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The initial effects of afforestation on the ground-dwelling spider fauna of Irish peatlands and grasslands

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Abstract

Across Europe, the majority of afforestation is carried out on former agricultural land. Given this current planting trend it is important to assess the impact that afforestation will have on the flora and fauna of habitats typically used for afforestation. The study aim was to investigate the initial effects of afforestation (5 years after planting) on the ground-dwelling spider fauna within three habitats (peatlands, improved grasslands and wet grasslands) in Ireland. A paired sampling approach was used where 24 pairs of unplanted and planted sites (eight within each habitat type) were matched for habitat, vegetation type, soil properties, and geographical location. The planted sites were comprised of 5-year-old stands of Sitka spruce (*Picea sitchensis*). Within each habitat pitfall traps were established in areas of vegetation cover representative of the site as a whole, as well as in supplementary features which may also contribute to the biodiversity of a site, for instance in hedgerows, wet flushes, and the edges of ditches or streams.

During the study 33,157 spiders were collected in 189 species and 18 families. Forty species sampled were associated with open habitats whereas 15 species were associated with forested habitats, 54 species were associated with wet habitats whereas two species were associated with dry habitats. Across the habitats fewer wet-associated species and fewer rare species were supported after afforestation. In particular areas of wet flush in the peatlands supported a unique and diverse spider fauna which was lost after afforestation. In contrast, the planted improved grasslands were more species rich, and supported a greater number of spider species associated with low vegetation than comparable unplanted sites. The hedgerow spider fauna did not differ notably in assemblage composition between the unplanted and planted sites. This study suggests that even in the early stages of the forest cycle (first 5 years) there is a change in the spider fauna, with the rare or specialist species being replaced by habitat generalists or species associated with forested habitats. It is also suggested that peatlands are particularly sensitive to afforestation, indicating that in terms of biodiversity loss, this habitat is the least suitable for afforestation.

Keywords: Spiders; Afforestation; Sitka spruce; Peatland; Grassland; Habitat specialists

1. Introduction

Afforestation causes major changes in both the abiotic and biotic aspects of an ecosystem. During the forest plantation cycle, as the habitat changes from an open to a forested environment, the greatest changes in the flora and fauna occur when the canopy closes (Wallace and Good, 1995; Humphrey et al., 1999; Jukes et al., 2001; Oxbrough et al., 2005). However, during the early stages of afforestation the silvicultural processes which take place (i.e. land preparation, chemical application, soil drainage) as well as the inevitable change in land-use that occurs (i.e. grazed to non-grazed land) are also likely to influence the organisms present.

Previous research examining the initial affects of afforestation on habitats has documented changes in soil properties (Bellot et al., 2004; Farley and Kelly, 2004), vegetation composition (Wulf, 2004), and bird diversity (Allan et al., 1997). There has however been less investigation of these effects on invertebrates, despite their prevalence in terrestrial ecosystems and importance in food webs. Spiders are a large group of terrestrial predators which are primarily affected by changes in habitat structure (Uetz, 1991). They can disperse aerially (Richter, 1970) as well as over land, giving them the ability to colonise habitats relatively quickly compared to other groups of invertebrates with a more sessile nature. This suggests that environmental changes, which occur over a relatively short period of time, for instance the first few years

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after afforestation, may be reflected by changes in the spider fauna.

Across Europe the majority of afforestation is carried out on former agricultural land (UNECE, 2003). Indeed, 90% of current Irish afforestation is carried out by agricultural land owners (Teagasc, 2005). Given these current planting trends it is important to assess the impact that afforestation has on the organisms which are found in pre-planting habitats, particularly less disturbed habitats of more limited extent. With this in mind the present study aimed to investigate the initial effects of afforestation on the ground-dwelling spider fauna within three habitat types: peatlands, improved grasslands and wet grasslands, which are typically used for afforestation in Ireland.

2. Methodology

2.1. Study areas and sampling design

A paired sampling approach was used in the present study. Ideally, researchers should be able to survey a location both before and after the event being investigated (Before–After–Control–Impact design: Green, 1979). However for investigations involving land-use changes such as afforestation, which take place over many years, a sampling design which tracks sites over time is difficult to implement. Paired-site sampling designs have been successfully utilised in previous research (Kladivko et al., 1997; Berger et al., 2002; Barnett et al., 2004). This approach was adopted in the present study to allow the influence of afforestation on ground-dwelling spider assemblages to be investigated over the course of one field season rather than over several years.

Ground-dwelling spider assemblages were surveyed in the following habitats: peatlands, improved grasslands, wet grasslands. Twenty-four matched pairs of unplanted and planted sites (eight within each habitat) were selected on the basis of habitat, soil type, and geographical location. The site-pairs within each habitat type were widely distributed across Ireland, although improved grassland sites were grouped in the south-east (Fig. 1). Where possible the paired sites were adjacent to each other, although three of the pairs were separated by 1–5 km. The habitat type of the planted sites prior to afforestation was determined by consultation with land owners, foresters' records

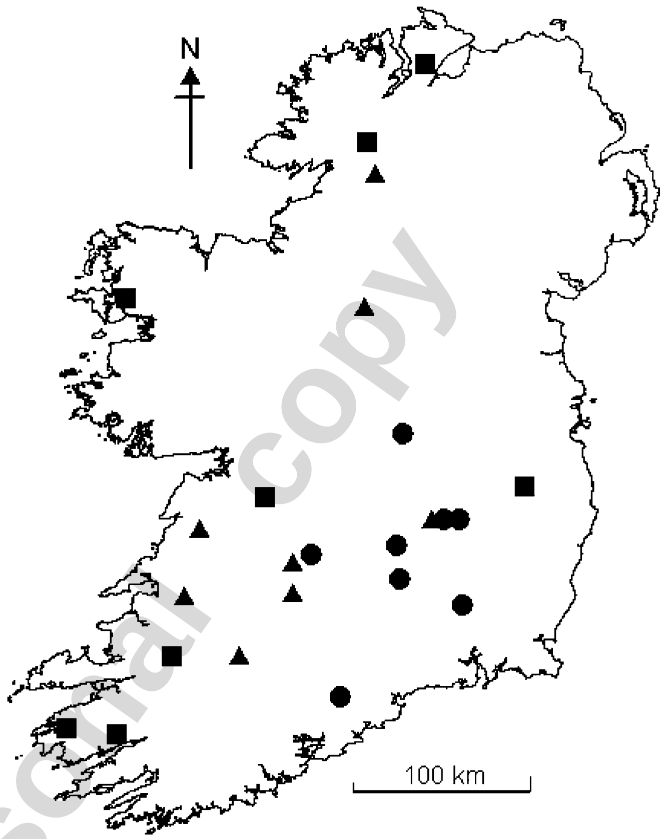

Fig. 1. Distribution of paired study sites across Ireland within the following habitats: (●) improved grassland; (▲) wet grassland; (■) peatland.

and the vegetation present at the site. The planted sites were comprised of 5-year-old stands of Sitka spruce (*Picea sitchensis*), which is currently the most widely planted tree species in Ireland, accounting for 65% of annual afforestation (Teagasc, 2005).

General environmental and habitat characteristics of the habitats surveyed are shown in Table 1. The management regime varied among the habitat types: the unplanted improved grasslands were subject to heavy grazing and were usually fertilised at least once per year. The peatlands and wet grasslands were generally under low to heavy grazing pressure, however approximately half of the wet grasslands were also

Table 1
Environmental and habitat characteristics among the habitats and planting types (U, unplanted; P, planted); mean ± S.D. and range of altitude is shown

Fossitt (2000) habitat type	Soil type	Altitude (m)	Drainage	Common plant species
Peatland (U)	Peat	143 ± 78, 20–250	Poor	*Molinia caerulea*, *Calluna vulgaris*, *Eriophorum angustifolium*, *Eriophorum vaginatum*, Sphagnum mosses
Peatland (P)	Peat	136 ± 73, 15–225	Moderate	*Molinia caerulea*, *C. vulgaris*
Wet grassland (U)	Gley	100 ± 42, 45–175	Moderate	*Juncus acutiflorus*, *Juncus effuses*, *Agrostis stolonifera*, *Molinea caerulea*
Wet grassland (P)	Gley	101 ± 53, 45–190	Moderate	*A. stolonifera*, *J. acutiflorus*, *J. effusus*, *Holcus lanatus*, *Molinea caerulea*
Improved grassland (U)	Brown earth/brown podzolic	164 ± 79, 45–300	Good	*Lolium perenne*, *A. stolonifera*, *H. lanatus*, *Cynosurus cristatus*
Improved grassland (P)	Brown earth/brown podzolic	166 ± 78, 45–290	Good	*A. stolonifera*, *H. lanatus*, *Elytrigia repens*, *Festuca rubra*

subject to annual silage cutting and fertilisation. In the planted sites the ground was generally prepared by mounding with drains established at frequent intervals, although drainage was much less frequent among the improved grasslands. Fertiliser was applied to most of the peatland and wet grassland planted sites though not the improved grasslands, and herbicide use was most frequent in the grassland sites in the years following planting. In all sites the spruce trees conformed to the standard spacing for conifers of 2 m × 2 m. Mean tree height in the wet grasslands was 4.3 m (±2.6 S.D.), compared to 3.1 m (±1.2 S.D.) in the improved grasslands and just 1.6 m (±0.7 S.D.) in the peatlands.

