Spider populations and their response to different habitat types

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Summary

The composition of a spider population in terms of species and numbers is influenced by many environmental factors. Examples of faunal differences between simple, uniform habitats and those which are much more diverse are discussed. This paper examines the characteristics of populations in different habitat types, some stable and others subject to use which causes disturbance. When adequate and accurate samples are taken of spider populations in a defined habitat it is usual to find a few Abundant species, a large number of Scarce, and a third category which is classified as Frequent. The species–numbers relationship can then be illustrated by calculating the proportion of the total population represented in each of the three groups. When graphed, an L-shaped curve is produced, which varies according to the structure and environmental conditions of the habitat, as well as to the sampling method used. A number of examples are described, and possible ecological interpretations are discussed.

There are no two species of indigenous spiders which occupy precisely the same position in nature's household.
F. Dahl (1906) (cited by Wise 1993)

Introduction

Spider populations and the habitats associated with them have attracted the attention of arachnologists for many years. One of the first systematic studies was made by Tretzel (1952). Since then, there have been numerous investigations, both at the landscape level (Hänggi *et al*. 1995; Duffey 2005; Hendrickx 2007), and by analysis of the microhabitat components of different habitat structures (Uetz 1979; Bultman & Uetz 1984). The selection of only one taxonomic group to study the species–numbers relationship has its dangers because the influence of other invertebrates which share the habitat is not known. In this case, we are only concerned with the role of the habitat in determining species and numbers.

The authors of many publications on invertebrate ecology seem to assume that each species can be allocated a specific habitat label which is a fixed characteristic wherever it occurs. This may be true for some invertebrate groups such as insects whose larvae feed on particular plants and a few spiders which are habitat specialists, but the majority of spiders in Britain and probably much of the rest of Europe are much more habitat tolerant. Duffey (2010), using habitat data collected by the British Arachnological Society, found that although some species showed a clear preference for a particular habitat they also occurred in other formations. For example, the lycosid *Arctosa perita* is commonly associated with coastal sand dunes but when the locality records were assigned to a habitat classification of 21 categories this species occurred in 15 of them. There were few records for the subsidiary habitats, but in southern France I found that *A. perita* was much more frequent in dry inland areas than in similar British habitats.

There are ecological and historical factors which may explain why habitat tolerance is so widespread. Over-specialization in habitat selection is an evolutionary trap which can lead to extinction if the landscape environment is changed by natural events. Habitat tolerance is an insurance for survival if a preferred site is destroyed and is even more effective if a species is able to adjust to different conditions in relation to geographical area (Duffey 2005).

Historically, the British landscape, modified by man for over 1000 years, has long since lost all undisturbed natural areas, with the possible exception of some mountain tops, rocky cliffs in coastal regions, and some saltmarshes. Consequently, the spider fauna today consists mainly of species which were able to survive the many habitat changes over time.

Spiders are a widespread group, including species which live successfully in some extreme environments, such as arctic regions, tropical deserts, marine habitats, and high mountains. Where habitat diversity is particularly well developed, as on tropical continents, spider faunas are very rich in species. In contrast, few species occur where the habitats have a simple uniform structure, as in arctic deserts. Such habitats are difficult to study because of climatic conditions, but some man-made environments with very simple structures colonized by spiders may illustrate how populations develop.

Nomenclature for spiders follows Russell-Smith (2008).

Spider diversity in simple, uniform habitats

The spider fauna of the filter beds at the Mimworth sewage treatment works in Birmingham was studied over 12 months (Duffey 1997). There were 48 filter beds covering an area of 18.2 ha. Each measured 166.5 m × 20 m × 1.85 m depth and had a volume of 6160 m^3. The material filling the beds was smooth, graded stones, mostly granite, each approximately 5.1 × 3.0 × 2.4 cm. The constant flow of nutrient-rich sewage water over the stones promoted the growth of protozoa, fungi and bacteria which maintained an invertebrate fauna of Oligochaeta, Acari, Copepoda, Collembola, Diptera, Coleoptera, and Araneae. In this environment of constant moisture, a temperature which never fell below 9°C, and an abundance of food, only two species were found: *Leptorhoptrum robustum* and *Erigone longipalpis*, forming a population of many thousands. During the study, two other species occurred: *Lessertia dentichelis* and *Porrhomma convexum*. Both were recorded with eggs, so were able to breed but, over 12 months, only 21 of the former, and 17 of the latter, were taken, so they were an insignificant part of the fauna.

The filter bed is a very simple environment with virtually no variation. In spite of the favourable conditions of moisture, free from frost, and ample food, a multi-species spider population could not develop because there was complete uniformity of habitat structure. Throughout the year there was a constant influx of other spider species by aerial dispersal, and 15 were recorded on trays placed on

