962a), while among the nocturnal running spiders, both *Clubiona reclusa* and *Agroeca proxima* require specific vegetation structures to which to attach their egg-sacs or retreats (Duffey, 1962b; Jones, 1983; Gibson *et al.*, 1992). The increase in the contribution of the sheet web spinners at these sites, both in terms of number of species and abundance, was due to the increased evidence of a number of species, such as *Minyriolus pusillus, Pocadicnemis pumila* and *Dismodicus bifrons,* which are typical of well vegetated habitats (Rushton *et al.*, 1987). This suggests a requirement for structural features of the vegetation, and indeed, *Pocadicnemis pumila* was also trapped at the structurally complex Site 6. However, a number of these species were absent from this site, suggesting that some other factor may also play a part in their distribution.

Increased vegetation density may be important in other respects. White & Hassall (1994), for instance, found that there was a significant increase in the numbers of both ambushers and diurnal running spiders with increased vegetation density, and considered that this may have been due to increased prey availability due to the link between structural diversity and plant taxonomic diversity at these sites. However, a number of studies have shown that spiders do not show a numerical response to increased food supply (Riechert, 1974; Schaefer, 1978; Wise, 1979), and Jocqué (1981) considered that this was probably because spider populations were limited by space. In this study, while the numbers of the ambushers declined, the diurnal running spiders did show an increase in numbers from early- to mid- successional habitats in tandem with vegetation density. However, this was largely due to the increased abundance of certain species, such as *Pardosa pullata, P. nigriceps and Alopecosa pulverulenta*, rather than the entire guild. The association of *P. nigriceps* with more complex vegetation has been discussed above, while *P. pullata* is a species of moist habitats (Vlijm & Kessler-Geschiere, 1967; Merrett, 1976), and the observed increase may be due at least in part to an increase in the extent of favourable conditions at the mid-successional habitats for certain species.

In addition, dense vegetation may reduce mortality in overwintering spiders, as Bayram & Luff (1993) found that overwintering lycosids were more abundant in denser tussock forming grasses, perhaps because these provided the most shelter from conditions of extreme cold (Luff, 1966; Bossenbroek *et al.*, 1977), while several studies (e.g. Edgar, 1969; Hallander, 1970) have suggested that certain species benefit from increased litter complexity due to the ability to avoid predation more effectively (Uetz, 1991), and this may also apply in the case of increased vegetation complexity.

Despite the similarity in density of the vegetation layer to Endgroup 1, by the time succession had reached the stage represented by Site 6, the species typical of the earlier sites had virtually disappeared. In terms of the diurnal running spiders and ambushers, it may be that the relatively small size of the clearing in which trapping took place meant that shading from the surrounding trees made the site unsuitable. If this is the case, the absence of the nocturnal running spiders may also imply that these species have some requirement for the higher temperatures at the early successional sites, perhaps for egg development.

Alternatively, it may be that these species are unable to colonise the clearings through the intervening woodland. While both immature diurnal running spiders and ambushers can disperse by ballooning, the behaviour does not appear to be uniformly well developed in either group (Duffey, 1956; Richter, 1970). In addition the relatively small size of these clearings would limit the size of the population which could be supported, and any population which did become established would be prone to extinction due to random fluctuation in numbers.

As a consequence of this, the spider community at Site 6 was dominated by species belonging to associations H, I and J, which despite the shallow litter layer at this site, had levels of abundance comparable to those at the plantation sites, probably as a consequence of generally more favourable conditions of humidity created by the almost total tree cover. While the majority of these species were present throughout the successional gradient *Lepthyphantes alacris* and *L. tenebricola* were absent or very uncommon at Endgroup 1. These species have been shown to be associated with wooded habitats (Lockett & Millidge, 1953; Huhta, 1971; Pajunen *et al.*, 1995), and it may be that they are relatively poor colonists. *Diplocephalus latifrons* also appears to be more closely associated with wooded habitats (Huhta, 1971), though this species was absent from Site 6, and may have some specific microclimatic or structural requirement which is only present in the deeper litter of the plantation sites.

Notwithstanding the presence of the small number of species which were more typical of Endgroups 1 or 2, and hence its high score on Axis 2 of the ordination, Site 6 was extremely similar to the plantation sites, both in terms of species composition and relative abundance, and despite the division of these sites into Endgroups 3 and 4, there was relatively little in the way of consistent differences in terms of the common species among them. Hence, while the relative scores of these sites on the ordination could be considered to represent gradients based on litter depth (Axis 1) and age (Axis 2), the relative scores were probably largely dependent upon the importance of different factors at different sites, rather than a gradient involving the change in one factor. The most important factor for Site 6 appears to be its open nature allowing the persistence of a vegetation layer and species more typical of Endgroup 1. This was likely due to a combination of its relatively young age in comparison to the other sites in Endgroups 3 and 4, but also to the presence of deciduous species, as plantations of this age would be expected to have a closed canopy (Hill, 1986). Site 2 was the most mature site, and also the only one of the plantation sites with a vegetation layer, and hence structure was perhaps important for this site. In the case of NOP, ROP and COP, which were particularly close to each other on the ordination diagram, the observed differences may have been due in part to chance, though at NOP the common plantation species tended to be more abundant than at the other sites, with the exception of Site 2, and as this site had a relatively high soil organic content, and hence water content, it may be that it was generally more suitable for these species. Conversely, ROP had the lowest soil organic content of these sites, and the abundance of these species tended to be lower.

5.3. Rate of change of spider communities during succession.

Ordination techniques provide a useful method for assessing the rate of change of communities along a successional gradient (Brown & Hyman, 1986), and this technique has been used in this context in a number of studies. Hence Brown & Southwood (1987), studying plant succession, found that there was a relatively rapid change in the positions of the sites on the first two ordination axes in the first five years, but a much slower change after this, while Brown & Hyman (1986) found a similar pattern studying succession in Heteroptera. In this study, the relative positions of the sites on the ordination diagram do suggest that the rate of community change slows as succession proceeds. The plantation sites were closer together on the ordination diagram than the Endgroup 1 and 2 sites, despite the fact that the latter represent a spread of ages less than half that of the former. Even with the inclusion of Site 6, which was clearly separated from the other wooded sites, and structurally very different from them, the dispersal of points for Endgroups 3 and 4, representing a difference in ages of roughly 40 years, did not differ greatly from that of Endgroups 1 and 2.

However, it is difficult to assess the rate of change of communities in the period represented by Endgroups 1 and 2, as the catch at these sites was affected by factors such as trap efficiency and site wetness which have been dealt with above. What is clear from a consideration of the abundance of the commonest species, which contributed most to the site ordination scores, is that the changes in community structure along the successional gradient in the period represented by these Endgroups were largely due to the effective accumulation of species, and as such this is in agreement with Gibson *et al.*, (1992).

For instance, of the 11 plant species which formed the initial wave of colonisers ('primary colonisers') in the communities studied by Southwood *et al.*, (1979), six species 'though at one time they were all very abundant' had disappeared within 18 months, and in this time period roughly 20 species had disappeared overall. In contrast, of the 23 common spider species present at NCF, representing the first year after clear-felling, only two did not occur at either of the nine year old Endgroup 1 sites, while of the 14 species in associations A and B, which were most closely associated with Endgroup 1, seven were not present at NCF. This is certainly related to the ability of spiders, in contrast to plants, to seek out suitable microclimatic conditions within what may be a generally unsuitable habitat.

As tree cover increases, extinction begins to play a part in the change in community structure, as the species characteristic of open habitats disappear due to the increasing unsuitability of the microclimatic conditions. Hence while the average number of species per site increased from 40.3 to 47.5 from Endgroup 2 to Endgroup 1, the values for Endgroups 3 and 4 were 26.7 and 26.5 respectively.

5.4. Changes in the attributes of spider life cycles with succession.

Brown (1985) considered that the predictions relating to life cycle strategies, arising from the successional models proposed by Margalef (1968) and Odum (1969), could be divided into three categories, namely the degree of niche specialisation (niche breadth), the size of the organism, and the nature of the life-cycle,.

Niche breadth has often been considered in terms of the range of food taken, and it is expected that the range of prey items taken, and hence niche breadth, will decrease along the successional gradient (Margalef, 1968; Odum, 1969; Southwood, 1977). This is due to the fact that in habitats in the early stages of succession resource availability is relatively low, and as such an organism cannot afford to overlook inferior prey items. However, as succession proceeds resource availability increases, leading to selective foraging and specialisation, with correspondingly narrow food niche breadths (Pianka, 1981). A number of previous studies have shown that this appears to be the case. Hence Brown (1985) found that in Heteroptera the proportion of generalist species, in terms of the number of plant species fed upon, declined along the successional gradient, while specialist species showed an increase, while Brown & Southwood (1983) found a similar decline in niche breadth in the entire exopterygote fauna.

In this study niche breadth, as represented by the range of prey taken by individual spider species, does seem to show a general decrease towards the late successional stages. Many of the species characteristic of Endgroups 1 and 2, such as the diurnal running spiders and ambushers, are relatively polyphagous, feeding on a wide range of insect groups and other spiders (Nentwig, 1986, 1987), while the sheet web spinners, such as those which characterise the later stages of succession at Hamsterley, are relatively selective feeders (Nentwig, 1980) and at altitude prey largely upon Collembola (Otto & Svensson, 1982; Coulson & Butterfield, 1986). However, as the abundance of many invertebrate groups tends to be decreased by afforestation (Butterfield, 1992) this does not appear to be the result of increased prey availability, but rather an artefact of the disappearance of the more polyphagous species due to reduced vegetation structure and increased tree cover, and the subsequent limited spider fauna of Endgroups 3 and 4.