2.2. Spider sampling

To investigate the initial effects of afforestation within the habitats two types of sampling plot were established. First, plots were located in areas of homogenous vegetation cover which took into account the major vegetation types present: these were termed standard plots; second, plots were located in various features present in the habitat which may contribute to the biodiversity of a site such as wet flushes and the edges of ditches or streams (in the peatlands) and hedgerows (in the grasslands): these were termed supplementary microhabitat plots. To identify suitable sampling plots, both unplanted and planted sites were examined and comparable areas of habitat within each were identified. Plots were then selected by walking a transect route through the centre of these habitat areas locating the plots approximately 50 m apart (although sometimes at a greater distance if no suitable habitat was located at 50 m) and at least 50 m from the edge.

Pitfall traps were used to sample the ground-dwelling spider assemblages within and among the habitat types. Pitfall trap catches are a function of a species' density, activity and behaviour, and as such, the data derived should not be considered a complete inventory of all the ground-dwelling species in a given habitat. Rather, they should be considered a representation of the active ground-dwelling spider fauna which are susceptible to this trapping method.

The pitfall traps consisted of a plastic cup (7 cm diameter by 9 cm depth) which had two drainage slits cut 1cm from the rim of the cup and were filled to 1cm depth with ethylene glycol to act as a killing and preserving agent. Although it has been found that a trap with a diameter of 11.1 cm may be the most efficient for sampling ground active spiders (Brennan, 2003) a 7 cm diameter was selected in the present study for logistical reasons. The cup was placed into a whole made with a bulb corer so that the rim of the cup was flush with the surface of the ground. To protect the trap from trampling in the heavily grazed sites a section of plastic piping (7 cm diameter by 10 cm depth), was inserted into the ground, and the plastic cup was then inserted within this ring. Each sampling plot consisted of five pitfall traps, which were arranged in a 4 m × 4 m grid, with one trap at each corner and one in the centre in the standard plots. In the supplementary plots which sampled linear features (such as hedgerows and ditch or stream edges) the traps were arranged in a line along the linear feature, with each trap spaced 2 m apart.

Six sampling plots were established within each site (three of each plot type), each separated by a minimum of 50 m. In two of the improved grassland planted sites however there were no supplementary features present, so only three standard plots were established. In the wet grasslands and peatlands this gave a total of 96 plots, with 48 plots each in the unplanted and planted sites, whereas in the improved grasslands there were a total of 90 plots with 48 in the unplanted and 42 in the planted sites. The traps were active from May to July (63–65 days) and were changed three times during this period, approximately every 21 days. A large number of traps were lost through trampling in five of the sites so the pitfall traps were maintained for an extra 21 days in these pairs of sites. Due to the large number of sites and the intensity of fieldwork involving invertebrates the sampling was carried out over two field seasons in 2002 and 2004. Four pairs of peatlands were sampled in 2002 and four in 2004; two pairs of wet grasslands were sampled in 2002 and six in 2004; two pairs of improved grasslands were sampled in 2002 and six in 2004.

A 50× magnification microscope was used to identify the spiders to species level and nomenclature follows Roberts (1993), however juveniles were not identified due to the difficulty involved in species identification. Determining the distribution, rarity and ecology of Irish spiders can be problematic due to the lack of previous research. To overcome this the *Provisional Atlas of British spiders* (Harvey et al., 2002) was used in conjunction with the published Irish records (van Helsdingen, 1996, 1997; Roberts, 1993; McFerran, 1997; Smith, 1999; Snazell and Jonsson, 1999; Nolan, 2000a,b, 2002a,b; Cawley, 2001; Fahy and Gormally, 2003). Species which occurred in less than five of the Irish counties and which are designated as either Nationally Scarce or recorded as Red Data Book species (Bratton, 1991) in Great Britain were considered to be rare. The species were assigned to habitat associations based on their preference for the following habitat and microhabitat characteristics: general habitat preference (open habitats, forested habitats or generalists); moisture preference (wet habitats, dry habitats or generalists); vegetation preference (ground layer, low vegetation, bushes and trees or generalists). These were determined using available literature (listed above), however due to the lack of published information on Irish spiders many of these associations were based on the species' habitat preferences in Great Britain. This was considered adequate because the climate and habitats in Ireland and Britain are similar, and it is likely that the species will respond in a similar way.

2.3. Habitat variables

Vegetation cover in a 1 m^2 quadrat surrounding each pitfall trap was measured in the following vertical layers: ground vegetation (0–10 cm), lower field layer (>10–50 cm) and upper field layer (>50–200 cm). Cover of other features such as deadwood, leaf litter and soil was also measured. Percentage cover of these variables was estimated using the Braun–Blanquet scale (Mueller-Dombois and Ellenberg, 1974), which gives numerical rankings to a range of percentages (+, <1%

cover; 1, 1–5%; 2, 6–25%; 3, 26–50%; 4, 51–75%; 5, 76–100%). For the analyses the appropriate median value within each range was substituted for the numerical ranking. At two locations within each plot a bulb corer was used to extract the top layer of the substrate to a depth of 15 cm. Organic content of the soil was then calculated using the method outlined in Grimshaw (1989). Each plot was classified by habitat type according to the Irish habitat classification scheme (Fossitt, 2000). Several of the flushes sampled were large enough to be designated as a poor fen and flush peatland habitat type, however as these areas were still not large enough to constitute a substantial area of the site they were still considered supplementary habitats.

2.4. Data analysis

NMS ordination analysis (for explanation see below) indicated that there was no difference in the spider assemblages sampled between the 2002 and 2004 fieldwork seasons, therefore these data sets were pooled in subsequent analyses. There was a significant effect of trap loss on the spider assemblages within the plots when three or more traps were missing (20% of the total per plot). Where possible pitfall traps from the extra sampling period were substituted for the missing traps, however where three or more traps were missing and no replacement traps were available these plots were excluded from the analyses.

Paired sample *t*-tests were used to examine the effect of afforestation on the spider assemblages of the standard and supplementary plots within each habitat type. The following response variables were tested: species richness, abundance, dominance and richness of the various habitat specialists. The Berger–Parker index (Berger and Parker, 1970) was used to indicate dominance, which calculates the proportion of the total abundance accounted for by the most abundant species. For these analyses the mean value of each response variable was calculated for each site. The response variables were tested for normality and homogeneity of variance and the Berger–Parker values were arcsin transformed. These analyses were carried out using SPSS (SPSS, 2002).

To examine the differences in spider assemblage composition between the unplanted and planted sites among the habitat types Global Non-metric Multi-dimensional Scaling Analysis (NMS), Blocked Multiple-response Permutation Procedures (MRBP) and Indicator Species Analysis were used. The NMS used plot data and the following parameter set-up: 6 initial axes, 20 runs with real data, stability criterion = 0.001, 10 iterations to evaluate stability, 250 maximum iterations, step down in dimensionality used, initial step length = 0.20, random starting coordinates and 50 runs of the Monte Carlo test. The environmental variables were correlated with the ordination axes and those with a Pearson $r^2 > 0.1$ were presented in a joint biplot ordination diagram. MRBP analysis tests the difference between pre-determined groups (site pairs) using the Euclidean distance measure. Differences are tested with the *A* statistic where $A = >0$ if the average distance is lower than that expected by chance within each group, $A = 0$ if average distance is equal to that expected by chance within each group and $A = 1$ if the assemblages are the same within each group. The *A* statistic is tested for significance by comparing observed and expected values. Indicator Species Analysis combines the relative abundance and relative frequency of species within each group, identifies species with high constancy and fidelity to groups and then tests the significance of the resulting indicator value with a Monte Carlo test. These analyses used relative abundance data (to account for differences in pitfall trap efficiency caused by variation in vegetation structure; Melbourne, 1999) and were carried out using PC-ORD (McCune and Mefford, 1997).