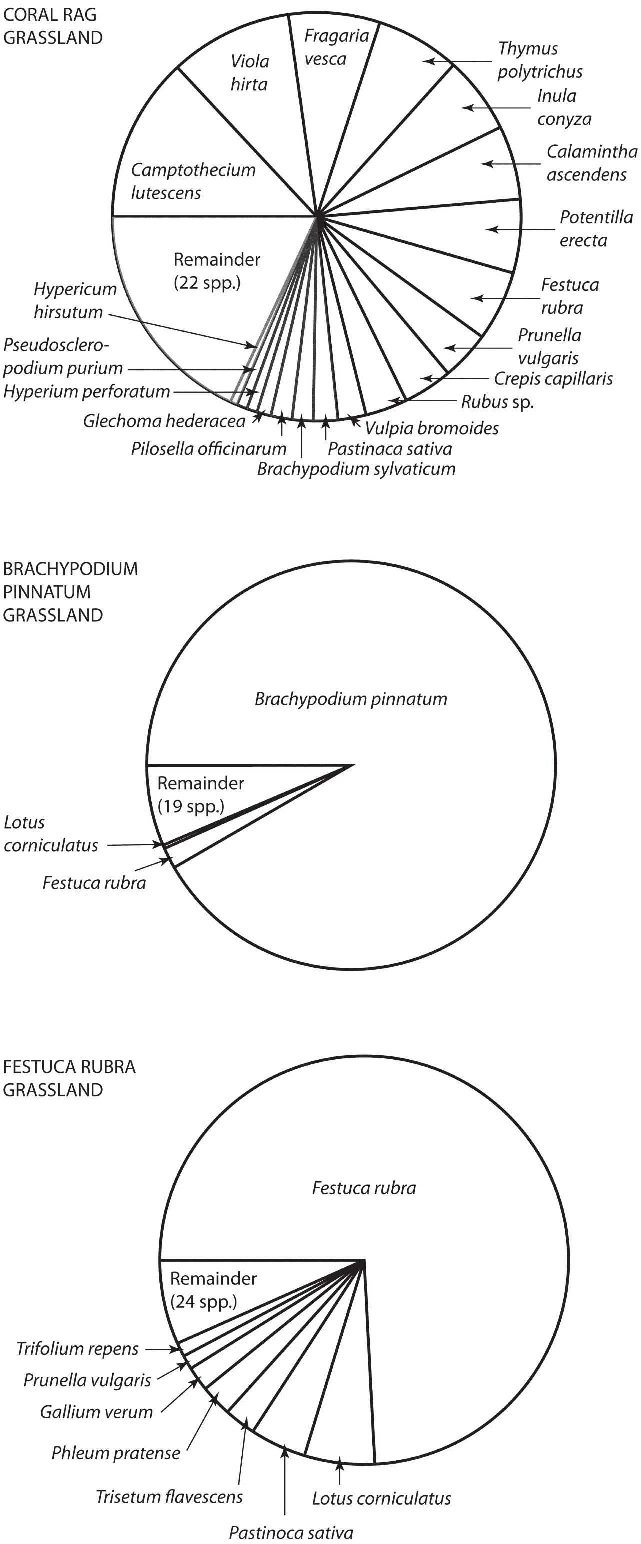

Fig. 1: Representation of the floral diversity in the three grasslands (nomenclature according to Stace 1997).

the filter-bed surface. None was able to establish a breeding population.

Two filter beds were studied. One was relatively undisturbed and recorded a density peak of 60,346 m^3 for *L. robustum* and 43,001 m^3 for *E. longipalpis*. At these density levels, each spider had only 3.2 × 3.2 cm of space available. This could be an effective deterrent for other species trying to establish themselves.

Nevertheless, *L. robustum* appeared to be better adapted to the filter-bed environment than *E. longipalpis*, which was less numerous. In nature, *L. robustum* is widespread in Britain, with most records from inland damp or marsh habitats, although it also occurs on saltmarshes (Harvey *et al*. 2002). *E. longipalpis* is also widespread in Britain but there are fewer records. It occurs primarily on coastal saltmarshes, with relatively few records on inland wet habitats. This suggests that *E. longipalpis* may be less well adapted to freshwater environments than *L. robustum*. It may be further handicapped by the need for free stone surfaces for the construction of its egg cocoons, whereas those of *L. robustum* are suspended in space.

Filter beds in other sewage treatment works had similar spider faunas but also included other species. Bristowe (1939) examined four filter beds in Yorkshire and found *L. robustum* to be the most numerous species, followed by *Erigone arctica* and *Porrhomma convexum*. The late G. H. Locket (pers. comm.) found *Prinerigone vagans* 'swarming' in filter beds near London. In recently constructed filter beds at Cambridge, Duffey (1997) found the most numerous species to be *P. vagans* and *L. dentichelis*, and a single, small filter bed by the Monks Wood Experimental Station, Huntingdon, had only a few *P. convexum*. It seems that when a new filter bed is constructed, the spider population which establishes depends on who gets there first, though only six species have so far been reported living successfully in this specialized habitat.

The influence of habitat disturbance on spider faunas

Elton (l966) demonstrated that 'no habitat component with an animal community is a closed system'. Even in the most stable habitats, which change very slowly, there are continuous losses and gains of species by dispersal, emigration, and immigration. A distinction has to be made between human-induced change, and natural processes (such as vegetation growth and plant succession). In the latter, the changes are slow and not disruptive, developing over seasons or even years, but the former can be severe and sudden. As an example, I placed four pitfall traps in an undisturbed hay crop in a semi-natural grassland with a rich flora. The field was normally used for cattle grazing but, in alternate years, the farmer removed the animals for 3 to 4 months to take a hay crop. The catch of spiders in the pitfall traps was recorded each week and averaged about 300. Trapping continued during the hay cut and for a further two weeks until the cattle returned. On the day of the hay cut the grass sward, 30 cm in height, was reduced to 2–3 cm in a few hours. I noticed a great deal of activity on the ground of small spiders reacting to the destruction of their habitat. At the end of the week which included the hay cut, the total trapped had jumped to 623. In the following week the catch fell to 348, and in the final week to 146. The spider fauna seemed to be returning to the low numbers and few species typical of the faunas in grasslands continuously grazed by cattle.

The influence of disturbance leading to food shortage was demonstrated in the filter-bed spider fauna. In 1980, the D4 filter bed at Mimworth suffered only 12 days when the flow of sewage water was stopped due to mechanical breakdown, while D5, the adjacent bed, lost 92 days. The *E. longipalpis* population in D5, which should have been similar to that in D4, was reduced by 94.9% and the *L. robustum* population by 60% (Duffey 1997), caused by the drying out of the stone filters. This was followed by a massive aerial dispersal by both species. The same event happened each year when the flow was stopped for several days for the sewage water distribution mechanism to be repainted. It demonstrates the vulnerability of faunas in habitats of extreme uniformity.

Semi-natural habitats which are stable and free from disturbance are rare in small overpopulated countries such as Britain. Modern agriculture must be intensive in order to produce more food from less land, and this creates an environment often inimical to wildlife. The management of nature reserves also includes disturbance activities, such as the use of grazing animals, reed and grass cutting, and coppicing in woodlands, which favour some wildlife but may be unfavourable to others. This aspect of nature conservation is poorly researched, especially in relation to grassland, which almost everywhere is used for agricultural, sporting, or recreational purposes.