In terms of the size of individual organisms, it is generally considered that there will be a tendency to increase in size along the successional gradient (Odum, 1969). However, in this study this does not seem to be the case, as many of those species more typical of the earliest stages, such as the nocturnal and diurnal running spiders and the ambushers, are larger spiders than the linyphiids which dominate the late successional sites. While this again may be as a result of the limited fauna of Endgroups 3 and 4 at Hamsterley, a number of recent studies have also found that size did not increase along the successional gradient. Hence, Brown (1985) found that the Heteroptera of early successional habitats were of intermediate size compared with those of the later stages, while Brown & Southwood (1987), looking at the changes in bird and small mammal communities during succession, found that neither group followed the expected pattern.

Odum (1969), who was one of the first to put forward this suggestion on the basis of successional changes of algae in a laboratory microcosm, was unsure whether the relationship between organism size and successional stage was characteristic of succession, or merely fortuitous, and Schoener & Janzen (1968) considered that small insects would not be liable to exploit habitats early in the successional process because they are vulnerable to attack by predators and are more prone to desiccation than larger species. However in habitats such as this small size could be considered an advantage as it would allow organisms to exploit the smallest areas of suitable habitat. Small size could also be an advantage in late successional habitats, as it might be expected that the increased competition in these habitats would push species to use smaller niches, and it may be that an increase in size is not a general rule along successional gradients.

Related to the size of organisms along a successional gradient, is the degree of morphological variation in the community. Previous research has suggested that as succession proceeds, so the range of variation, in terms of both size and shape should increase. Hence Brown (1982) found that the range of variation in Heteroptera along a successional gradient increased, with those in the early successional stages being fairly consistent in terms of both size and shape, and Brown (1982) also considered this true of the species in Southwood *et al.*, (1979). In the case of this study, it is certainly the case that these factors show the opposite trend, though again this appears to be an artefact of the limited nature of the communities at Endgroups 3 and 4.

Life-cycles can be considered in terms of the r-K continuum (MacArthur & Wilson, 1967). In relation to succession, organisms in early successional stages, where communities are not saturated and populations not at equilibrium (Southwood *et al.*, 1979), would be expected to tend towards r-selection, developing rapidly, producing large numbers of offspring in a relatively short time, and, as these habitats are relatively transitory, having a well developed dispersal ability. As succession proceeds, organisms would become more K-selected developing more slowly, having relatively longer life-cycles, producing their offspring over an extended period, and having a relatively poorly developed dispersal ability (MacArthur & Wilson, 1967; Odum, 1969; Pianka, 1970; Southwood, 1977; Krebs, 1978; Brown & Southwood, 1983). Hence Brown (1985) found that the number of generations per year and proportion of bi- or multivoltine species among Heteroptera was greater in the early stages of succession than subsequent stages, while Brown & Southwood (1983) found a similar pattern with all exopterygote herbivores. In spiders, a number of studies have found that early successional communities, or similar habitats with poorly developed vegetation structure, tend to be dominated by a relatively small number of linyphiid species such as *Bathyphantes gracilis*, and species of the genera *Oedothorax* and *Erigone,* which are highly invasive, and are able to produce a number of generations a year (Meijer, 1977; Rushton *et al.*, 1987; Maelfait & de Keer, 1990; Gibson *et al.*, 1992), though at Hamsterley these species did not make up a significant part of the catch at any site.

In terms of voltinism, a consideration of the monthly catches at Hamsterley, and of time of occurrence given in Lockett & Millidge (1951, 1953) and Jones (1983), did not indicate that spiders characteristic of the earlier stages of succession completed more generations in a year than those later in the process. Seasonal occurrence of adult spiders does show some variation, with the common species at Endgroups 3 and 4 generally being active for all or most of the year, likely due to the protective nature of the leaf litter, while a number of species in Endgroups 1 and 2 have a more limited seasonality, usually from spring to autumn. In addition, a number of those species which were most characteristic of Endgroup 2 have seasonal occurrences which avoid high summer, namely *Pardosa amentata, Trochosa terricola* and *Xysticus sabulosus.*

Huhta (1971) pointed out that while summer daytime temperatures in clear-felled habitats were higher than in the preceding woodland, the increased heat loss at these sites due to the removal of tree cover resulted in relatively low night-time and winter temperatures. At Hamsterley heat loss is also likely to be higher from the Endgroup 2 sites (NCF, CCF90, CCF89 and RCF with 1- 60% ground cover) than those of Endgroup 1 (Site 1 and Site 5 with 95-100% ground cover), as the dense and extensive vegetation layer of the latter is likely to provide a degree of insulation at these sites. Hence an important consideration for species at the Endgroup 2 sites would be how to survive the relatively low temperatures during the winter months. This is certainly of importance for the diurnal running spider *Pardosa amentata,* as Bayram & Luff (1993) found immatures of this species active during the winter at temperatures just above freezing, and considered that this species, and other winter-active lycosids, probably overwintered in a non-diapausing state, and would therefore be susceptible to the effects of low temperature. Immatures of this species have been shown to overwinter in the litter-layer (Maelfait & de Keer, 1990), and at Hamsterley are presumably able to utilise the patches of leaf-litter remaining after clear-felling to this end. However, while the depth of leaf litter at the Endgroup 2 sites shows a decrease from NCF (first year after clear-felling) to CCF89 (third year), the numbers of this species trapped showed an increase, despite the increased vegetation density and associated decrease in trap efficiency, and it may be that this species was also able to utilise the increasing vegetation layer to provide protection during winter, though Bayram & Luff (1993) did not find *P. amentata* in large numbers in grass tussocks during this time. *Trochosa terricola* gains protection from low temperatures during the winter by overwintering in a burrow in the ground lined with silk for extra insulation (Engelhardt 1964). This is particularly important for members of this genus, as the temperature at which their rate of metabolism becomes too low to allow movement (chill-coma, Kirchner, 1987) can be as high as +2.5 °C (Engelhardt, 1964). Under these conditions neither feeding nor escape from predators is possible, and an important aspect in the choice of overwintering sites for both *P. amentata* and *T. terricola*, in addition to protection from extreme temperatures, may be that they provide protection from predation when temperatures are not low enough to be fatal, but are sufficient to induce chill-coma. Lack of ability to feed is perhaps not so much of a problem for these species, as spiders are able to go for extended periods of time without feeding (Strazny & Perry, 1987), and in addition a number of lycosid species, including *P. amentata*, have been shown to feed during the winter when temperatures are high enough to allow activity (e.g. Bayram & Luff, 1993; Aitchison, 1987).

I could find no information regarding overwintering phase or physiological adaptations to low winter temperatures for the ambusher *Xysticus sabulosus*, though as this species does seem to be closely adapted to habitats with a low percentage of ground cover (Merrett, 1976), it might be expected that such adaptations exist. As the reproductive period of this species is from late summer to early autumn (Lockett & Millidge, 1951; Jones, 1983) it may fall into the category of 'stenochronous species reproducing in autumn' (Schaefer, 1987). Many of these species hibernate in the egg stage (Schaefer, 1987) which has been shown to be the most resistant stage of many spider species to low temperatures, and would thus be the optimal stage for survival during freezing conditions (Kirchner, 1987).

In contrast to the above species, for *Leptothrix hardyi* low winter temperatures are likely to be a pre-requisite, as this species occurs as an adult, and has its reproductive season, during the winter months (Merrett, 1976). In another winter-mature linyphiid, *Stemonyphantes lineatus*, males are only able to mate after having been exposed to low temperatures for some weeks, and the ovaries of females only develop after exposure to cold under short-day conditions (Schaefer, 1976, 1987). However, winter-mature species are not necessarily resistant to low temperatures. The linyphiid *Centromerus silvaticus*, for instance, has been shown to have a low resistance to cold, and the mortality rate of this species can be high and is directly related to the severity of the winter (Schaefer, 1977). It may be that the apparent absence of *L. hardyi* from NCF, where ground cover was less than 2%, was because of the particularly severe weather conditions at this site during the winter, though this species has been recorded in the northern Pennines at heights up to 520m (Coulson *et al.*, 1984), and it may be that some other factor played a part, perhaps unsuitable conditions during the spring and summer when this species is immature. Alternatively, as clear-felling took place at this site in late winter 1990-1991, it may be that this site only became available for colonisation after the main dispersal period of *L. hardyi*, though this would depend on the exact timing of dispersal, and the rate at which suitable habitat became available during the felling process.

In terms of dispersal, changes in this ability along the successional gradient are difficult to assess, as while dispersal by ballooning has been observed in many spider families (Duffey, 1956; Richter, 1970; Decae, 1987) the ability varies even between closely related species (Duffey, 1956; Richter, 1970) and information on particular species is often lacking. The ability is best developed in the Linyphiidae, but while this family was dominant in terms of species at all stages of succession, among the species most characteristic of Endgroup 2, only three species were members of this family. Of these only *Lepthyphantes mengei* has been recorded as an aeronaut (Duffey, 1956), while of the eight other common species of this family in associations A, B and F which occurred at Endgroup 2, references to this behaviour were found for *Dismodicus bifrons, Micrargus herbigradus,* and *Cnephalocotes obscurus* (Duffey, 1956; Huhta, 1971). I could find no references to ballooning in the plantation species, though this does not mean it does not occur, and as one of the advantages of this sort of dispersal is that it minimises overcrowding (Foelix, 1982) we might suppose that the possession of this ability in late successional species, where densities are highest, would be advantageous.

The remaining species characteristic of Endgroup 2 belonged either to the Thomisidae or Lycosidae, and while ballooning has been observed for both families, it may not be general, and is not equally well developed in all species. Both Bristowe (1929) and Nielsen (1932) reported ballooning behaviour in immature thomisids, the latter of an unidentified species, the former in a member of the genus *Xysticus*, while Duffey (1956) did not find any members of this family as aeronauts in grassland. Of the lycosids, Richter (1970) considered both *Pardosa amentata* and the Endgroup 1 species *P. pullata* as displaying a poor dispersal capacity, while that of another Endgroup 1 species, *P. nigriceps*, was much better developed.