3. Results

Over 14% of the traps were lost due to animal trampling. The majority of these were in the unplanted improved grasslands where nearly 27% of the traps were lost. With these plots excluded from the analyses this gave a total of 86 plots in the peatlands (43 planted and 43 unplanted), 70 in the improved grasslands (37 unplanted and 33 planted) and 90 in the wet grasslands (45 unplanted and 45 planted). For the paired site analyses this resulted in 6 paired peatlands, 7 paired wet grasslands and 5 paired improved grasslands.

There were 33,157 individuals captured from 189 species and 18 families: of these spiders 3448 were juveniles and so were excluded from the analyses. The most abundant species in the unplanted sites were *Pardosa pullata* (Clerck, 1757), *Pardosa amentata* (Clerck, 1757), *Silometopus elegans* (O. P.-Cambridge, 1872), *Oedothorax fuscus* (Blackwall, 1834) and *Pachygnatha degeeri* (Sundevall, 1830), each of these species constituting greater than 5% of the total adult catch within these sites. In the planted sites, *P. pullata* and *P. amentata* were the most abundant species, also constituting greater than 5% of the total adult catch each.

There were 40 species sampled that were associated with open habitats and 15 species associated with forested habitats; furthermore, two species were associated with dry habitats and 54 species associated with damp or wet habitats. The majority of species sampled were typical ground layer species (111), although 37 species were associated with low vegetation and one species associated with trees and shrubs. A full list of the species and their authorities, including their habitat associations is given in Appendix A.

There were five rare species found in the standard plots, the majority of which were only sampled in the unplanted sites. *Satilatlas britteni* (Jackson, 1913) is associated wet locations and was sampled in lowland and upland blanket bogs. Both *Nigma puella* (Simon, 1870) and *Zelotes lutetianus* (Koch, 1866) were sampled in the lowland blanket bogs, *N. puella* is usually found on trees and bushes, and *Z. lutetianus* is associated with coastal marshes and sand dunes (Harvey et al., 2002). *Milleriana inerrans* (O. P.-Cambridge, 1885) frequently utilises aerial dispersal and is therefore found in a variety of habitats in Britain (Harvey et al., 2002) though it has only been recorded once in Ireland. This species was sampled in the unplanted wet grasslands. Only one rare species was found

Table 2
Mean ± S.E. species richness, abundance, dominance and richness (S) of habitat specialists per standard plot in the unplanted and planted sites within each habitat type (paired sample *t*-test statistics and associated significance between the unplanted and planted sites within each habitat are shown)

	Peatland			Wet grassland			Improved grassland		
	Unplanted	Planted	*t* (d.f. = 7)	Unplanted	Planted	*t* (d.f. = 7)	Unplanted	Planted	*t* (d.f. = 5)
Species richness	24.1 ± 1.6	23.0 ± 1.6	0.82	22.0 ± 2.3	20.0 ± 1.1	1.15	16.3 ± 1.5	20.9 ± 0.9	−3.63*
Total abundance	198 ± 42	91 ± 17	4.25**	182 ± 32	77 ± 13	4.41**	173 ± 42	99 ± 19	2.04†
Berger–Parker dominance	0.32 ± 0.09	0.21 ± 0.03	4.01**	0.35 ± 0.04	0.26 ± 0.03	1.5	0.33 ± 0.05	0.31 ± 0.05	0.32
Open-associated S	6.6 ± 0.6	5.0 ± 0.4	2.71*	7.6 ± 0.8	5.5 ± 0.5	4.47**	7.5 ± 0.7	5.5 ± 0.7	2.48*
Forest-associated S	0.7 ± 0.2	1.3 ± 0.2	−2.60*	0.5 ± 0.1	1.1 ± 0.4	−1.77	0.5 ± 0.2	1.2 ± 0.1	−3.31*
Wet-associated S	8.0 ± 0.9	5.8 ± 0.5	2.16†	8.5 ± 0.9	6.4 ± 1.0	3.85**	6.8 ± 0.3	4.4 ± 0.6	3.31*
Ground-layer associated S	17.2 ± 1.3	15.8 ± 1.4	1.64	14.5 ± 1.6	13.9 ± 0.8	0.51	9.6 ± 0.6	13.4 ± 1.1	−2.98*
Low vegetation associated S	2.9 ± 0.3	2.5 ± 0.5	0.73	2.6 ± 0.5	2.5 ± 0.4	0.35	1.6 ± 0.5	2.6 ± 0.3	−3.00*

† $P = 0.1$–0.05; * $P < 0.05$; ** $P < 0.01$.

solely in the planted sites, *Episinus truncatus* (Latrielle, 1809), which was sampled in an improved grassland site and is usually associated with heathlands (Roberts, 1993). *Baryphyma gowerense* (Locket, 1865), was sampled in a wet grassland standard plot (as well as in a poor fen and flush supplementary peatland plot) and has previously been found in brackish marshes (Harvey et al., 2002).

There were four rare species found in the supplementary microhabitat plots, the majority of which were only sampled in the unplanted peatlands. *Meioneta mollis* (O. P.-Cambridge, 1871) which was a new Irish record, and is associated with damp conditions, and *S. britteni*, were both sampled in poor fen and flush peatlands. *B. gowerense* was sampled in a poor fen and flush unplanted peatland plot (as well as in wet grassland standard plot). *Maro sublestus* (Falconer, 1915) and *S. britteni*, were also sampled on the edges of streams in lowland blanket bogs. Both of these species are associated with wet habitats (Harvey et al., 2002). *Saloca diceros* (O. P.-Cambridge, 1871) was found in both unplanted and planted hedgerows in the wet grasslands and is associated with a variety of wet habitats such as saltmarshes and *Sphagnum* bogs (Harvey et al., 2002).

3.1. The affects of afforestation on species richness and abundance

The mean number of species per standard plot within each habitat type is shown in Table 2. Total species richness did not differ significantly between the unplanted and planted peatland and wet grasslands; however in the improved grasslands mean species richness was significantly greater in the planted sites. Across the habitats total abundance and the number of open-associated and wet-associated species was greater in the unplanted sites, though for abundance this difference was not significant among the improved grasslands. In contrast, the number of species associated with forested habitats was higher in the planted sites across the habitats, though not significantly so in the wet grasslands. The number of species associated with the ground layer did not differ significantly between the unplanted and planted peatlands and wet grasslands; however in the improved grasslands the number of ground layer species supported was significantly greater in the planted sites. Similarly, the number of low vegetation species did not differ significantly among the unplanted and planted sites in the wet grasslands and peatlands, however there were significantly more of these species supported in the improved grassland planted than the unplanted sites.

In the peatlands the number of species associated with wet habitats was significantly lower in the planted supplementary plots compared to the unplanted plots ($t = 3.60$, $P = 0.009$, $n = 8$). The number of ground layer species in the peatlands showed a similar trend, however this difference was not significant ($t = 1.95$, $P = 0.09$, $n = 8$). The remaining species variables however (total richness, abundance, dominance and various habitat specialists) did not differ significantly in the peatlands. In addition to this there were no significant differences in any of the measures of the above-mentioned species variables between supplementary plots in the planted and the unplanted sites within the wet and improved grasslands.

3.2. The effects of afforestation on spider assemblages

The grassland and peatland spider assemblages were distinct in both the richness of the various species groups and the rare species supported (see above text, Table 2 and Appendix A) so these were analysed in separate ordinations. The NMS ordination of spider assemblages among the unplanted and planted grassland standard plots accounted for 84% of the variation in the data with three axes best explaining this variation (Fig. 2). Axis 1, which accounted for 31% of the variation, separated the unplanted from the planted plots. Axis 2, which represented 30% of the variation, distinguished the unplanted improved grasslands from both the unplanted and planted wet grassland plots. Axis 3, which accounted for a further 22% of the variation in the species data, represented a further separation of the unplanted and planted plots. Within the habitats the spider assemblages in the unplanted and planted improved grasslands differed significantly (MRBP: $A = 0.291$, $P = 0.008$), whereas unplanted and planted wet grasslands plots did not (MRBP: $A = 0.045$, $P = 0.139$).