Grassland leaf litter, an important spider micro-habitat, can be damaged or destroyed by raking in the spring to encourage grass growth, grazing by cattle or horses, cutting for hay, and treading by people. Duffey (1975) investigated the influence of human treading on spiders, beetles and other invertebrates in grassland leaf litter by using hay in mesh-bags (Table 1) which allowed the small species in the fauna to colonize but excluded rodents. For 12 months, 25 bags were subjected to 5 treads per month, 25 bags to 10 treads per month, and 22 bags were controls. A comparison between the control bag fauna and the treated bags showed that after 12 months the 10-tread treatment had reduced the spider population by 84%, though one species had increased slightly and two others were not greatly affected. Morris (1968) studied the changes in the fauna of plant bugs (Auchenorrhyncha) on sheep-grazed and ungrazed chalk grassland. Van Wingerden & Dimmers (1993) and Offereins & Van Wingerden (1995) investigated similar changes for grasshoppers in Dutch grazed and ungrazed grasslands. Most forms of disturbance reduce habitat diversity and result in poorer faunas. This trend can be reversed by adding even small additional microhabitats. Schaefer (1978) found that he could treble the population of the spider *Floronia bucculenta* by adding frames with chicken wire as a base for web construction. Rypstra *et al*. (1999) reported that the soil-living spiders in agroecosystems increase dramatically when the leaf litter is enhanced to create more retreats and hiding places, as well as moderating extremes of temperature and humidity. Uetz (1979) studied the leaf-litter spider fauna in woodlands and found that depth was more influential than structural complexity in developing a forest-floor spider population.

	Control	5 treads per week	10 treads per week	Significance level
Coleoptera	2003	349	320	<0.001
Araneae	275	75	44	<0.001
Isopoda	412	12	8	<0.001
Diplopoda	113	5	8	<0.001
Mollusca	340	148	113	<0.001

Table 1: The fall in numbers of five invertebrate groups in grassland leaf litter at two levels of trampling intensity (Duffey 1975). All were significantly reduced in numbers but Diptera larvae increased and Annelida were little affected.

The spider fauna in long-undisturbed grassland

A grassland of *Festuca rubra* L. on limestone in the Oxford University Wytham estate was selected for studies on the spider population (Duffey 1962) because it had been undisturbed for about 10 years and had developed during a long period of stability. Adjacent to it was a grassland of *Brachypodium pinnatum* (L.) P. Beauv., also undisturbed for the same period, and a recovering grassland on a Coral Rag limestone substrate with 10% bare ground dominated mainly by mosses and prostrate, creeping, and other small plants. The recovering area had 0–10 cm depth of vegetation and no leaf litter. An analysis of the fauna of three contrasting grasslands must include a study of the habitat components of the vegetation as well as the animal species and numbers. The structural and environmental differences of the three grasslands were expected to be reflected in their spider fauna. The main differences in the structure of the grasslands are shown in Fig. 1 and Table 2. The *F. rubra* sward averaged 25–30 cm in height, excluding the scattering of taller field-layer plants. The uniform stem density of 1900 in a quadrat of 25 × 25 cm provided shelter, hiding places, moisture, and avoided extremes of temperature. The *B. pinnatum* grassland was twice the height of the *F. rubra*, with broader leaves and fewer stems per unit area, which tended to be in groups with bare spaces in between. It was a very uniform structure, as over 90% of this part of the study area consisted of this species. The leaves of *B. pinnatum* have a high silica content and are not palatable to most herbivores. The leaf litter breaks down very slowly in contrast to *F. rubra*. This component of the ground vegetation generally accounts for the largest proportion of the ground-living species, especially small Linyphiidae. If the dead leaves are palatable to many small invertebrates this provides an important food supply.

	B. pinnatum	*F. rubra*	Coral Rag
Plant species (see Fig. 1)	22	32	42
Number of leaves and stems in quadrat 25 × 25 cm	343	1900	-
Mean population density of spiders/m² after 12 months' quadrat sampling	252	615	169
Spider species recorded by quadrat sampling	58	69	47
Adult spiders as a mean % of total from quadrat samples	21.7%	26.5%	17.2%

Table 2: Comparison of the spider fauna in three adjacent, but different, grasslands in relation to habitat. Population density and number of species calculated from 29 quadrat samples (25 × 25 cm) in each grassland over 12 months. Plant stem density was assessed in a 25 × 25 cm quadrat; not applicable to Coral Rag grassland.

	Numbers per species
5 Abundant species accounting for 70% of all spiders	267, 143, 42, 42, 35
14 Frequent species accounting for 18% of all spiders	8, 9, 12, 16, 10, 10, 8, 11, 6, 10, 11, 8, 9, 8
43 Scarce species accounting for 12% of all spiders	3, 3, 5, 1, 1, 2, 1, 2, 3, 1, 2, 5, 5, 2, 1, 3, 2, 1, 1, 2, 5, 4, 1, 3, 1, 1, 1, 1, 2, 3, 1, 1, 2, 1, 1, 2, 1, 5, 2, 1, 4, 1, 1

Table 3: The numbers of 71 species of spiders obtained from an undisturbed *Festuca rubra* grassland. The spiders were recorded from 32 quadrats (25 × 25 cm) on each of three dates in September, using a heat-gradient extraction system. Each figure represents the total number of individual spiders recorded for a particular species. Total spiders = 750.

These three grasslands were adjacent to each other without barriers to movement (Duffey, 1962), so there was probably frequent interchange of species between them. In spite of this, all three grasslands were characterized by different species which were rare or absent in the others. The data in Table 2 suggest that the *F. rubra* grassland habitat is a more favourable environment than the *B. pinnatum*. The Coral Rag vegetation, in spite of having the greatest floristic diversity, which should increase the variety of microhabitats, could not develop a high population density because there was insufficient depth and no litter layer in the plant cover.