An interesting point to come from Richter's study was that, in general, species which occurred in widespread and abundant habitats did not show a well developed ability to balloon. Hence, while there does appear to be a greater evidence of aeronautic species at the early successional in this study, the fact that it is not more evident is perhaps not surprising, as the majority of species characteristic of the earlier stages of succession at Hamsterley are not pioneers in the strict sense that they are closely adapted to the conditions found in these habitats, rather they are probably species which were available to colonise them when they became available and are able to tolerate the conditions they found. While there is little evidence for the occurrence of the species characteristic of Endgroups 1 and 2 in the late successional habitats at Hamsterley, species such as the diurnal running spiders *Pardosa amentata, P. pullata* and *Alopecosa pulverulenta* are common and widespread species in Britain (Lockett & Millidge, 1951; Jones, 1983; Roberts, 1985), occurring in a wide range of open habitats, and populations of these species may occur in woodland rides at Hamsterley. The early successional habitats at Hamsterley were generally dominated by *Calluna vulgaris* at the time of trapping, and both the sheet web weaver *Lepthyphantes mengei* and the diurnal running spider *Trochosa terricola* are associated with habitats of this nature (Lockett & Millidge, 1951; Coulson & Butterfield, 1986). Hence these species are probably widespread on the surrounding moorland at Hamsterley, and in this case at least *L. mengei* appears to be an accomplished aeronaut.

Brown (1985), studying Heteroptera, found that the in the early stages of succession a higher proportion of species overwintered as adults, and considered that this fact, combined with the higher dispersal ability of species at these stages, would allow rapid invasion of new habitats and immediate reproduction. Unlike insects, in which reproductive and dispersal ability are linked, many spiders are only able to disperse in immature stages, and for those species which can disperse as adults, i.e. linyphiids, the season when this occurs is limited, again unlike insects. In the case of the linyphiids aerial dispersal takes place during the autumn and winter (Foelix, 1982), when many members of this family have their reproductive season, which is in essence the same as insects overwintering as adults. However, as many linyphiids appear to have their reproductive season at this time of year, there seems little point in trying to link this characteristic with particular stages of succession.

In the case of families other than the Linyphiidae, aerial dispersal takes place in the immature stages, and hence in order for the life-cycle of a non-linyphiid spider to approximate to that of early successional insects, the species in question would be required to balloon as a late instar immature. This would allow the shortest possible developmental period between arrival at a habitat and the commencement of reproduction. Again it is difficult to assess this in the early successional species at

Hamsterley due to the lack of information on ballooning behaviour in individual species, let alone the developmental stage at which it occurs. However, *Pardosa amentata*, which was characteristic of Endgroup 2, begins it reproductive period in spring and does overwinter as a late instar immature (Richter, 1970). However, the poor dispersal ability of *P. amentata* has already been dealt with above, and in addition, Richter (1970) found that dispersal ability in this species was best developed in young instars, and was absent in sub-adults, which are the most mature stage at which this species overwinters. Richter (1970) also investigated the ballooning behaviour of the closely related *P. purbeckensis*. This species is not strictly speaking a colonist, but is found on mud flats, which are local in their occurrence, and *P. purbeckensis* did show a well developed dispersal ability. In addition, aeronautic behaviour occurred more frequently in the later instars of *P. purbeckensis* than those of *P. amentata*, and in fact was observed in adults of this species. Hence it may be that non-linyphiid spider species in early successional habitats will be found to be able to disperse in later instars than those in more mature habitats.

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Appendix 1. Spider species list for 11 sites studies at Hamsterley Forest.

SPECIES	SITE 1	SITE 5	NCF	CCF89	CCF90	RCF	SITE 2	COP	ROP	NOP	SITE 6
Amaurobiidae											
Amaurobius fenestralis							10				
Segestriidae											
Segestria senoculata											1
Gnaphosidae											
Drassodes cupreus	6	4			1	10					
Haplodrassus signifer	44	8		4	2	10	2				1
Gnaphosa leporina					1						
Micaria pulicaria	7	2				2					
Clubionidae											
Clubiona reclusa	18	2				1					
C. trivialis	1	1				1					
C. diversa	5	6									
Agroeca proxima	9	6		1	3	19			1		
Thomisidae											
Xysticus cristatus	9	1	19	6	2	11					
X. sabulosus			1	17	2						
Salticidae											
Heliophanus flavipes			1	2							

Appendix 1.(continued).

SPECIES	SITE 1	SITE 5	NCF	CCF89	CCF90	RCF	SITE 2	COP	ROP	NOP	SITE 6
Lycosidae											
Pardosa palustris			7	3	6						
P. pullata	252	439	67	46	40	60				1	
P. amentata	19	5	42	102	78	89					
P. nigriceps	56	32	10		2	8					
Alopecosa pulverulenta	231	173	37	20	21	178					
A. barbipes	1										
Trochosa terricola	3	3	7	3		17			1		
Pirata piraticus						1					
Agelenidae											
Coelotes atropos		1		4		17	9	3	2		
Cryphoeca silvicola	2	1			2	1	74	4	13		2
Mimetidae											
Ero furcata	2		1								
Theridiidae											
Robertus lividus	29	6		1		1			2		5
Pholcomma gibbum								1			
Theonoe minutissima									1		
Tetragnathidae											
Pacygnatha degeeri	1										
Meta segmentata			1			1	1				

Appendix 1.(continued).

SPECIES	SITE 1	SITE 5	NCF	CCF89	CCF90	RCF	SITE 2	COP	ROP	NOP	SITE 6
Tetragnathidae(cont.)											
M. mengei							1	1			
Linyphiidae											
Ceratinella brevipes	5	4		2	1	1	1			1	8
Walckenaeria nudipalpis	1										
W. antica			5	1		4			2	1	1
W. acuminata	19	22		6	2			10			
W. cucullata	6	7	22	1	6	17	14	9	12	27	8
Dicymbium tibiale		1								2	4
Dismodicus bifrons	14	4	2		1	9					
Hypomma bituberculatum	1										
Metopobactrus prominulus						2	1				
Gonatium rubens	19	26	1	1		1					
Maso sundevalli											8
Peponocranium ludicrum	5	2			1						
Pocadicnemis pumila	51	128	3			2					4
Oedothorax gibbosus										1	
O. fuscus				1							
O. retusus	1					1					
Pelecopsis mengei	4				2						
Silometopus elegans	3	1	1	12	4	1					
Cnephalocotes obscurus	65	11				7					
Minyriolus pusillus	7	20	1								2
Tapinocyba pallens	6	18	21		10	15	51	26	16	32	14

Appendix 1.(continued).

SPECIES	SITE 1	SITE 5	NCF	CCF89	CCF90	RCF	SITE 2	COP	ROP	NOP	SITE 6
Linyphiidae(cont.)											
Monocephalus fuscipes	23	43	36	9	21	12	101	61	29	54	49
Gongylidiellum vivum	1	5	1		1			1			
Micrargus herbigradus	4	8		1	3	1	1	3			
Erigonella hiemalis	2	2									4
Savignia frontata				1							
Diplocephalus latifrons			3	3	18	2	25	24	7	70	
D. picinus							3				5
Typhochrestus digitatus				2	1						
Erigone dentipalpis			2								
E. promiscua				1							
E. atra				1							
Leptothrix hardyi				28	3						
Porrhomma pygmaeum		1									
P. pallidum			1		1		4		5	3	
P. micropthalmum								1			
P. montanum									1		1
Agyneta conigera			7				1		4	5	1
A. ramosa											10
Meioneta gulosa			2	1							
Maro minutus	5	3				1					1
Centromerus sylvaticus	1				1					1	2
C. prudens		1	1	1	2			3	1	3	
C. arcanus				1	3			8			1
C. dilutus		1	1	2		2	5		6	2	6

Appendix 1.(continued).

SPECIES	SITE 1	SITE 5	NCF	CCF89	CCF90	RCF	SITE 2	COP	ROP	NOP	SITE 6
Linyphiidae(cont.)											
Centromerita concinna				6	7	2					
Saaristoa abnormis	7	4	4	2	1	2	4	3	1	2	3
Macrargus rufus					2		3		1		
Bathyphantes gracilis	1		2			2					
B. parvulus	1	37			1						12
Diplostyla concolor											1
Poeciloneta variegata	1	1		1					1		
Drapetisca socialis								1			
Tapinopa longidens					2						
Stemonyphantes lineatus						1					
Bolyphantes luteolus			1		1						
B. alticeps						2					
Lepthyphantes alacris		2	10				9	14	7	25	20
L. obscurus								1	1	2	
L. tenuis	1		2	1				1		1	
L. zimmermanni	10	5	25	10	24	9	52	21	25	39	26
L. cristatus											3
L. mengei	4	4	8	4		13	1				1
L. flavipes					1		1				
L. tenebricola		2	4		5	2	23	22	9	42	6
L. ericaceus	1	5	4	1	7	2		8		2	1
L. pallidus	2			1	1			1	1	1	1
L. expunctus	1						1				
Linyphia hortensis.							3				2

Appendix 1.(continued).

SPECIES	SITE 1	SITE 5	NCF	CCF89	CCF90	RCF	SITE 2	COP	ROP	NOP	SITE 6
Linyphiidae(cont.)											
Neriene montana							1				
N. clathrata							1				
N. peltata							1				1
Microlinyphia pusilla	1	2				1	1				
TOTAL	968	1060	363	310	293	542	405	227	149	317	215

Appendix 2a. Species list for grassland and habitat edge at Wilton Moor.