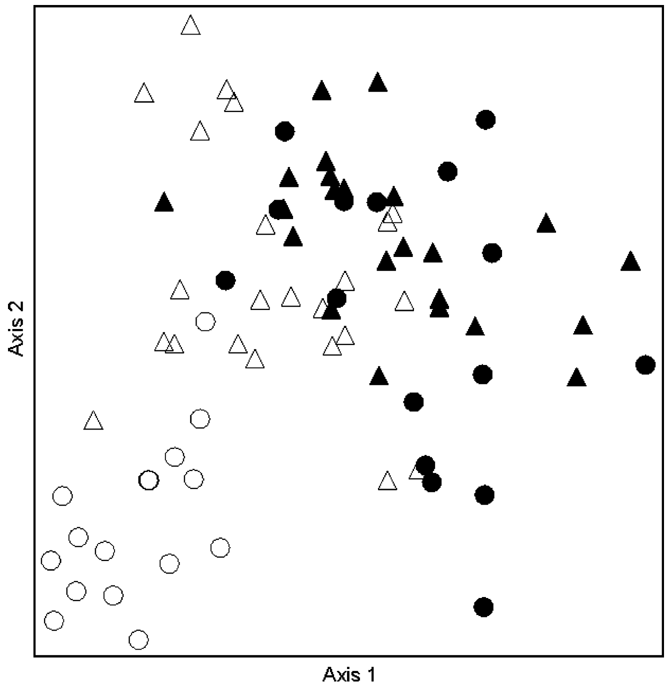

Fig. 2. NMS ordination of the spider assemblages among the unplanted and planted standard plots in the grasslands: (○) improved grassland unplanted; (●) improved grassland planted; (△) wet grassland unplanted; (▲) wet grassland planted. Final stress for a three-dimensional solution = 13.54; final instability = 0.0004.

The NMS ordination of the peatland standard plots accounted for 86% of the variation in spider assemblage composition (Fig. 3) and was represented by three axes. Axis 1, which explained over 53% of the variation in the species data, distinguished the unplanted and planted plots which also differed significantly in assemblage composition (MRBP: $A = 0.162$, $P = 0.004$). Across axis 2 (which accounted for 17% of the variation) the planted plots exhibited greater variation than the unplanted plots. There was also some separation of the unplanted plots by Irish habitat classification (Fig. 3). Axis 3, which accounted for 15% of the variation in the species data, further separated the planted plots, distinguishing several lowland and upland blanket bog plots from the remaining plots.

The species with high indicator values in the unplanted sites (Table 3) are mostly species commonly found in open habitats, however several species associated with wet habitats were identified as indicators in the wet grasslands and peatlands. In the planted sites most of the species with high indicator values were generalist species commonly found in a broad range of open habitats, although *Robertus lividus* is a ubiquitous species which is found in both open and forested habitats, and two species associated with forested habitats were identified.

The NMS ordination of the spider assemblages among the supplementary plots in the unplanted and planted grasslands accounted for 70% of the variation in the species data with three axes best explaining this variation (Fig. 4). Axis 1, which accounted for 28% of the variation, separated the unplanted improved grassland plots from the planted plots to some degree, with the planted plots forming a relatively tight cluster. However, the assemblages of the unplanted and planted supplementary plots did not differ significantly from each other: $A = -0.020$, $P = 0.243$ and $A = 0.014$, $P = 0.170$ in the improved grasslands and wet grasslands, respectively. The remaining two axes each explained 21% of the variation among the spider assemblages represented some unknown variation in the supplementary plots (hedgerows) unrelated to habitat type or site.

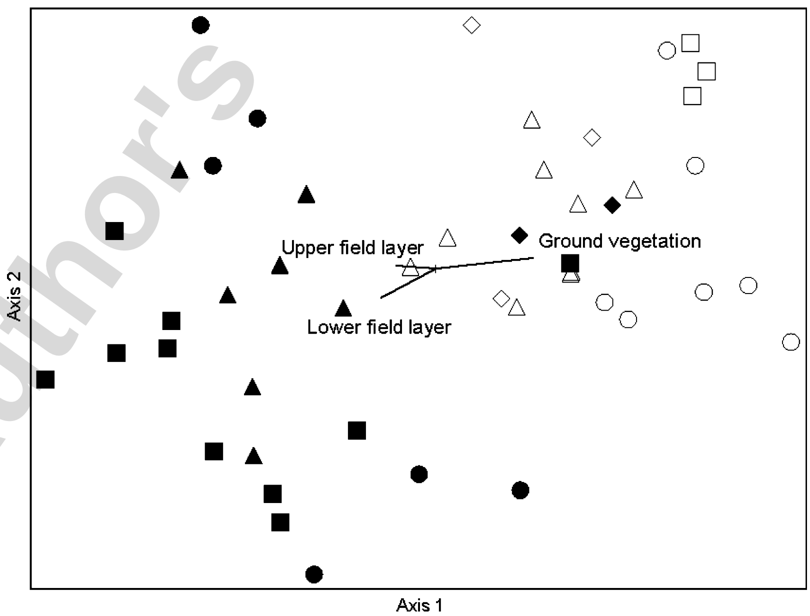

Fig. 3. NMS ordination of the spider assemblages among the unplanted and planted standard plots in the peatlands by Irish habitat classification: (○) wet heath unplanted; (●) wet heath planted; (△) upland blanket bog unplanted; (▲) upland blanket bog planted; (□) lowland blanket bog unplanted; (■) lowland blanket bog planted; (◇) cutover bog unplanted; (◆) cutover bog planted. Habitat variables with a Pearson correlation r^2 value with the axes >0.1 are shown. Final stress for a three-dimensional solution = 12.83; final instability = 0.0004.

Table 3
Indicator species analysis of the standard plots in the unplanted (U) and planted (P) sites within each habitat group

	Habitat	Peatland		Wet grassland		Improved grassland	
		U	P	U	P	U	P
Pardosa pullata	O, GL	**70*****	15	50	40	26	49
Pirata piraticus	W, GL	**67****	16	**71*****	4	1	11
Silometopus elegans	O, W, GL	**58***	14	12	0	9	2
Walckenaeria vigilax	W, GL	**54****	3	36	16	1	5
Pocadicnemis pumila	O	16	**83*****	12	**66****	2	**75*****
Lepthyphantes zimmermanni	F, GL	3	**73*****	10	42	3	31
Oedothorax gibbosus	O, W, GL	10	**65*****	7	**52***	14	30
Bathyphantes gracilis	GL	1	**54****	61	31	49	51
Robertus lividus	GL	5	**50****	2	**51****	0	**56****
Oedothorax fuscus	O, W, GL	7	1	**63*****	0	**100*****	0
Erigone atra	O, GL	11	1	**50****	5	**97*****	1
Bathyphantes parvulus	GL	8	40	13	**64****	0	**79*****
Lepthyphantes ericaeus	GL	6	49	10	56*	0	**62*****
Erigone dentipalpis	O, GL	12	1	26*	0	**100*****	0
Pardosa palustris	O, GL	27	0**	40*	1	**69*****	0
Pocadicnemis juncea	O	4	41*	19	45	2	**72****
Monocephalus fuscipes	F, GL	6	7	0	34**	0	**62*****
Walckenaeria acuminata	GL	6	8	5	16	0	**56****

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Species with a significant maximum indicator value >50% and associated significance (Monte Carlo test) are indicated by bold type. The habitat association of each species is also shown: O, open habitats; F, forested habitats; W, wet habitats; GL, ground layer.

The NMS ordination of the spider assemblages among the supplementary plots in the unplanted and planted peatlands accounted for 77% of the variation in the species data (Fig. 5). Three axes best explained the variation in the spider assemblages with axis 1 accounting for 40%, axis 2, 20% and axis 3, 17%. Axis 1 distinguished the spider assemblages of the unplanted and planted supplementary plots, which differed significantly (MRBP: $A = 0.143$, $P = 0.006$). The planted plots were associated with higher cover of upper and lower field layer vegetation whereas the unplanted plots were associated with higher cover of ground vegetation. Axis 2 reflected differences in organic content and soil cover among the plots.