The data on species and numbers in this study are based only on adult spiders because identification of most immature specimens is uncertain or impossible. The proportion of adults in the *F. rubra* grassland fell to less than 10% in July–August and reached a peak of 45% in November–January. With a mean of 26.5% (Table 2), nearly three-quarters of the total population cannot be taken into account in the analysis.

Graphical representation of the species–numbers relationship

As I looked again at the Wytham study and subsequent work on spider populations I found that there was a consistent pattern of species and numbers which could be separated into three groups. There were a few species which were so abundant that they accounted for the majority of the total spiders (Abundant), others were frequent but contributed less to the total (Frequent) and, finally, there were numerous scarce species present in very low numbers (Scarce) (Table 3).

This pattern of species numbers in invertebrate populations is widespread in published data which describe the fauna of particular habitats. It has some similarity to the Equitability Index J, which is based on the number of species and the index of diversity. However, only minimum equitability can occur in wildlife populations because all species are different in behaviour, tolerance or intolerance of habitat, interactions with other species and food needs. As F. Dahl said in 1906 (quoted in Wise 1993): ‘no two species in a population are equal’. Duffey (2005, 2010) used

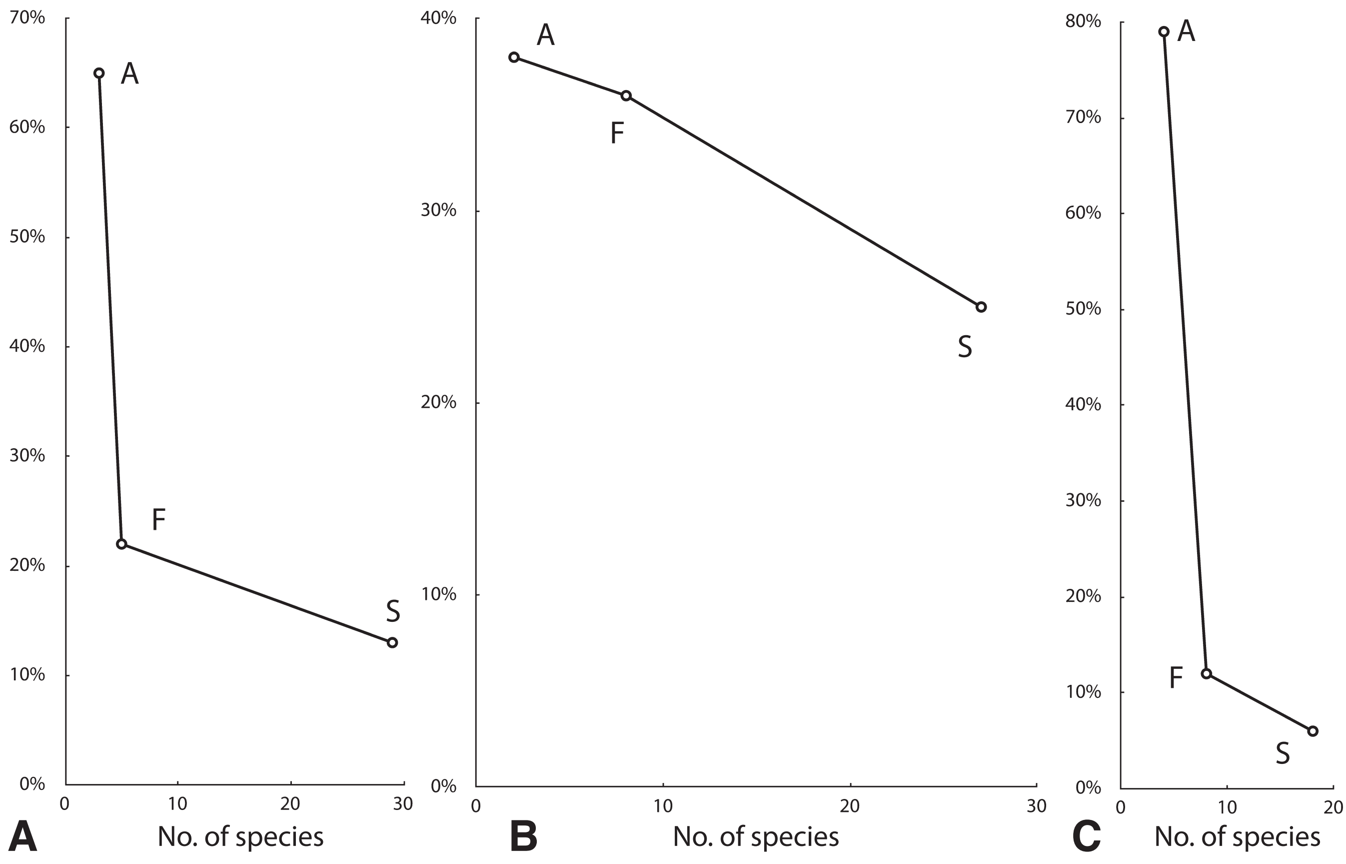

Fig. 2: Wytham Estate, Oxfordshire. **A** Templet for *Festuca rubra* grassland using quadrat data, April–June; **B** *Brachypodium pinnatum* grassland, quadrat data, January–July. **C** *Festuca rubra* grassland, pitfall data, May–June.

habitat data collected by the British Arachnological Society to draw habitat profiles of spider species based on a habitat classification system, and did not find two which were identical. It is in the nature of wild species to evolve differently because it is by this means that habitats and resources will be found which are not used by others.