SPECIES	9m			7.5m			6m			4.5m			3m			1.5m			Edge		
Amaurobiidae																					
Amaurobius fenestralis					1											2					
Gnaphosidae																					
Drassodes cupreus	1		6							1			1			8		4	1	7	1
Haplodrassus signifer			3		1						1		1			4	1	3	4	15	6
Gnaphosa leporina	1																				
Micaria pulicaria																			2	3	4
Thomisidae																					
Xysticus cristatus		1		1	3																
Lycosidae																					
Pardosa palustris			2															1			
P. pullata	7	9	66	14	49		3		3	3	16	3	6	2		23	19	47	5	12	2
P. nigriceps				2													1				
Alopecosa pulverulenta		1	3	1	3					1	2		1			4	4	1	1	5	3
Trochosa terricola	1	1	1		2											1		2			
Agelenidae																					
Coelotes atropos																					1
Cryphoeca silvicola			2		1					1	1					1			2	1	1

Appendix 2a. (continued).

SPECIES	9m			7.5m			6m			4.5m			3m			1.5m			Edge		
Mimetidae																					
Ero furcata												1									
Theridiidae																					
Robertus lividus	1		1	1	1						1		1	1		1	1	3	3	5	2
Tetragnathidae																					
Pacygnatha degeeri	5	3	27	11	23	1	3	2	4	2	24	6	7	8	1	11	15	14	7	7	2
Linyphiidae																					
Ceratinella brevis					1					1	1		1		1	6	3	1	2	6	2
C. brevipes																1		1	2	1	1
Walckenaeria acuminata														1		1		1	2		1
W. vigilax	1	4	1	3	6											1					
Dicymbium nigrum	1		1	1					1	1	1		1			1		1			
f. brevisetosum		1												1		1					
D. tibiale		1					1	1				1								1	4
Dismodicus bifrons			1				1														1
Hypomma bituberculatum							1														
Gonatium rubens			1						2		1				1				1	1	
Peponocranium ludicrum																					1
Pocadicnemis pumilla				1							1			1		1	2	1	2	11	4
Oedothorax fuscus			2		4					1											
O. retusus	16	10	17	17	40		6		10	7	13	5	4	6	1	8	6	4	1	1	2

Appendix 2a. (continued).

SPECIES	9m			7.5m			6m			4.5m			3m			1.5m			Edge		
Linyphiidae (cont.)																					
Pelecopsis mengei	2		1	1	1		2			1	2		1	2		1		4	11	13	17
Silometopus elegans		2	8	2	5		1			2	1			1							
Tiso vagans	1		1	1	5		1			1	5			3		7	13	6	9		
Tapinocyba pallens																			2	1	2
Gongylidiellum vivum			2		5		3		1		3		2	4	1	2	3	2	1		
Micrargus herbigradus			1		1		1		1	1			4	2	1		2	5	8	8	4
M. subaequalis																		1			1
Erigonella hiemalis											1			1		1	1		1		
Savignya frontata					2						1										
Diplocephalus latifrons																1			2		
Erigone dentipalpis	4	6	23	3	7		2		1	1	7		3		1	15	2			1	
E. atra	2		1	2														1			
Meioneta saxatilis			1	1	3	1				1	1	1	2		1	1	4	11	20	12	28
M. beata																		1			
Centromerus sylavaticus																				1	
Centromerita bicolor	1																1				
Saaristoa abnormis									1											1	
Macrargus rufus			1																		
Bathyphantes gracilis	6	4		4			3	4	1		1	2	6	3		1			1		1
B. parvulus		1		1	2		6	1	6				5		1		1	3	1	1	1
Diplostyla concolor														1					1		
L. tenuis	2	1		3	3	1	5	2	1	1	1	6	6	5	3	1	2	5		2	4
L. zimermanni			1					1				1						1		1	

Appendix 2a. (continued).

SPECIES	9m			7.5m			6m			4.5m			3m			1.5m			Edge		
Linyphiidae (cont).																					
L. mengei				3			1	1			3	1		1		1	4	2	3	2	7
L. ericaceus	1	1	1		4		9	1	7	3	5	3	5	5	1			9	4	4	6
L. pallidus							1														
Allomengea scopigera							1						1								
TOTALS	53	46	175	73	173	3	51	13	39	29	93	30	58	48	13	106	85	135	99	123	109

Appendix 2b. Species list for plantation at Wilton Moor.

SPECIES	1.5m			3m			4.5m			6m			7.5m			9m		
Gnaphosidae																		
Drassodes cupreus			1		1	1												
Haplodrassus signifer	1		2			1		1					2	1			1	
Micaria pulicaria		1	1															
Lycosidae																		
Pardosa palustris														1				
P. pullata		3	5					1							1			
P. nigriceps					1													
Alopecosa pulverulenta			2		1											1		
Trochosa terricola		1											2					
Agelenidae																		
Cryphoeca silvicola	3	1	9	1	3	6		1	1		2	1	1	2	3	1		2
Theridiidae																		
Robertus lividus	3	2	3	1	2	3		2	2	1			3	1	1		1	3
Tetragnathidae																		
Pacygnatha degeeri	4	2	4		2				1						1			
Linyphiidae																		
Ceratinella brevis	3	1	8	2	5	3	2	4	2		2		2	6	1	11	5	5
C. brevipes	1	2	5	1	1	2	1	1	4			1		1	1	1	1	2

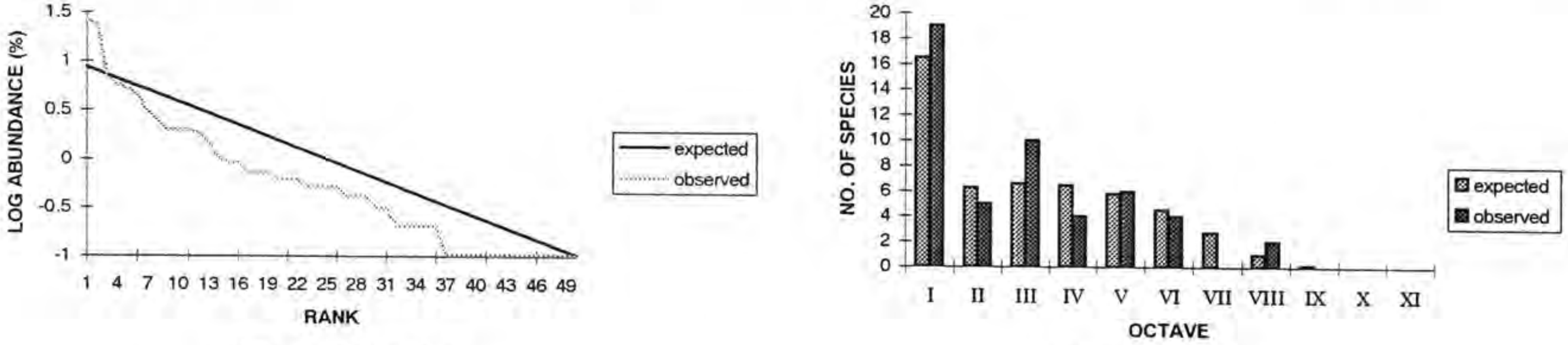
Appendix 2b. (continued).

SPECIES	1.5m			3m			4.5m			6m			7.5m			9m		
Linyphiidae (cont).																		
Walckenaeria acuminata		1			1											1		1
Dicymbium nigrum	2																	
D. tibiale		1				1						1						
Dismodicus bifrons		1	2	1					2	1								
Gonatium rubens																1		
Maso sundevalli												1						
Pocadicnemis pumilla		2	4			1			1									
O. retusus			1		1									1				
Pelecopsis mengei	1	9	6	1	6	2	3	2	2		1	1		5	2	5	1	1
Silometopus elegans			2											1				
Cnephalocotes obscurus																1		
Tiso vagans			1		1						1							
Monocephalus fuscipes						1		1										
Gongylidiellum vivum		3	3	1						1				1				
Micrargus herbigradus	11	5	5	3	13	2	2	3	6	8		1	4	3	2	1	1	1
Erigonella hiemalis	1		2															
Diplocephalus latifrons			3	1	3			2	13	9			1	8	2	4	3	1
Agyneta cauta																		1
A. conigera					2													
Meioneta saxatilis	4	10	16	5	4	1		2	3			1		1		1		1
Centromerus sylavaticus																1		
C. dilutus														2			1	
Saaristoa abnormis										1	2		3			1	2	

Appendix 2b. (continued).

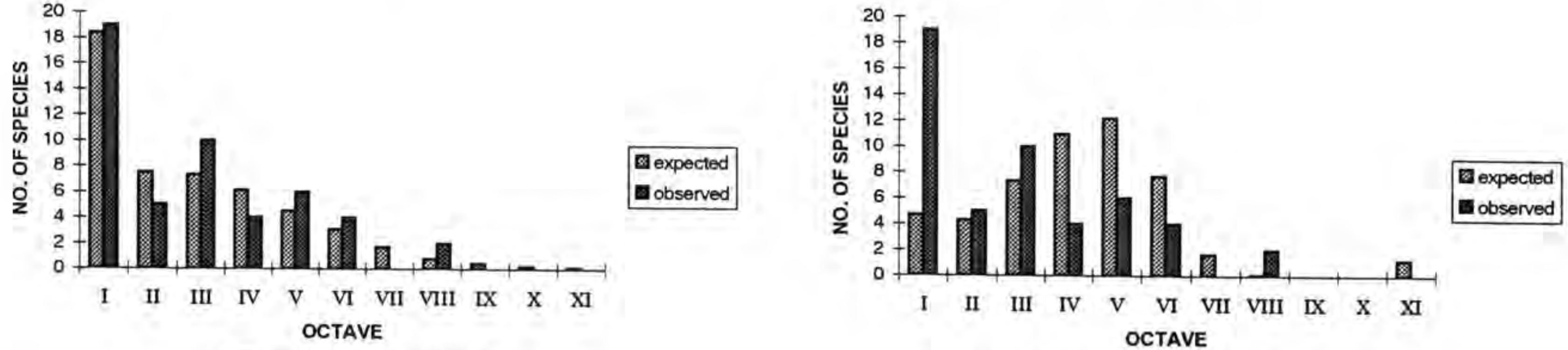
SPECIES	1.5m			3m			4.5m			6m			7.5m			9m		
Linyphiidae (cont).																		
Macrargus rufus		1			3		1	2			1			1			1	
Bathyphantes gracilis												1	3					
B. parvulus		3	2	1	1		1	1	3							1		
Stemonyphantes lineatus						1												
Lepthyphantes alacris					2		1	1	5			3			2	2		2
L. tenuis	2	3	2		1			3	2			2						
L. zimermanni	1	4			7	9	12	10	7		4	4	1	6	2	2		2
L. mengei	3	3	1		7	3		1						1				
L. tenebricola		1						1	2					1		2	2	1
L. ericaceus	3	6	4		3	3	2	10	5		8	1	5	5	9	3	1	7
L. pallidus		1																
TOTALS	43	67	94	18	71	40	25	49	61	21	21	18	27	48	27	40	20	30