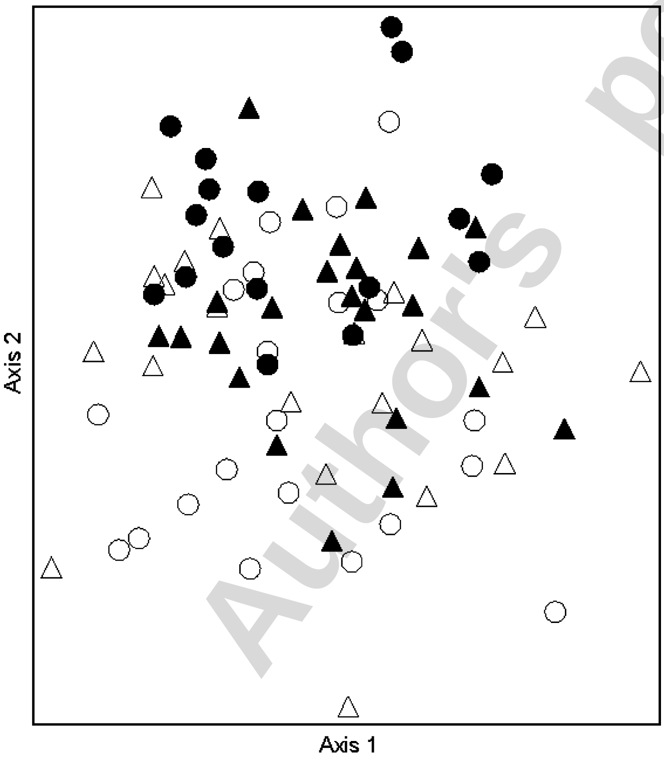

Fig. 4. NMS ordination of the spider assemblages among the unplanted and planted supplementary plots in the grasslands: (○) improved grassland unplanted; (●) improved grassland planted; (△) wet grassland unplanted; (▲) wet grassland planted. Final stress for a three-dimensional solution = 19.37; final instability = 0.0008.

The indicator species identified in the supplementary plots among the unplanted and planted sites are shown in Table 4. The unplanted sites were characterized by open as well as generalist species, although one species was associated with wet habitats. In the planted sites species with high indicator values are associated with both open and forested areas.

4. Discussion

During the forest cycle there is a fundamental change in the flora and fauna at the time of canopy closure (Wallace and Good, 1995; Humphrey et al., 1999; Jukes et al., 2001; French, 2005; Oxbrough et al., 2005). Indeed, prior to this the spider assemblages resemble that of the pre-planting habitat type (Oxbrough et al., 2005). In addition to this, the present study also suggests that even in the first 5 years of the forest cycle the spider fauna is affected by afforestation. In particular, species associated with specific habitat characteristics of the unplanted sites were replaced by habitat generalists. Furthermore, after afforestation, a greater number of species associated with forested habitats were supported, even at this early stage in the forest plantation cycle. For instance, two forest species (*Lepthyphantes zimmermanni* and *Monocephalus fuscipes*) were identified as indicators of the planted peatland and improved grassland sites respectively. The 5-year-old spruce trees in this study had not yet reached canopy closure: the trees

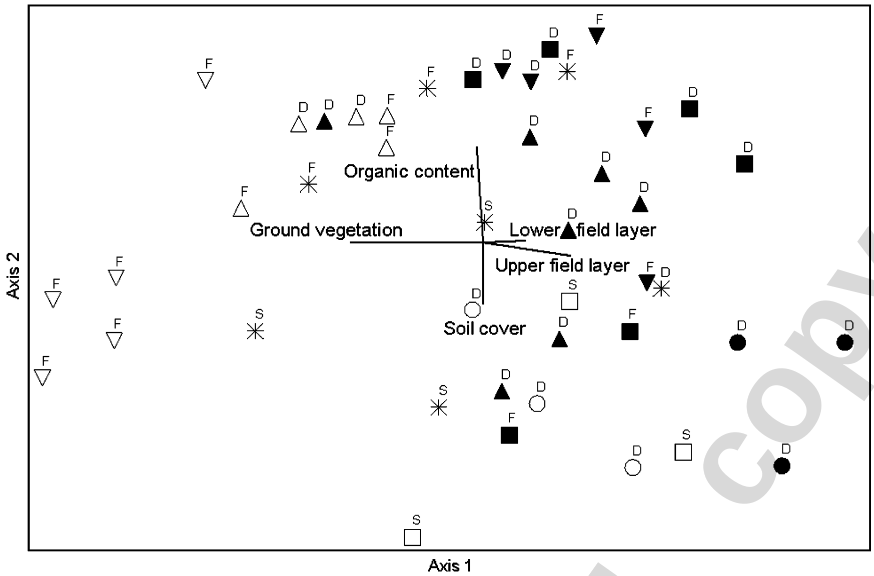

Fig. 5. NMS ordination of the spider assemblages among the unplanted and planted supplementary plots in the peatlands by Irish habitat classification: (○) wet heath unplanted; (●) wet heath planted; (△) upland blanket bog unplanted; (▲) upland blanket bog planted; (□) lowland blanket bog unplanted; (■) lowland blanket bog planted; (▽) poor fen and flush unplanted; (▼) poor fen and flush planted; (✳) cutover bog unplanted. Letter above plot symbol denotes supplementary plot type: F, flush; S, edge of stream; D, edge of ditch. Habitat variables with a Pearson correlation r^2 value with the axes >0.1 are shown. Final stress for a three-dimensional solution = 15.67; final instability = 0.0004.

were spaced 2 m apart and were generally 2–3 m high (mean 2.2 m ± 0.9 S.D., range 0.1–4.3 m). However, for ground-dwelling spiders this may create some of the conditions characteristic of forested environments such as protection from the wind and stable microclimates (Pollard, 1968).

4.1. Peatland spider fauna

There was no overall difference in the number of species supported in the peatlands after afforestation, however the composition of the spider assemblages differed between the unplanted and planted sites, being distinguished by a reduction in rare and specialist wetland species. Prior to afforestation the unplanted areas are prepared for plantation establishment to encourage more suitable conditions for tree growth. This includes the establishment of drains, which on particularly wet sites are created at frequent intervals: for instance the recommended spacing for mound drains is 8 m (Forest Service, 2003). Indeed, in the present study the majority of the sites had an extensive network of drains established (personal observation). The peatlands were generally the wettest sites surveyed and so drainage may have had the greatest influence on the soil moisture content in this habitat, a factor known to influence spider distribution (Usher, 1992).

The extent of the drainage may be of particular importance for the supplementary microhabitats sampled in the peatlands, especially those larger areas which were designated as poor fen and flush habitats. These areas supported a distinct spider fauna with several rare species compared to those in the planted sites. The Irish *Forestry and Water Quality Guidelines* (Forest Service, 2000b) stipulate that aquatic zones (‘a permanent or seasonal river, stream or lake’) which are marked on ordnance

Table 4
Indicator species analysis of the supplementary microhabitat plots in the unplanted (U) and planted (P) sites within each habitat group

	Habitat	Peatland		Wet grassland		Improved grassland	
		U	P	U	P	U	P
P. pullata	O, GL	**87*****	10	15	29	15	29
W. vigilax	W, GL	**69*****	3	17	9	17	9
Pachygnatha degeeri	LV	**50****	5	12	1	12	1
Pocadicnemis pumila	O	22	**78****	23	27	23	27
Pocadicnemis juncea	O	8	45*	19	**54***	22	**61***
Lepthyphantes tenuis	GL	39	12	23	18	**75*****	8
E. atra	O, GL	4	0	13	0	**65*****	1
Leptorhoptrum robustum	W, GL	0	5	30	1	**50***	3
B. parvulus	GL	17	16	6	49*	17	**73*****
L. ericaeus	GL	27	41	20	30	13	**66****
W. acuminata	GL	16	5	7	17	5	**50***

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Species with a significant maximum indicator value >50% and associated significance (Monte Carlo test) are indicated by bold type. The habitat association of each species is also shown: O, open habitats; W, wet habitats; GL, ground layer; LV, low vegetation.

survey 6 inch maps should be protected during the afforestation process by a minimum buffer zone of 10 m. These current guidelines are likely to exclude the supplementary flushes sampled within this survey because they are either not included in this definition or because of they are too small to be included on the 6 inch maps, and so they may be afforded little protection during the afforestation process.

In the peatlands the vegetation structure and composition changed dramatically after afforestation. The unplanted peatlands were dominated by a mixture of mosses, sedges, low herbs and some grasses and low ericaceous shrubs. After planting, purple moor-grass (*Molinia caerulea*), a coarse tussocky grass, was dominant in many of the peatland sites. This may explain why the numbers of species associated with low vegetation was significantly lower in the planted peatlands; these species may have been specialised to the particular vegetation structure present on the site prior to afforestation. Changes in vegetation structure and composition could be attributed to the drier soil conditions after afforestation, but also the application of fertiliser (phosphate) which was used after afforestation on all of the peatland sites. Although fertiliser is applied to encourage crop tree growth it is also likely to influence the ground and herb vegetation present.