The division of species numbers into three categories can be criticized for being arbitrary. In practice, providing that adequate and accurate data have been obtained, the Abundant and Scarce categories are usually obvious, so that the remainder form the Frequent group (Table 3). This is the method used here until a satisfactory mathematical solution can be found. Three methods of graphical representation were tried: histograms, pie-charts, and line diagrams, but only the last showed clear differences between faunas of different habitats. By plotting the number of species and the proportion of the total fauna they represent, the values of Abundant, Frequent and Scarce (A–F–S) form an L-shaped curve (Fig. 2A). This example from the already described *Festuca rubra* grassland, undisturbed for over 10 years, is regarded as a templet for the spider fauna in a relatively stable habitat where the structural environment is only modified by climatic conditions and plant growth changes. It shows a balance between the three abundance groups in which they are approximately equal, without one dominating. This is in contrast to some of the other examples presented. In the *Brachypodium pinnatum* grassland this species accounted for 93% of the vegetation cover and so had a much more uniform structure and a poorer fauna. The A–F–S curve, a diagonal straight line, reflected this difference (Fig. 2B).

Most published spider population studies are based on pitfall catches, not quadrats, with the inevitable bias in favour of the more mobile species and against those that are sedentary. The effect of this can be demonstrated in the A–F–S curve because the *F. rubra* grassland was sampled both by quadrat samples and pitfall traps in the same year. Fig. 2C illustrates the curve based on pitfall sampling for comparison with Fig. 2A. Fig. 3 was drawn using pitfall data from a bog in Lithuania (Relys *et al*. 2002). The bog was described as consisting of *Pinus sylvestris* L., *Ledum palustre* L. and *Sphagnum* spp. The curve is quite different from that of the templet in Fig. 2A. It shows the exaggerated dominance of the mobile species and the bias against those more sedentary. A comparison of some sedentary species recorded in the same year in pitfall traps and quadrats in

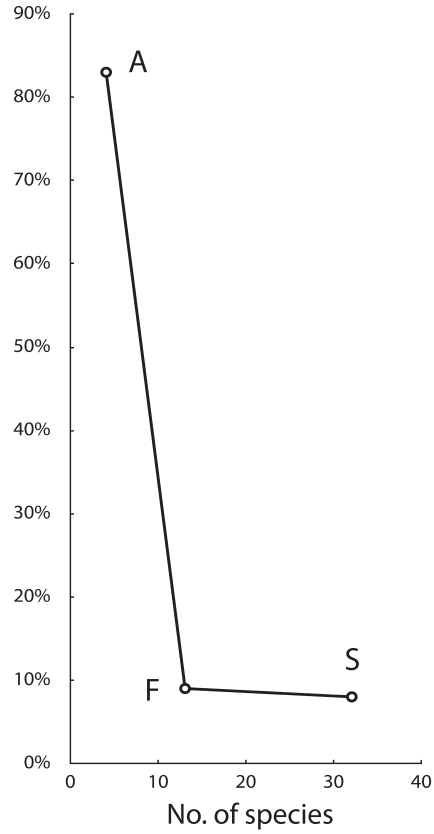

Fig. 3: Lithuania bog, Site LA99; pitfall data.

F. rubra grassland is shown in Table 4. A true comparison is not possible because the catching area of a pitfall trap is not known. Relys *et al*. (2002) commented that 'pitfall trapping could provide valuable information about the relative abundance of species'. This is not supported by the results reported in this paper.

Reliable field data are of great importance when comparing species–numbers curves from different habitats. It is essential that the sampling method gives each species and their numbers an equal chance of being recorded. The removal of measured quadrats, followed by heat-gradient treatment or hand sorting, to obtain the fauna is the best method as there is no bias in representation of the fauna, and a true estimate can be made of the numbers of each species per unit area. Some of the A–F–S curves illustrated in this paper are based on timed hand collecting, which appears to be reliable in habitats which are easily examined,

		J	F	M	A	M	J	J	A	S	O	N	D
Tapinocyba praecox	Quadrats	337	240	233	97	132	121	60	64	288	384	339	352
	Pitfalls	3	3	3	2	0	0	0	0	0	0	0	0
Cnephalocotes obscurus	Quadrats	10	11	30	7	4	0	6	24	26	75	20	24
	Pitfalls	0	0	1	42	8	10	10	11	1	0	0	0
Meioneta mollis	Quadrats	12	6	5	2	0	0	0	0	10	10	25	8
	Pitfalls	0	0	0	0	0	1	0	2	1	0	0	0
Savignia frontata	Quadrats	44	13	7	0	0	0	0	0	5	32	32	8
	Pitfalls	1	1	0	0	0	0	0	0	0	0	0	0

Table 4: Comparison between monthly pitfall catch and quadrat samples of four sedentary species in *Festuca rubra* grassland. Quadrat (25 × 25 cm) totals in m^2; average of 19 samples per month; 12 pitfalls, operated for 12 months.