Appendix 3a. Fit of the geometric series, log series, log normal and MacArthur's broken stick to Site 1 species abundance data.



a) Geometric series

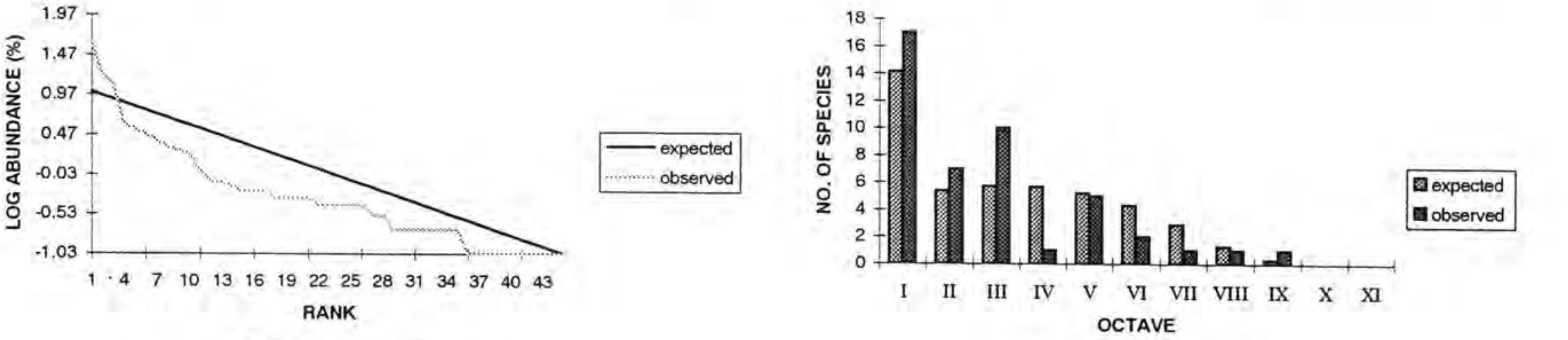
b) Logarithmic series



c) Truncated log normal

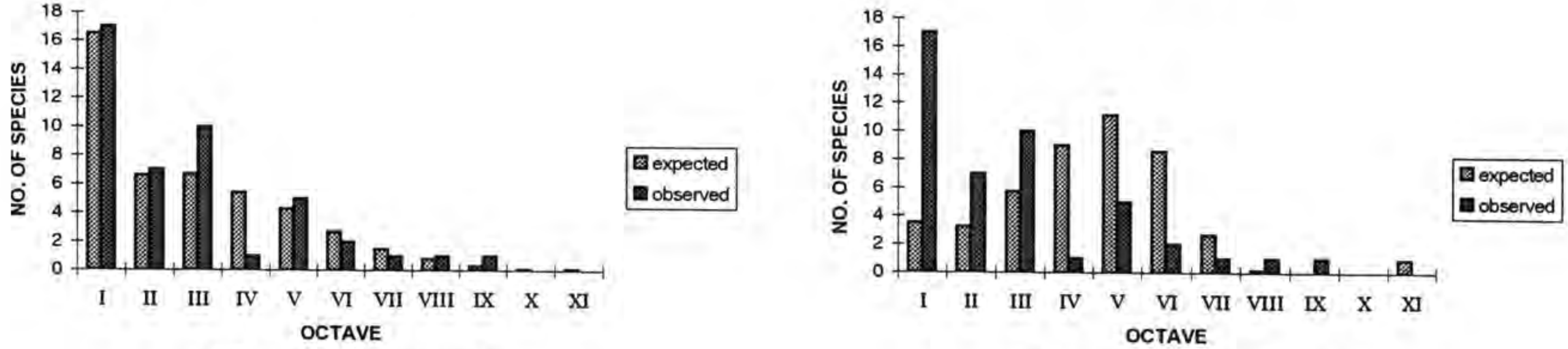
d) Macarthur's Broken Stick

Appendix 3b. Fit of the geometric series, log series, log normal and MacArthur's broken stick to Site 5 species abundance data.



a) Geometric series

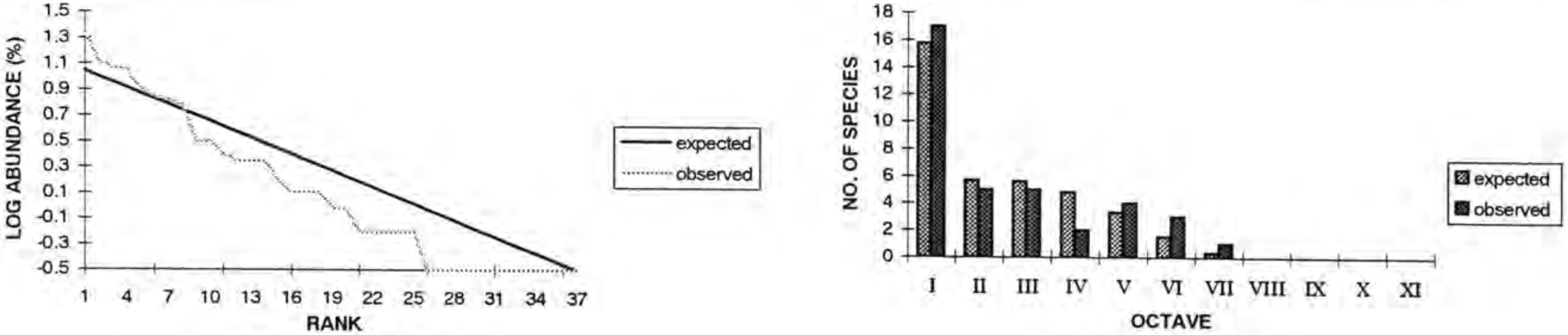
b) Logarithmic series



c) Truncated log normal

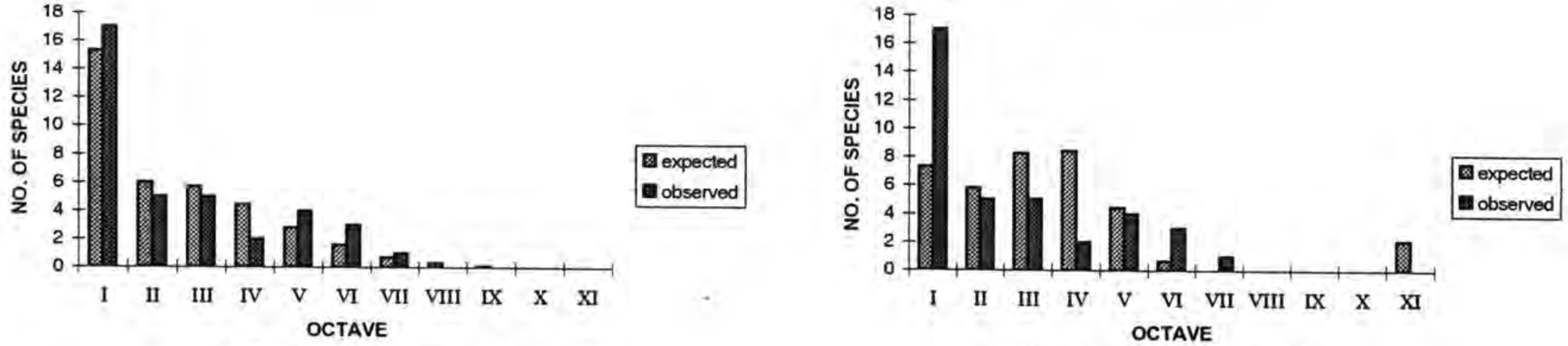
d) Macarthur's Broken Stick

Appendix 3c. Fit of the geometric series, log series, log normal and MacArthur's broken stick to NCF species abundance data.