4.2. Grassland spider fauna

Among the grasslands the number of specialist wetland species and rare species was reduced after afforestation, again probably reflecting the influence of soil drainage but also fertiliser application in the wet grasslands. In addition to this the spider fauna of the grasslands, and in particular the improved grasslands, may have been influenced by a release from grazing pressure. The improved grassland sites were the most intensively managed of the habitats surveyed prior to afforestation, with the heaviest level of grazing. This can be seen in the present study where the unplanted improved grasslands were characterised by species such as *Erigone atra*, *Erigone dentipalpis* and *O. fuscus*, which are pioneer species frequently found dominating disturbed habitats (Cole et al., 2003). However after afforestation there was an increase in the overall number of species supported and also in the number of species associated with low vegetation (rather than ground vegetation). Grazing pressure has been found to directly influence spider diversity through the resulting decrease in vegetation structure (Dennis et al., 1998, 2001). This may suggest that afforestation initially benefits the spider fauna of improved grasslands, however this is unlikely to persist after canopy closure (Oxbrough et al., 2005).

It is unsurprising that the hedgerows sampled in the grasslands did not differ to a great degree in either species richness or assemblage composition between the unplanted and planted sites. Whilst hedgerows are likely to be adversely affected by the effects of shading when the trees are more developed, at this early stage in the forest plantation cycle trees of 2–3 m in height are unlikely to have a large impact. Furthermore, the Irish *Forest Biodiversity Guidelines* (Forest Service, 2000a) recommend that hedgerows be regarded as areas for biodiversity enhancement within plantations, meaning that they should remain undisturbed during the afforestation process and a 3 m buffer zone should be established around them (Forest Service, 2000a). This is presumably to protect them from shading and disturbance by machinery. In addition to this hedgerows may support species which inhabit the upper vegetation layers (and hence not sampled by pitfalls), so the protection of these features during the afforestation process may be important for plantation biodiversity.

5. Conclusions

This study indicates that peatlands are the most sensitive to afforestation of the habitats surveyed, suggesting that in terms of biodiversity loss, this habitat is the least suitable for afforestation. In particular, small areas of wet flush within peatlands, which support distinct and rare species, should be protected during the afforestation process. Furthermore, the loss of specialist species across all of the habitats after afforestation indicates that retained areas which are selected for biodiversity enhancement when plantations are established will benefit from as little disturbance to the habitat and pre-planting management regime as possible.

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Appendix A

The number of individual spiders sampled within each habitat type, site type (unplanted and planted) and plot type (S, Standard, M, Supplementary microhabitat); *n*, number of plots

	Peatlands				Wet grasslands				Improved grasslands				Habitat
	Unplanted		Planted		Unplanted		Planted		Unplanted		Planted		
	S ($n = 35$)	M ($n = 13$)	S ($n = 29$)	M ($n = 18$)	S ($n = 24$)	M ($n = 24$)	S ($n = 24$)	M ($n = 24$)	S ($n = 24$)	M ($n = 24$)	S ($n = 24$)	M ($n = 18$)	
Agelena labyrinthica (Clerck, 1757)	0	0	0	0	1	0	0	0	0	0	0	0	LV
Agroeca proxima (O. P.-Cambridge, 1871)	1	0	0	2	1	0	0	0	0	0	0	0	LV
Agyneta cauta (O. P.-Cambridge, 1902)	10	0	26	0	0	0	0	0	0	0	0	0	GL
Agyneta conigera (O. P.-Cambridge, 1863)	3	0	5	2	0	2	2	2	0	3	0	2	–
Agyneta decora (O. P.-Cambridge, 1871)	66	45	45	15	5	0	0	0	12	4	1	0	–
Agyneta olivacea (Emerton, 1882)	293	176	178	146	2	1	0	1	0	0	1	0	W, GL
Agyneta ramosa (Jackson, 1912)	4	9	5	6	8	29	4	20	0	4	1	8	W, GL
Agyneta subtilis (O. P.-Cambridge, 1863)	63	49	64	35	6	48	8	57	0	21	0	8	GL
Allomengea vidua (Koch, 1879)	0	0	0	0	0	0	1	0	0	0	0	0	W, LV
Alopecosa pulverulenta (Clerck, 1757)	61	7	0	3	14	1	4	4	3	1	9	3	O, GL
Antistea elegans (Blackwall, 1841)	116	10	18	4	38	7	6	8	0	0	0	0	O, W, GL
Aphileta misera (O. P.-Cambridge, 1882)	0	1	0	0	0	0	0	0	0	0	0	0	O, W
Araeoncus crassiceps (Westring, 1861)	18	0	0	0	0	0	0	0	0	0	0	0	W, GL
Arctosa leopardus (Sundevall, 1843)	95	1	0	1	0	0	0	0	0	0	0	0	O, W, GL
Asthenargus paganus (Simon, 1884)	0	0	0	0	0	0	1	0	0	2	0	1	F, GL
Baryphyma gowerense (Locket, 1965)	1	0	2	1	4	0	0	0	0	0	0	0	O, W
Baryphyma trifons (O. P.-Cambridge, 1863)	3	1	2	5	14	3	17	4	1	1	19	0	O, W, GL
Bathyphantes approximatus (O. P.-Cambridge, 1871)	0	0	0	0	8	2	4	0	0	0	6		W, GL
Bathyphantes gracilis (Blackwall, 1841)	12	57	96	94	188	27	73	35	197	50	172	41	GL
Bathyphantes nigrinus (Westring, 1851)	2	0	0	2	5	29	14	26	1	8	38	14	GL
Bathyphantes parvulus (Westring, 1851)	17	37	35	19	39	20	103	62	7	52	192	158	GL
Bathyphantes setiger (O. P.-Cambridge, 1894)	1	0	0	0	0	0	0	0	0	0	0	0	W, GL
Bolyphantes luteolus (Blackwall, 1833)	0	0	1	0	0	0	0	0	0	0	0	0	–
Centromerita bicolor (Blackwall, 1833)	0	0	0	0	0	0	0	0	0	0	1	0	GL
Centromerita concinna (Thorell, 1875)	15	2	2	0	3	1	0	0	0	1	0	0	GL
Centromerus sylvaticus (Blackwall, 1841)	0	0	0	0	1	0	0	0	0	0	0	1	GL
Centromerus dilutus (O. P.-Cambridge, 1875)	3	0	6	3	0	0	2	0	1	1	1	0	GL
Ceratinella brevipes (Westring, 1851)	107	66	110	70	14	5	10	11	1	6	7	8	GL
Ceratinella brevis (Wider, 1834)	32	0	13	15	1	3	0	2	0	7	1	0	GL
Ceratinella scabrosa (O. P.-Cambridge, 1871)	0	0	1	0	7	85	5	65	2	47	7	32	GL
Clubiona comta (C.L. Koch, 1839)	0	0	0	0	0	5	0	4	0	4	0	0	UV
Clubiona diversa (O. P.-Cambridge, 1862)	3	0	0	1	0	0	0	0	0	0	0	0	LV
Clubiona lutescens (Westring, 1851)	0	0	0	0	0	0	0	0	0	0	0	1	–
Clubiona neglecta (O. P.-Cambridge, 1862)	0	0	0	0	0	0	0	0	1	0	0	0	LV
Clubiona reclusa (O. P.-Cambridge, 1863)	2	0	0	3	1	5	1	3	0	3	8	2	LV
Clubiona stagnatilis (Kulczynski, 1897)	2	0	1	0	0	0	0	0	0	0	0	0	W, LV
Clubiona trivialis (C.L. Koch, 1843)	1	0	1	0	0	0	0	0	0	0	0	0	D, LV
Cnephalocotes obscurus (Simon, 1884)	19	6	4	0	2	0	0	0	0	0	0	0	GL
Cryphoeca sylvicola (C.L. Koch, 1834)	0	0	0	1	0	1	0	2	0	1	2	1	–
Dicymbium nigrum (Blackwall, 1834)	13	26	5	2	55	8	21	14	32	4	38	7	–
Dicymbium tibiale (Blackwall, 1836)	2	0	4	4	4	0	2	0	3	2	3	0	GL
Diplocephalus cristatus (Blackwall, 1833)	1	0	0	0	0	0	0	0	0	0	0	0	GL
Diplocephalus latifrons (O. P.-Cambridge, 1863)	1	0	0	0	0	4	1	10	1	3	1	6	F, GL
Diplocephalus permixtus (O. P.-Cambridge, 1871)	12	4	3	2	39	11	4	9	4	0	1	2	W, GL