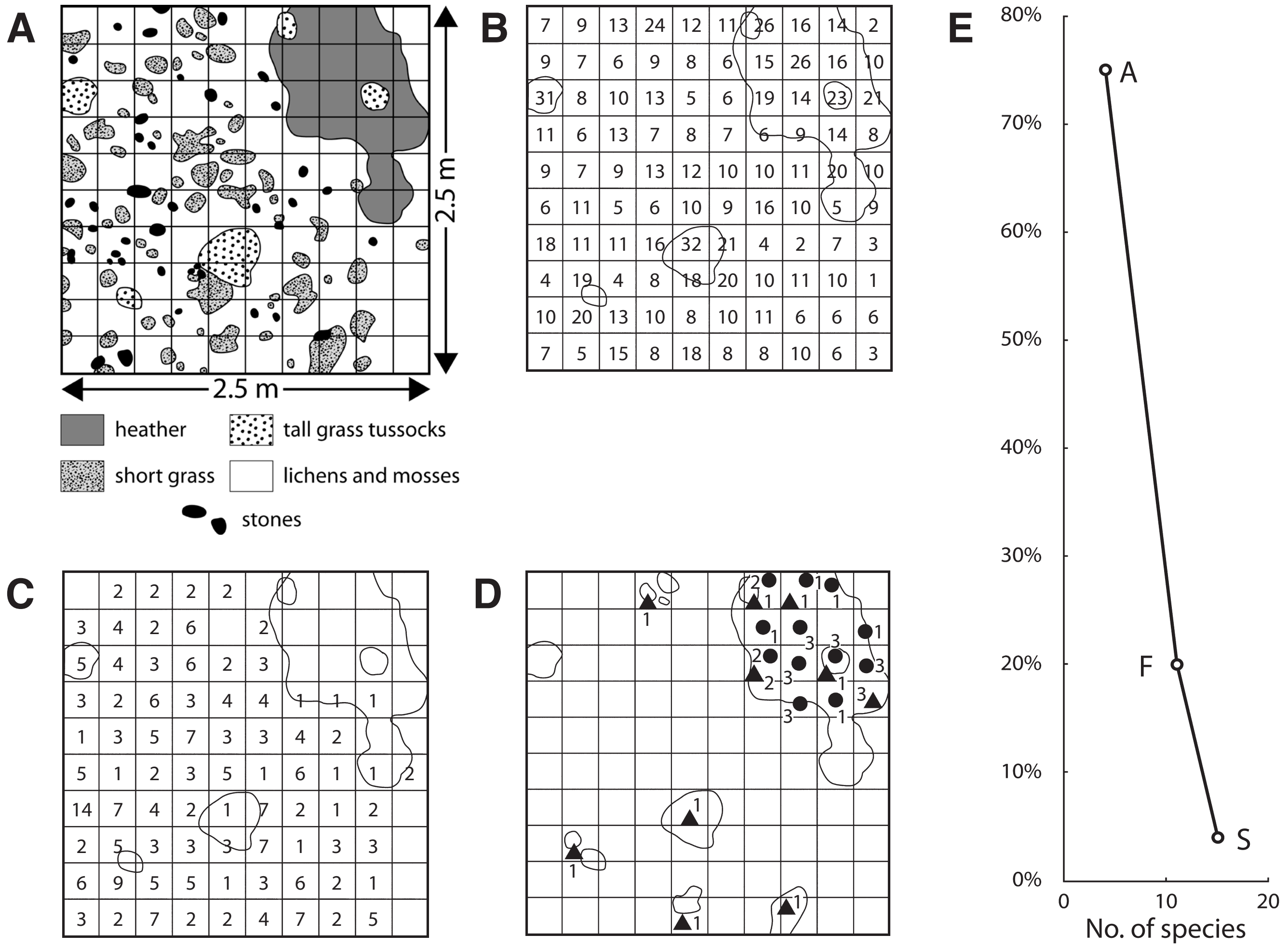

Fig. 4: Mols heathland, Denmark. **A** Vegetation map of 2.5 × 2.5 m study plot. **B** Numbers of spiders recorded in each 25 × 25 cm quadrat. **C** Distribution of the spider *Trichopterna cito* in the 100 quadrats on the Mols heathland. **D** Distribution of the spiders *Dipoena prona* (▲) and *Scotina gracilipes* (●) in the 100 quadrats on the Mols heathland. **E** The A–F–S curve of the Mols heathland spider fauna.

but perhaps is less so in tall, dense vegetation. This method also requires several field collectors working together. In the work described in Duffey (1968), and especially in Duffey (2009), it was necessary to collect for nine hours before no new unrecorded species, or very few, were found. This was achieved by recruiting a team of nine people working together for one hour in a designated habitat.

Faunal characteristics of structurally diverse habitats

Most wildlife habitats are variable in structure because they have a diverse flora which creates numerous micro-habitats. The characteristics of the fauna in a habitat which is structurally complex can be illustrated by a study of a heathland at Mols in Denmark in September 1966 (Duffey 1974). A plot measuring 2.5 × 2.5 m was selected for the study as there appeared to be no disturbance. The vegetation map (Fig. 4A) included a patch of *Calluna* heather, scattered tussocks of the grass *Deschampsia flexuosa* (L.) Trin. more than 15 cm in height, short grass areas of *Corynephorus canescens* (L.) P. Beauv., carpets of mosses and lichens, and about 10% bare ground. The plot was divided into 100 quadrats, 25 × 25 cm. Each quadrat was removed and hand sorted in the laboratory to collect the spiders and beetles. Thirty species and 813 spiders were recorded, of which 3 Abundant species accounted for 75.5% of the total, 11 Frequent species 20%, and 14 Scarce species 4.5%. Figs. 4B, C and D illustrate the number of spiders taken in each 25 × 25 cm square, and the distribution of two species in relation to the vegetation. The resulting A–F–S curve (Fig. 4E) is a near-vertical straight line, suggesting a fixed relationship between the species and their numbers due to habitat diversity. The A–F–S curve for the beetle fauna is closer to the templet curve (Fig. 2A). Near-vertical straight lines were also found in the rich floras of three fens in the Norfolk Broads, where the sampling method was by timed hand collection (Fig. 5). In this case, greater habitat diversity was inadvertently introduced by the sampling method. The team of nine people spread out over the designated fen habitat covered a considerably larger area than 2.5 × 2.5 m. Consequently, each person collected in a slightly different area and so sampled a more diverse range of species and numbers.

Spider populations in agricultural crops

Invertebrate predators, particularly spiders, have attracted many studies to ascertain whether they are numerous enough to control crop pests. Raatikainen & Huhta (1968) studied the spider fauna of Finnish oat fields using sweep nets. They

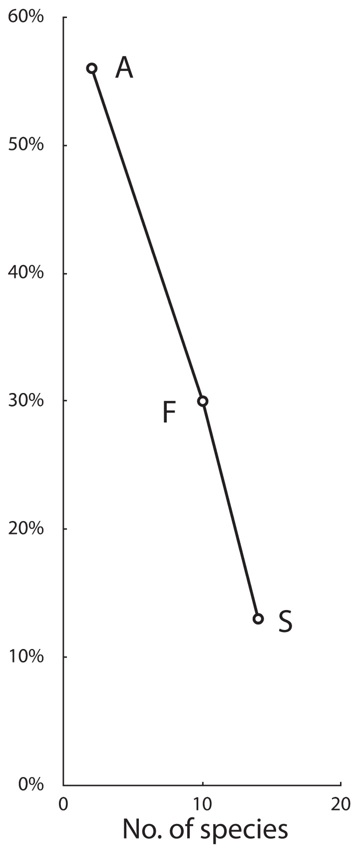

Fig. 5: Sutton Broad, Norfolk, fenland spider fauna by timed hand collection.