a) Geometric series

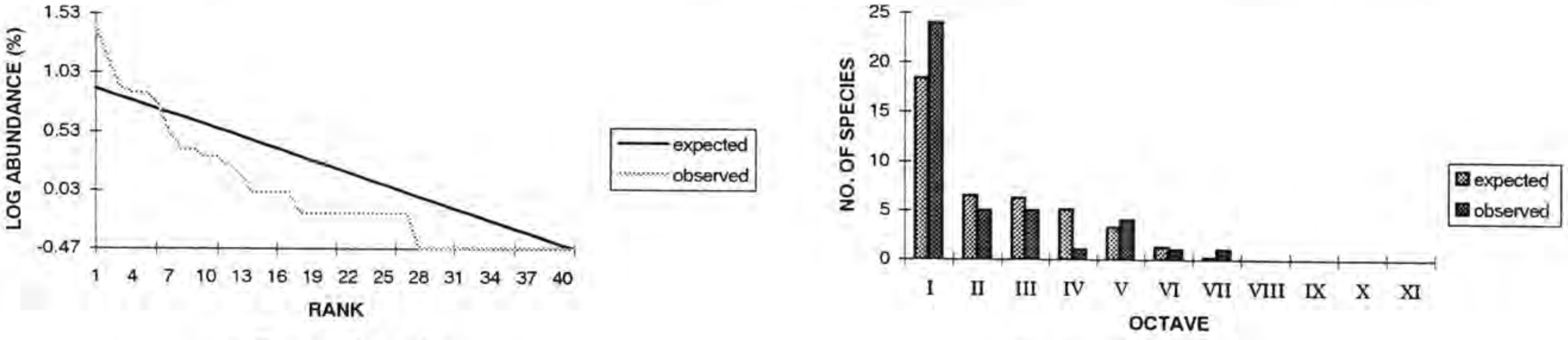
b) Logarithmic series



c) Truncated log normal

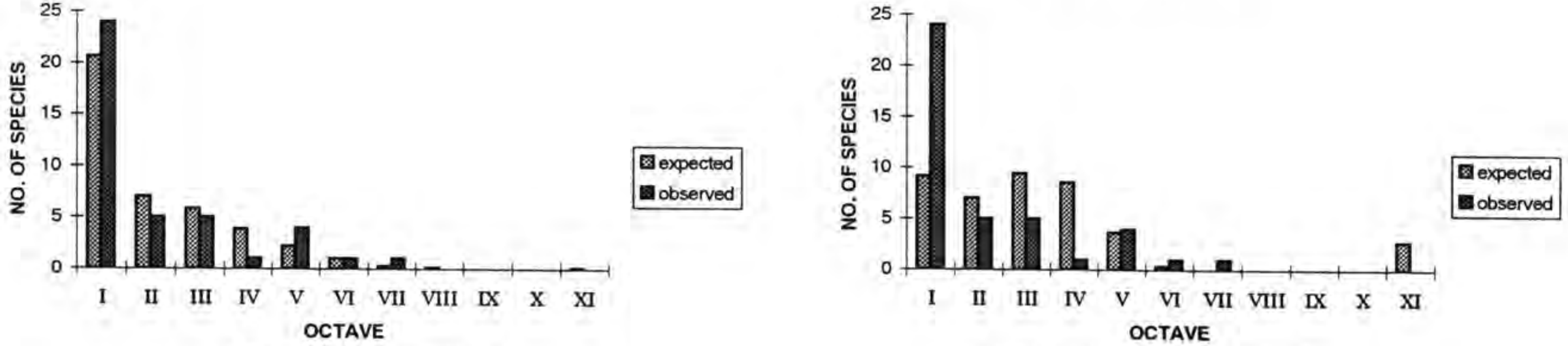
d) Macarthur's Broken Stick

Appendix 3d. Fit of the geometric series, log series, log normal and MacArthur's broken stick to CCF90 species abundance data.



a) Geometric series

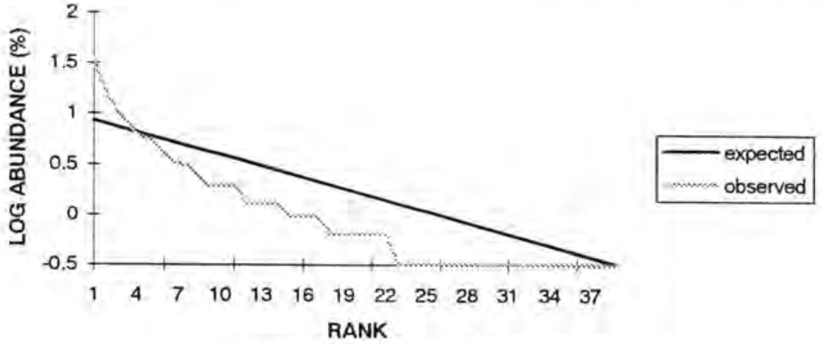
b) Logarithmic series



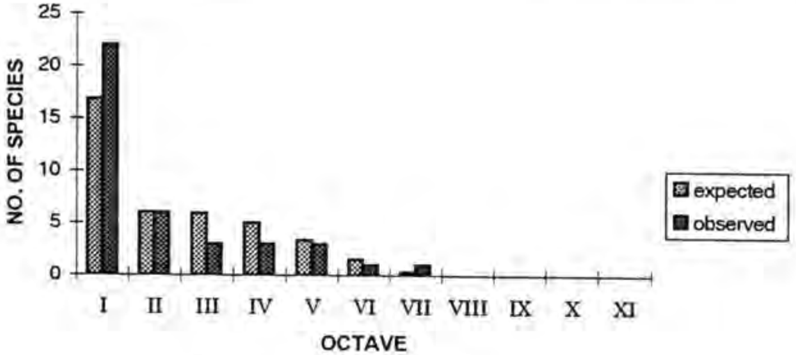
c) Truncated log normal

d) Macarthur's Broken Stick

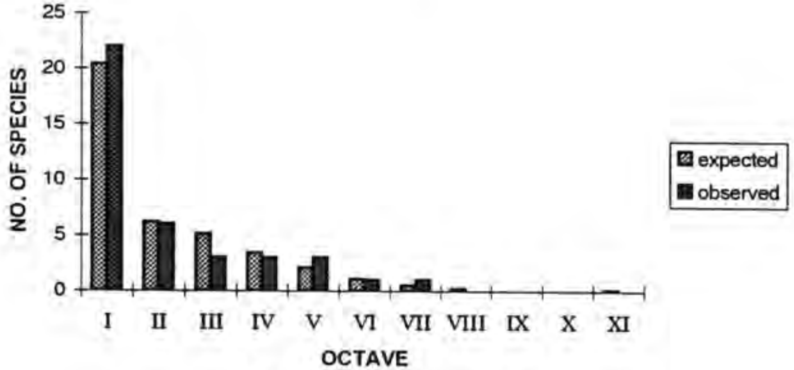
Appendix 3e. Fit of the geometric series, log series, log normal and MacArthur's broken stick to CCF89 species abundance data.



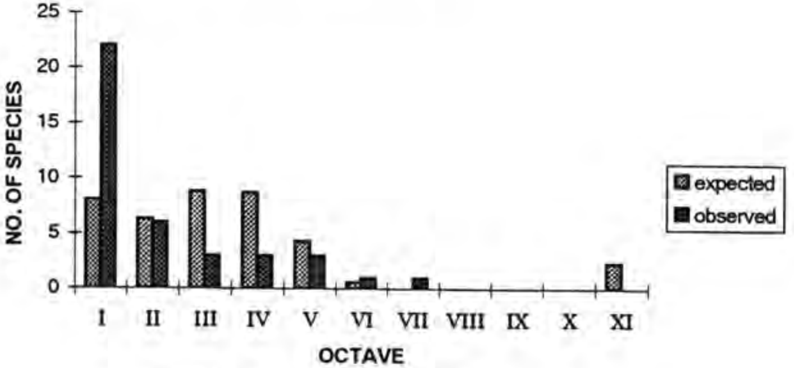
a) Geometric series



b) Logarithmic series

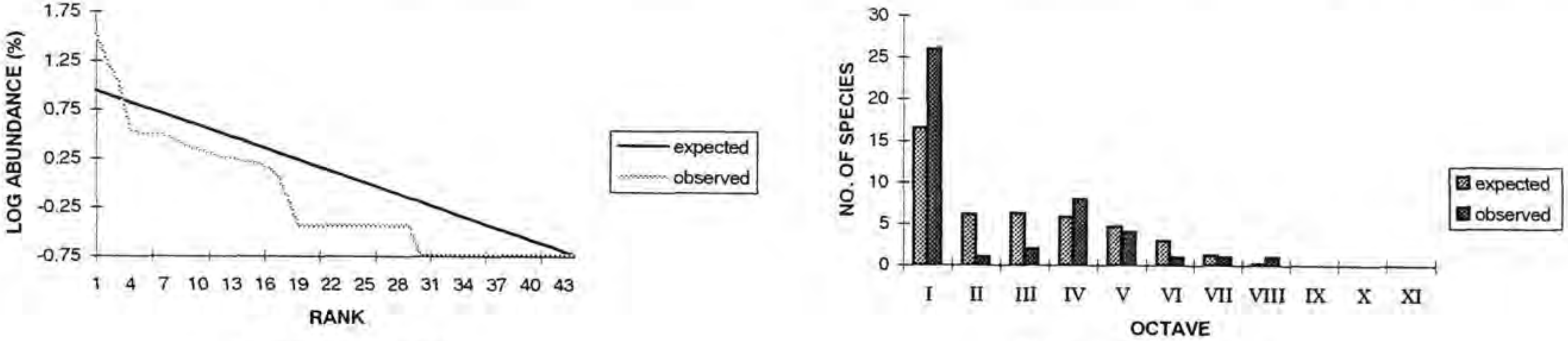


c) Truncated log normal



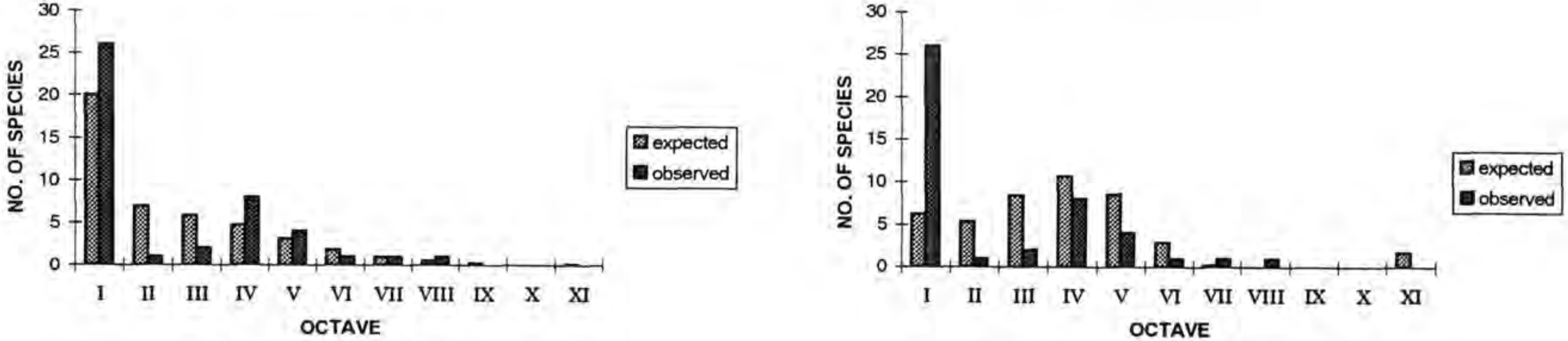
d) Macarthur's Broken Stick

Appendix 3f. Fit of the geometric series, log series, log normal and MacArthur's broken stick to RCF species abundance data.