Appendix A (*Continued*)

	Peatlands				Wet grasslands				Improved grasslands				Habitat
	Unplanted		Planted		Unplanted		Planted		Unplanted		Planted		
	S ($n = 35$)	M ($n = 13$)	S ($n = 29$)	M ($n = 18$)	S ($n = 24$)	M ($n = 24$)	S ($n = 24$)	M ($n = 24$)	S ($n = 24$)	M ($n = 24$)	S ($n = 24$)	M ($n = 18$)	
Diplocephalus picinus (Blackwall, 1831)	1	0	0	0	2	0	0	0	1	1	0	0	GL
Diplostylor concolor (Wider, 1834)	0	0	0	0	0	15	0	5	0	9	8	18	GL
Dismodicus bifrons (Blackwall, 1841)	22	7	28	12	7	35	13	34	17	30	37	18	GL
Dolomedes fimbriatus (Clerck, 1757)	5	0	2	3	0	0	8	0	0	0	0	0	O, W
Drassodes cupreus (Blackwall, 1834)	18	0	0	1	0	0	0	0	0	0	0	0	O, GL
Drassodes lapidosus (Walckenaer, 1802)	1	1	1	0	0	0	0	0	1	0	0	0	O, GL
Drepanotylus uncatus (O. P.-Cambridge, 1873)	1	0	0	0	0	0	0	0	0	0	0	0	O, W
Dysdera crocata (C.L. Koch, 1838	0	0	0	0	0	0	0	0	0	2	0	0	W
Enoplognatha ovata (Clerck, 1757)	0	2	5	0	0	3	4	2	0	8	3	3	LV
Enoplognatha thoracia (Hahn, 1833)	1	0	0	0	0	0	0	0	0	0	0	0	LV
Episinus angulatus (Blackwall, 1836)	0	0	1	0	0	0	0	0	0	1	0	0	W, GL
Episinus truncatus (Latrielle, 1809)	0	0	0	0	0	0	0	0	0	0	1	0	–
Erigone atra (Blackwall, 1833)	7	0	1	0	115	8	23	1	539	62	15	3	O, GL
Erigone dentipalpis (Wider, 1843)	10	0	0	0	24	0	0	0	364	12	1	0	O, GL
Erigone longipalpis (Sundevall, 1830)	0	0	0	0	0	0	0	0	2	1	0	0	W, O, GL
Erigonella hiemalis (Blackwall, 1841)	1	0	0	0	0	3	1	0	1	3	5	4	F, GL
Erigonella ignobilis (O. P.-Cambridge, 1871)	1	0	0	1	0	0	0	0	1	0	0	0	GL, W
Ero cambridgei (Kulczynski, 1911)	4	0	9	3	5	2	2	1	1	1	2	0	LV
Ero furcata (Villers, 1789)	0	0	0	0	0	0	0	0	0	0	0	1	LV
Euryopsis flavomaculata (C.L. Koch, 1836)	35	3	0	0	0	0	0	0	0	0	0	0	W, GL
Gnathonarium dentatum (Wider, 1834)	0	1	2	1	18	2	18	1	1	2	1	0	W, GL
Gonatium rubens (Blackwall, 1833)	2	0	5	1	0	0	0	0	0	2	1	0	O, GL
Gongylidiellum vivum (O. P.-Cambridge, 1875)	20	19	16	12	26	11	21	20	27	19	62	21	W, GL
Gongylidiellum latebricola (O. P.-Cambridge, 1871)	6	1	13	1	0	0	0	0	0	0	0	0	W, GL
Gongylidum rufipes (Linnaeus, 1758)	1	0	0	0	0	5	0	8	0	4	1	1	W, LV
Hahnia montana (Blackwall, 1841)	2	0	0	0	0	0	0	0	0	0	0	0	GL
Hahnia nava (Blackwall, 1841)	0	0	0	0	1	0	0	0	0	0	0	0	O, GL
Haplodrassus signifier (C.L. Koch, 1839)	5	4	6	1	0	0	0	0	0	0	0	0	O, GL
Hilaira excisa (O. P.-Cambridge, 1870)	0	0	0	1	0	0	0	0	0	0	0	0	W, GL
Hypomma bituberculatum (Wider, 1834)	20	14	12	11	14	8	9	2	8	4	7	3	W
Hypomma cornutum (Blackwall, 1833)	1	0	0	1	0	0	1	0	0	0	0	0	F, LV
Hyposinga pygmaea (Sundevall, 1831)	3	0	1	0	0	0	0	0	0	0	0	0	O, LV
Hypselistes jacksoni (O. P.-Cambridge, 1902)	9	1	2	1	0	0	0	0	0	0	0	0	O, W, GL
Kaestneria dorsalis (Wider, 1834)	0	0	0	0	0	0	0	0	0	0	0	1	LV
Kaestneria pullata (O. P.-Cambridge, 1863)	13	3	4	3	0	2	2	0	0	0	3	3	W, LV
Lepthyphantes alacris (Blackwall, 1853)	0	1	27	9	0	7	2	5	1	5	0	13	F, GL
Lepthyphantes angulatus (O. P.-Cambridge, 1871)	0	0	0	0	0	0	6	0	0	0	0	0	–
Lepthyphantes cristatus (Menge, 1866)	0	0	2	1	1	0	4	5	1	2	6	4	GL
Lepthyphantes ericaeus (Blackwall, 1853)	36	32	71	60	21	27	28	29	1	19	66	37	GL
Lepthyphantes flavipes (Blackwall, 1854)	0	0	3	0	0	8	0	15	1	3	0	3	F, GL
Lepthyphantes mengei (Kulczynski, 1887)	81	31	98	85	39	16	20	6	0	6	4	2	GL
Lepthyphantes minutus (Blackwall, 1833)	0	0	0	1	0	0	0	0	0	0	0	0	F
Lepthyphantes obscurus (Blackwall, 1841)	0	1	4	0	0	10	0	1	0	2	0	0	F
Lepthyphantes pallidus (O. P.-Cambridge, 1871)	0	0	0	0	0	1	1	0	0	0	2	2	GL
Lepthyphantes tenebricola (Wider, 1834)	0	0	0	0	1	4	2	13	0	7	1	4	F, GL
Lepthyphantes tenuis (Blackwall, 1852)	19	36	24	12	145	30	70	22	123	65	113	15	GL
Lepthyphantes zimmermanni (Bertkau, 1890)	10	6	93	32	14	39	22	55	5	34	10	18	F, GL
Leptorhoptrum robustum (Westring, 1851)	0	0	0	1	27	11	8	3	42	31	18	6	W, GL