worked in 12 different regions of Finland, sampling up to 25 fields in each, excluding any which had been treated with herbicides. A sample of 60 sweeps was made in each field, and a grand total of 65 species and 701 spiders from all regions were recorded. The numbers per region were low and, in 7 out of the 12, no Abundant species occurred. In region 12 (Fig. 6A), where 21 species and 93 spiders were taken, there was no difference in the proportion of the total accounted for by the Abundant and Frequent categories so the A–F–S curve was reversed. In region 7, where only 78 spiders were recorded, the curve took a different shape because Scarce species scored a higher proportion of the total than the Frequent category (Fig. 6B). The inadequate data obtained per region were unable to produce a curve characteristic of the oat-field spider fauna. However, if all 276 samples from about 100 oat fields surveyed by sweep-netting in the 12 regions are combined, the A–F–S curve becomes more like the templet L-shape (Fig. 2A), because there were numerous slight differences in the faunas of such a large number of structurally uniform habitats.

Samu *et al*. (2010) studied the spider fauna in two alfalfa (lucerne) fields by suction sampling. The alfalfa was cut three times per year. The authors carried out a short-term survey, taking a total of 20 samples between May and November 2001, recording 18 species and 1128 spiders. The A–F–S curve (Fig. 7) is almost a straight line because 4 Abundant species accounted for over 90% of the total spiders and both the Frequent and Scarce categories scored very low values. On the other field of alfalfa they conducted a long-term study lasting five years from 1995 to 2000

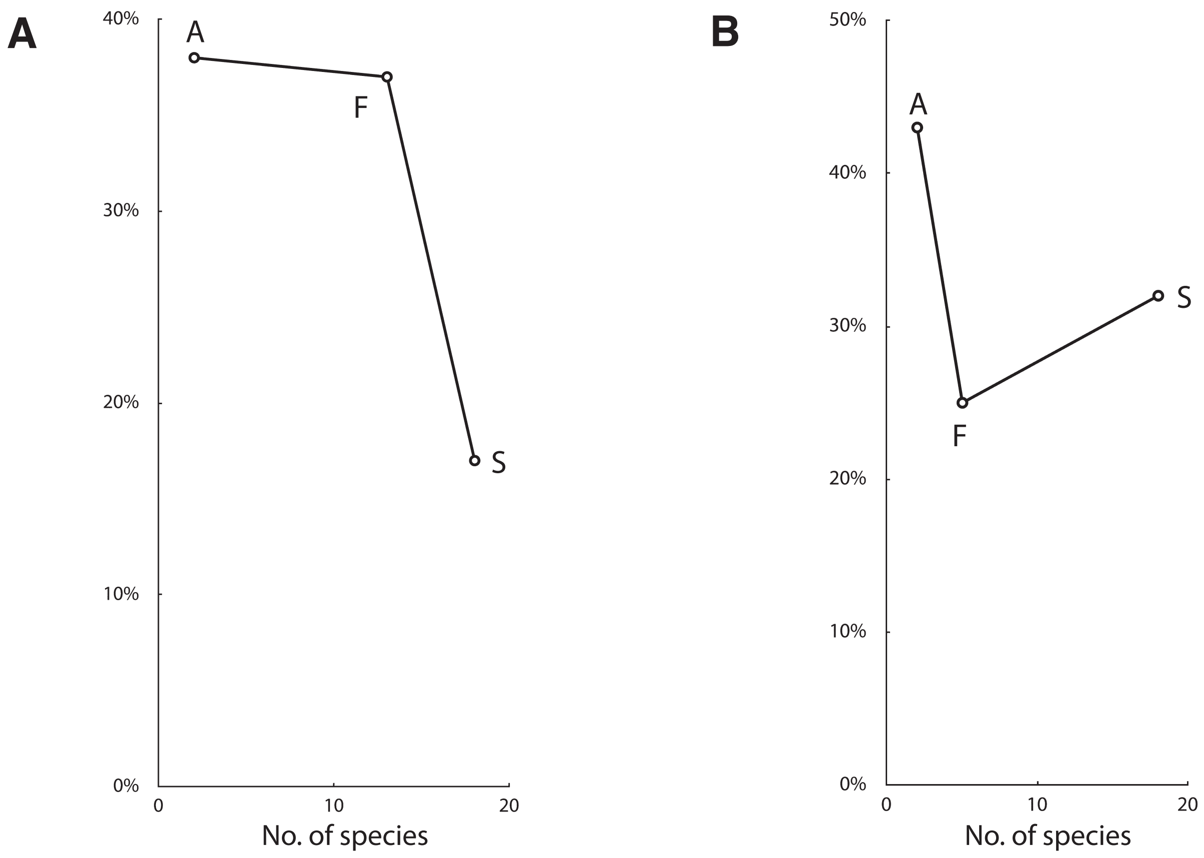

Fig. 6: Finland oat-field survey; collections by sweep net. **A** Site 12; **B** Site 7.

(excepting 1999). Suction samples were taken six times per year (February–April, May–August, September–October) and a total of 43 species and 919 spiders was recorded. The two curves are similar, the only difference being the larger number of Scarce species in the long-term study. The curves are close to those typical for pitfall-trap data.

Samu *et al*. (2010) commented that, if left alone, alfalfa fields convert into meadows and after three to four years the spider fauna reaches 'its climatic and maximal abundance'. Duffey (2009) noted that 9-hour collections made in two different parts of a single fen habitat on the same day produced different species but similar abundance totals. These records suggest that there may be a carrying-capacity limit in any specific habitat.

Figure 8 illustrates the A–F–S curve obtained in a pasture normally grazed by cattle. The animals were removed for nearly four months in 1987 (April–July) to grow a crop of hay, providing an opportunity to use pitfall traps. The six most abundant species, out of a total of 33, accounted for 92% of the total fauna (Duffey 2000). The A–F–S curve is distorted because only a few species dominated the fauna, as recorded by pitfall traps. Although the traps were operating during a period of no disturbance the results seem to reflect the characteristics of the poor fauna normally associated with a pasture subject to cattle grazing.