a) Geometric series

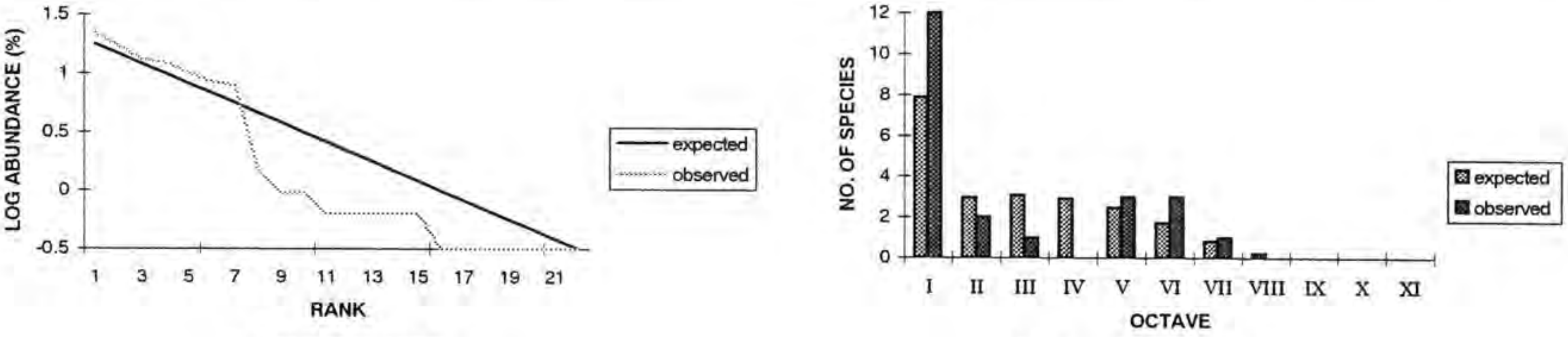
b) Logarithmic series



c) Truncated log normal

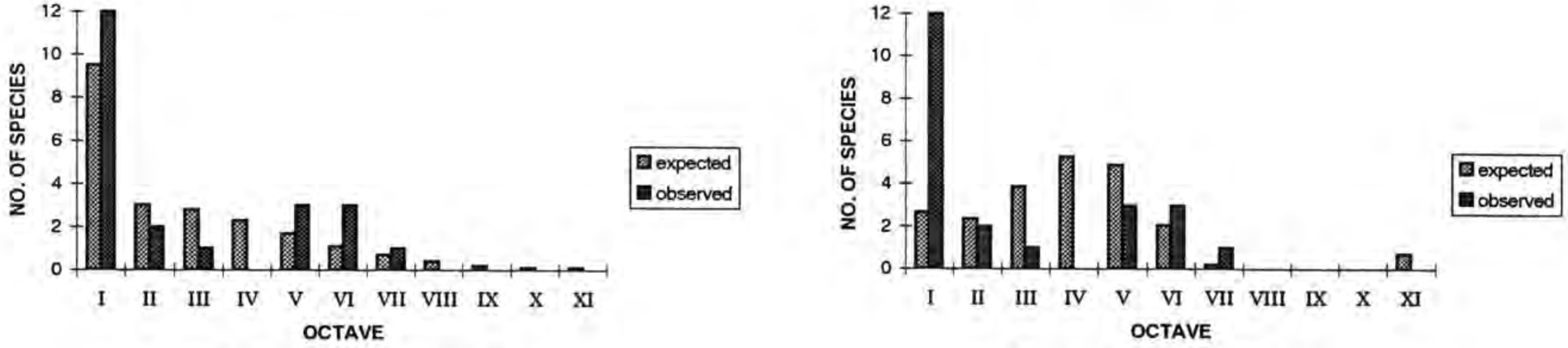
d) Macarthur's Broken Stick

Appendix 3g. Fit of the geometric series, log series, log normal and MacArthur's broken stick to NOP species abundance data.



a) Geometric series

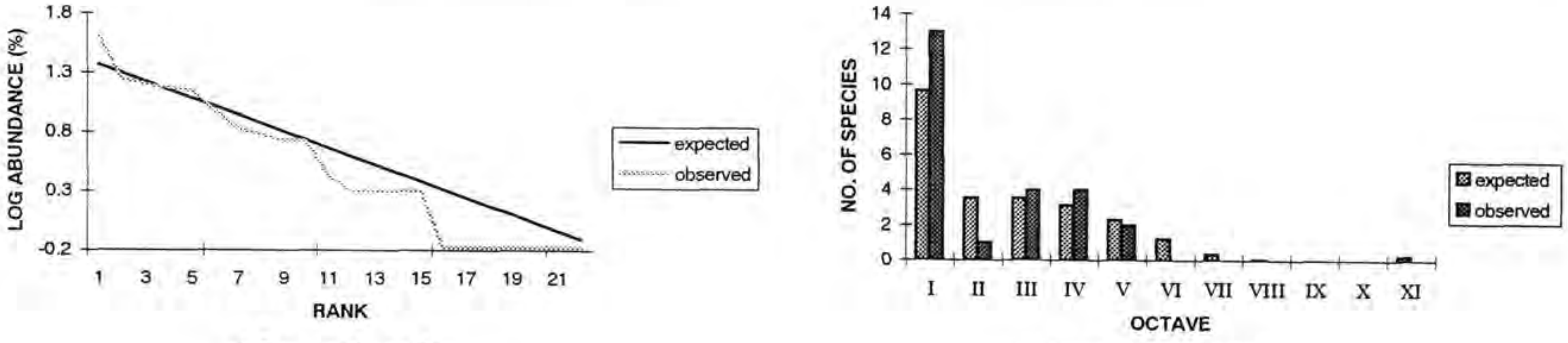
b) Logarithmic series



c) Truncated log normal

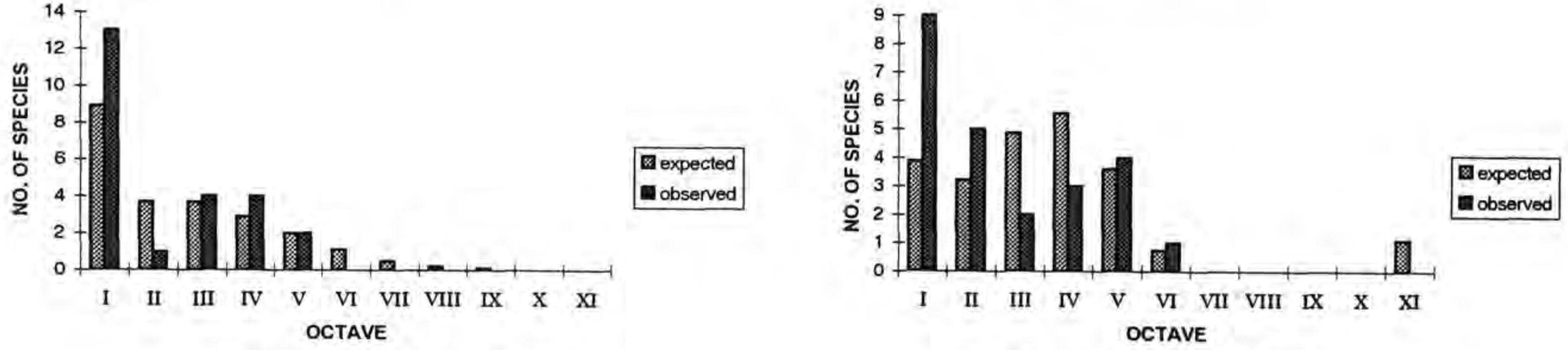
d) Macarthur's Broken Stick

Appendix 3h. Fit of the geometric series, log series, log normal and MacArthur's broken stick to COP species abundance data.



a) Geometric series

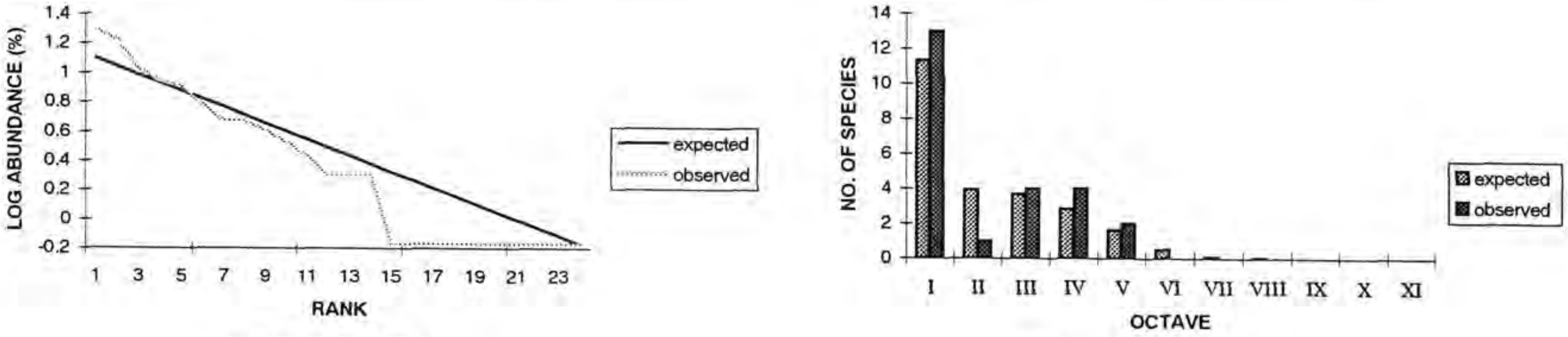
b) Logarithmic series



c) Truncated log normal

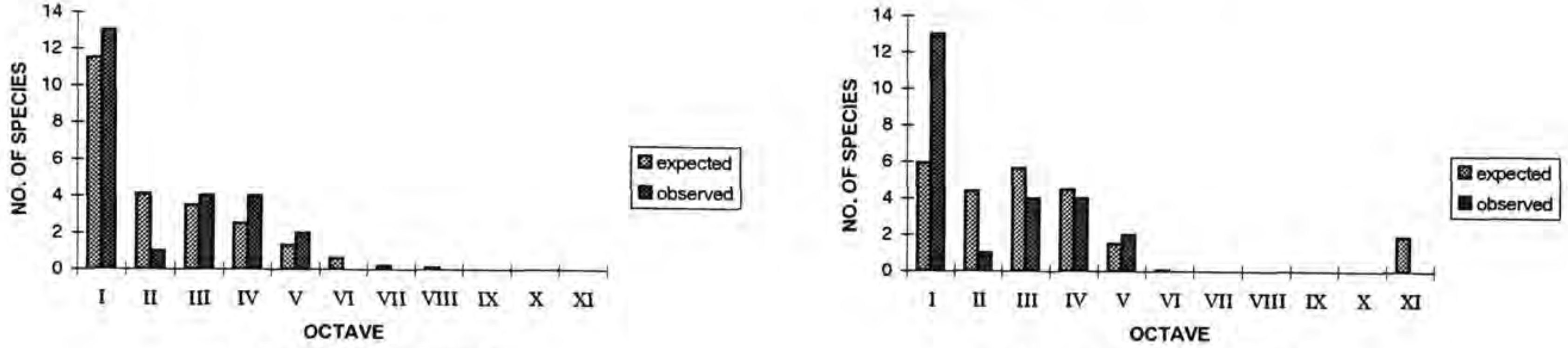
d) Macarthur's Broken Stick

Appendix 3i. Fit of the geometric series, log series, log normal and MacArthur's broken stick to ROP species abundance data.



a) Geometric series

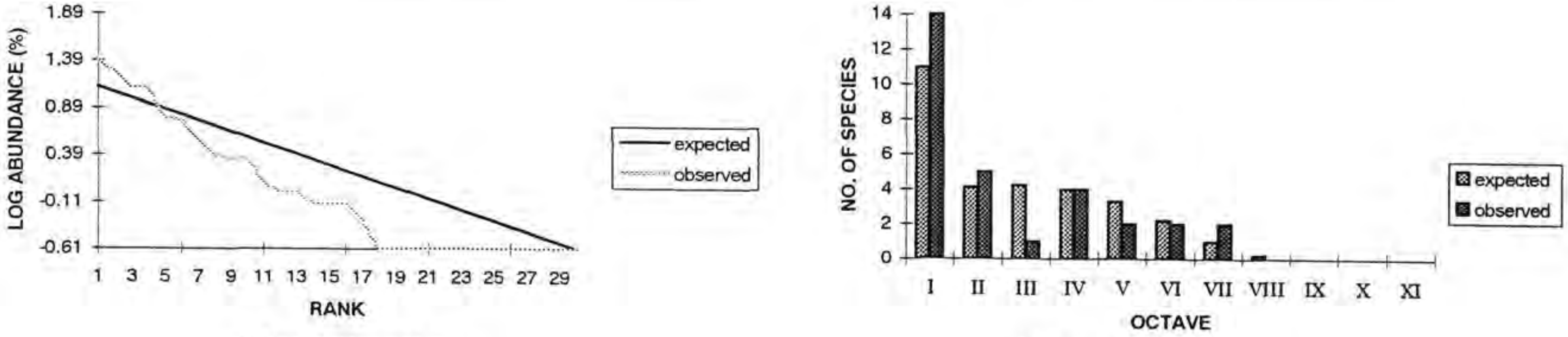
b) Logarithmic series



c) Truncated log normal

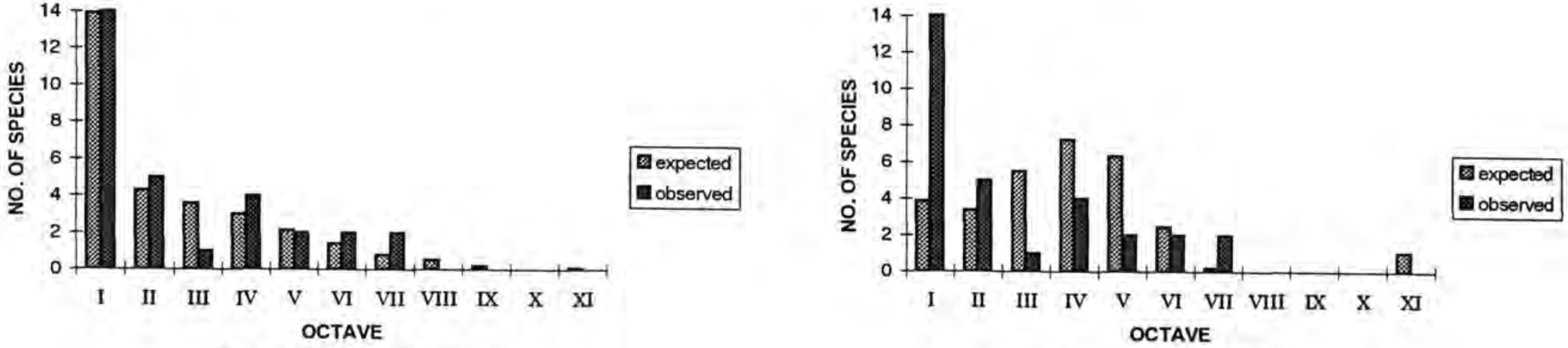
d) Macarthur's Broken Stick

Appendix 3j. Fit of the geometric series, log series, log normal and MacArthur's broken stick to Site 2 species abundance data.



a) Geometric series

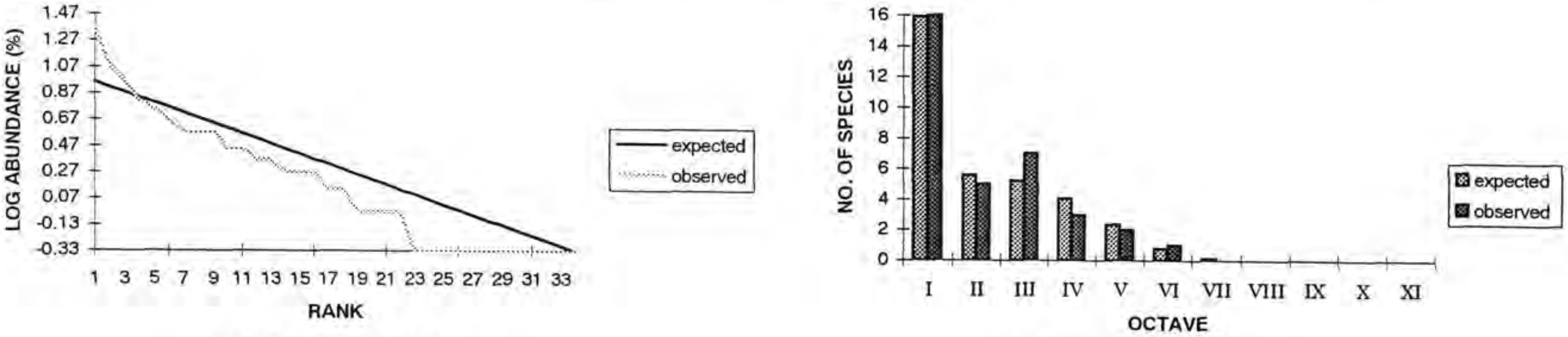
b) Logarithmic series



c) Truncated log normal

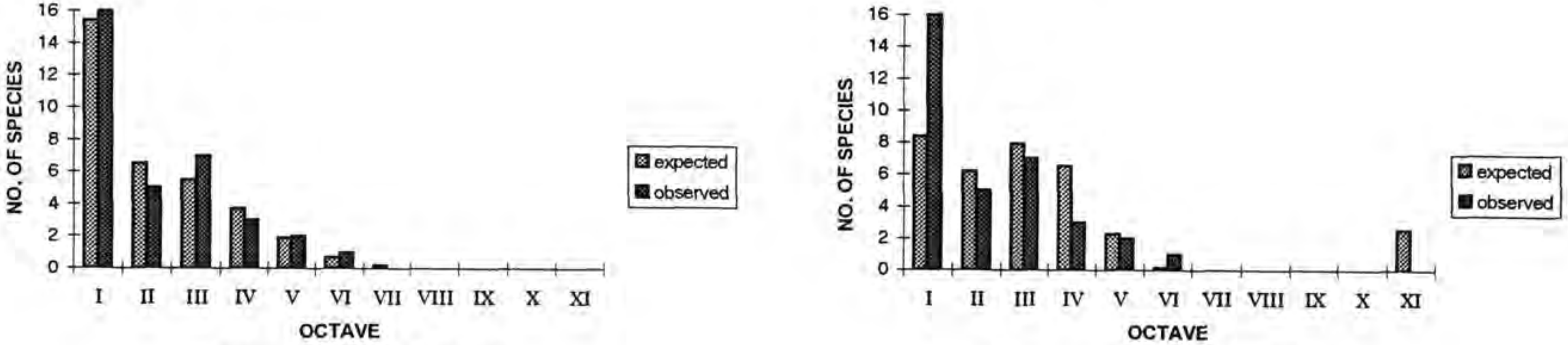
d) Macarthur's Broken Stick

Appendix 3k. Fit of the geometric series, log series, log normal and MacArthur's broken stick to Site 6 species abundance data.



a) Geometric series

b) Logarithmic series



c) Truncated log normal

d) Macarthur's Broken Stick