Discussion and provisional conclusions

1. The study of wildlife populations is part of community ecology but we have little information on how the species and numbers of spiders organize themselves in relation to the environmental characteristics of the landscape where they occur. Although the terms 'habitat' and 'niche' are useful concepts, their use in many publications gives the impression that a fixed label can be attached to each species to describe its living space and the resources it needs. The more we learn about the biology and distribution of spiders throughout their total range, the more we realize that fixed labels are not accurate descriptions because so many species are able to tolerate and exploit many types of environmental conditions (Duffey 2005). Of the approximately 665 species known in Britain, nearly half (46.5%) have been recorded in the very different landscapes and climatic conditions of all four regions: Scotland, Wales, Northern England (above 53°N) and Southern England (below 53°N) (data from Harvey *et al*. 2002). Some are common everywhere while others show a preference for one or more regions. There are numerous examples of species which adapt to different habitats according to the region in which they occur so that the species–numbers relationship also changes.

2. This attempt to characterize a spider population according to particular environmental conditions is provisional and needs more study and analysis, especially for agricultural crops, some of which may not be appropriate for this type of analysis. The three categories of Abundant, Frequent and Scarce were found in nearly all population studies for which there were adequate and accurate data. All the semi-natural habitat types used in making the graphs were three-dimensional, having length, breadth and depth, but there are well-known examples which are two-dimensional, having a ground-cover vegetation of lichens

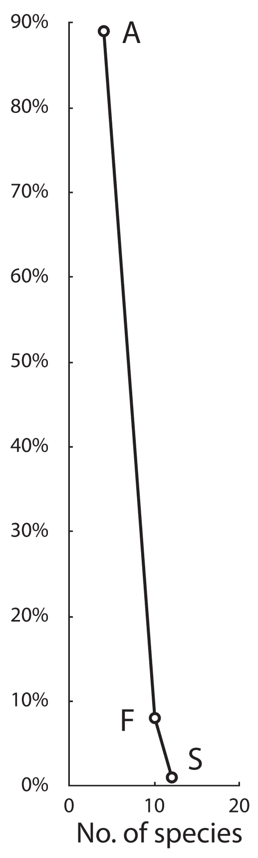

Fig. 7: Alfalfa spider survey by suction sampler; short-term study, Hungary.

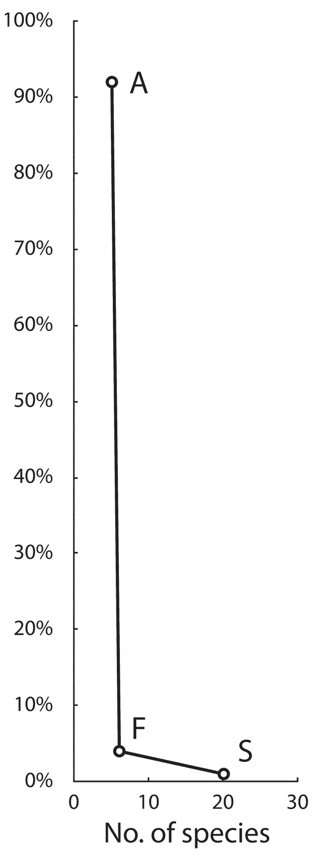

Fig. 8: Cattle-grazed pasture; pitfall study during period of hay crop, Northamptonshire.

and mosses, or prostrate and creeping plants with minimum depth and no litter layer. Very little seems to be known of how the species–numbers relationship of spider populations varies in two- and three-dimensional formations. Observations suggest that the former are usually low in numbers but may, in some circumstances, be rich in species if the ground surface flora is diverse. In such cases is the turnover rate high for some species having a short residence time while new ones are continually attempting to colonize? If so, could this be an opportunity to look for the elusive evidence of competition?

3. The templet curve derived from undisturbed *F. rubra* grassland in September illustrates the characteristic species–numbers relationship in the spider population at that time. In some of the other months, for example April, May and June, the data for each were inadequate for analysis but if all the records for the three months are combined the A–F–S curve was similar to the templet. A more extreme example occurred in the oat-field survey where individual fields never provided adequate data for analysis but when the survey results from all 100 fields were combined the curve was similar to the templet. The explanation seems to be that the fauna of each individual survey is slightly different from the others so that when all the differences are combined a more balanced species–numbers relationship is obtained.

The A–F–S curve seems to be sensitive to small differences in faunal characteristics. Adequate data from single sites which are structurally and floristically rich, for example the Mols heathland, produce a near-vertical straight line while the undisturbed *Brachypodium pinnatum* grassland, which has a poor fauna because of structural uniformity, forms a diagonal straight line. The bias in pitfall trap data always produces a curve with a long A–F section. This was particularly emphatic in the fauna in a cattle-grazed pasture where the few Abundant species accounted for more than 90% of the total spiders.

4. Although the causes of the numerous changes in the Abundant, Frequent and Scarce categories described in this paper have not yet been investigated thoroughly, a partial explanation is because environmental conditions change with season. The vegetation develops or declines from spring to autumn and spider species have different breeding and dispersal periods. No immature spiders were included in the analyses as the majority cannot be determined with accuracy. This means that at certain times of the year some common species are not recorded although their offspring may be numerous. The few species that can be identified in the later stages of development before becoming adult were not included because this would create a bias in their favour.

5. The combined data from suction sampling in the alfalfa-crop long survey over several years produced a curve similar to that typically associated with pitfall catches, emphasizing the long A–F section and the short F–S. Suction sampling does not have the biases of pitfalls, though other limitations are known (Duffey 1980), but it is possible that the alfalfa curve may be nearer a true reflection of the species–numbers relationship. This was not recorded for oat crops in Finland where the agrobiont spider fauna and the sampling method were different.

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