Lophomma punctatum (Blackwall, 1841)	2	11	8	10	12	1	6	3	0	0	21	1	W, GL
Maro minutus (O. P.-Cambridge, 1906)	7	1	2	2	0	7	0	3	0	0	1	3	GL
Maro sublestus (Falconer, 1915)	0	2	0	0	0	0	0	0	0	0	0	0	W, GL
Maso sundervalli (Westring, 1851)	26	22	43	25	6	69	15	50	1	27	2	17	GL
Meioneta beata (O. P.-Cambridge, 1906)	15	0	0	0	0	0	0	0	0	0	0	0	O, GL
Meioneta mollis (O. P.-Cambridge, 1871)	19	0	0	0	0	0	0	0	0	0	0	0	–
Meioneta saxatilis (Blackwall, 1844)	23	14	3	1	1	0	0	2	6	13	4	4	GL
Meta mengei (Blackwall, 1869)	0	0	0	0	0	1	0	3	0	0	3	0	LV
Meta merianae (Scopli, 1763)	0	0	0	0	1	0	0	0	0	0	0	0	W
Meta segmentata (Clerck, 1757)	0	0	0	0	0	3	0	2	0	2	1	0	LV
Metopobactrus prominulus (O. P.-Cambridge, 1872)	21	3	21	8	0	0	0	11	2	5	55	13	–
Micrargus herbigradus (Blackwall, 1854)	12	6	13	6	3	0	6	7	0	0	2	1	GL
Micrargus subaequalis (Westring, 1851)	8	0	2	0	0	4	0	2	10	7	9	5	GL
Microlinyphia pusilla (Sundevall, 1830)	5	2	3	7	1	2	0	0	0	0	0	0	LV
Microneta viaria (Blackwall, 1841)	0	0	0	0	0	0	0	3	0	0	0	0	F, GL
Milleriana inerrans (O. P.-Cambridge, 1885)	0	0	0	0	1	0	0	0	0	0	0	0	GL
Minyriolus pusillus (Wider, 1834)	1	0	0	0	0	8	0	0	0	0	0	1	–
Monocephalus fuscipes (Blackwall, 1836)	5	5	3	5	19	74	22	168	1	58	44	100	F, GL
Neon reticulatus (Blackwall, 1853)	5	0	7	0	0	0	0	0	0	0	0	0	–
Nereine clathrata (Sundevall, 1830)	0	1	2	5	9	24	16	31	0	17	4	23	LV
Neriene montana (Clerck, 1757)	0	0	0	0	1	1	0	0	0	0	0	0	F, LV
Neriene peltata (Wider, 1834)	0	0	0	0	0	3	1	2	0	0	0	0	LV
Nigma puella (Simon, 1870)	1	0	0	0	0	0	0	0	0	0	0	0	LV
Oedothorax fuscus (Blackwall, 1834)	29	12	2	0	285	25	4	1	802	17	4	0	O, W, GL
Oedothorax gibbosus (Blackwall, 1841)	59	54	126	152	26	4	45	18	26	2	60	17	O, W, GL
Oedothorax retusus (Blackwall, 1851)	1	23	1	2	38	11	9	6	120	35	36	9	O, GL
Oxyptila trux (Blackwall, 1846)	152	29	20	13	18	13	14	14	22	41	10	5	LV
Pachygnatha clercki (Sundevall, 1823)	34	10	23	6	50	10	15	3	1	1	8	4	W, LV
Pachygnatha degeeri (Sundevall, 1830)	526	33	29	6	129	10	24	1	353	8	113	38	LV
Pardosa agricola (Thorell, 1856)	0	0	0	0	1	0	0	0	0	0	0	0	O, GL
Pardosa amentata (Clerck, 1757)	12	49	0	1	1183	338	404	132	163	95	351	83	O, W, GL
Pardosa nigriceps (Thorell, 1856)	168	28	33	5	36	5	18	6	10	11	30	22	LV
Pardosa palustris (Linnaeus, 1758)	4	0	0	0	123	25	17	2	163	9	0	0	O, GL
Pardosa pullata (Clerck, 1757)	1628	188	230	67	731	51	360	49	253	112	392	262	O, GL
Pelecopsis mengei (Simon, 1884)	1	2	0	0	40	0	1	0	0	0	0	0	W, GL
Pelecopsis nemoralis (Blackwall, 1841)	0	0	0	0	0	0	0	1	0	0	0	0	F
Pelecopsis parallela (Wider, 1834)	4	0	2	0	0	0	0	0	0	0	0	0	–
Pepnocranium ludicrum (O. P.-Cambridge, 1861)	23	10	21	2	0	0	0	0	1	0	0	0	–
Pholcomma gibbum (Westring, 1851)	0	0	2	3	0	8	1	5	0	0	0	2	GL
Pirata hygrophilus (Thorell, 1872)	19	1	8	3	0	0	0	0	0	0	0	0	O, W, GL
Pirata latitans (Blackwall, 1841)	0	0	1	0	2	0	0	0	0	0	0	0	O, W, GL
Pirata piraticus (Clerck, 1757)	472	108	75	28	281	36	16	4	3	1	8	3	W, GL
Pirata uliginosus (Thorell, 1856)	71	3	96	46	1	0	0	0	1	1	4	0	O, GL
Pisaura mirabilis (Clerck, 1757)	0	0	0	0	0	0	1	0	0	1	0	0	LV
Pocadicnemis juncea (Locket & Millidge, 1853)	13	19	42	35	83	31	90	84	26	105	197	210	O
Pocadicnemis pumila (Blackwall, 1841)	111	54	269	274	40	42	75	51	9	8	58	10	O
Poeciloneta globosa (Blackwall, 1841)	0	1	1	0	0	1	1	1	0	0	0	0	O
Porrhomma egeria (Simon, 1884)	0	0	0	0	0	1	0	0	0	0	0	0	–
Porrhomma pygmaeum (Blackwall, 1834)	0	0	1	0	0	1	0	1	0	0	0	0	W
Robertus arundineti (O. P.-Cambridge, 1871)	3	2	2	4	0	0	0	0	0	0	0	0	GL
Robertus lividus (Blackwall, 1836)	28	21	46	30	3	4	23	6	2	4	43	34	GL
Robertus neglectus (O. P.-Cambridge, 1871)	0	0	0	0	0	0	0	0	0	1	0	0	GL
Saaristoa abnormis (Blackwall, 1841)	5	17	29	12	0	3	8	8	0	0	11	2	GL
Saaristoa firma (O. P.-Cambridge, 1905)	0	1	1	0	0	0	0	0	0	0	2	1	–

Appendix A (*Continued*)

	Peatlands				Wet grasslands				Improved grasslands				Habitat
	Unplanted		Planted		Unplanted		Planted		Unplanted		Planted		
	S (n = 35)	M (n = 13)	S (n = 29)	M (n = 18)	S (n = 24)	M (n = 24)	S (n = 24)	M (n = 24)	S (n = 24)	M (n = 24)	S (n = 24)	M (n = 18)	
Saloca diceros (O. P.-Cambridge, 1871)	0	0	0	0	0	6	0	6	0	0	0	0	W, GL
Satilatlas britteni (Jackson, 1913)	79	1	0	0	0	0	0	0	0	0	0	0	O, W, GL
Savignya frontata (Blackwall, 1833)	0	0	0	0	4	0	0	0	16	1	1	0	–
Scotina gracilipes (Blackwall, 1859)	1	0	0	0	0	0	0	0	0	0	0	0	GL
Segestria senoculata (Linnaeus, 1758)	0	0	0	0	1	1	0	4	0	4	1	1	–
Silometopus elegans (O. P.-Cambridge, 1872)	749	491	214	108	13	1	6	1	10	0	3	2	O, W, GL
Tallusia experta (O. P.-Cambridge, 1871)	0	1	0	0	7	1	2	1	0	0	1	0	W, GL
Tapinoba longidens (Wider, 1834)	1	0	0	0	0	0	0	0	0	0	0	0	GL
Tapinocyba insecta (L. Koch, 1869)	0	0	0	0	1	0	0	0	0	0	0	0	GL
Tapinocyba pallens (O. P.-Cambridge, 1872)	2	0	0	2	0	0	0	0	0	0	0	0	F, GL
Taranucnus setosus (Simon, 1884)	1	0	16	11	7	2	12	7	1	1	12	7	W, LV
Tetragnatha montana (Simon, 1874)	0	0	0	0	0	1	0	0	0	0	0	0	LV
Textrix denticulata (Olivier, 1789)	0	0	0	0	0	1	0	1	0	0	0	0	–
Theonoe minutissima (O. P.-Cambridge, 1879)	0	1	6	4	0	0	2	0	0	0	0	0	GL
Theridion bimaculatum (Linnaeus, 1767)	1	0	3	2	0	0	0	0	0	0	0	0	LV
Theridion instabile (O. P.-Cambridge, 1870)	2	0	0	0	0	1	1	2	0	0	0	3	LV
Theridion pallens (Blackwall, 1834)	0	0	1	0	0	0	0	0	0	0	0	0	–
Theridiosoma gemnosum (Koch, 1877)	0	0	0	0	0	0	0	1	0	0	0	0	W, LV
Tibellus maritimus (Menge, 1875)	1	1	0	0	0	0	0	0	0	0	0	0	LV
Tibellus oblongus (Walckenaer, 1802)	2	0	1	0	0	0	0	0	0	0	0	0	LV
Tiso vegans (Blackwall, 1834)	37	47	1	0	1	0	0	1	3	0	6	0	GL
Trichopterna thorelli (Westring, 1861)	165	1	2	0	0	0	0	0	4	0	0	0	W, GL
Trochosa ruricola (De Geer, 1778)	8	0	0	0	0	1	0	0	16	0	5	1	GL
Trochosa spinipalpis (O. P.-Cambridge, 1895)	6	0	1	0	59	16	26	4	1	1	3	0	W, GL
Trochosa terricola (Thorell, 1836)	69	43	39	9	32	3	28	7	2	4	6	1	GL
Troxochrus scabriculus (Westring, 1851)	0	1	0	0	0	0	0	0	14	0	0	4	D, GL
Walckenaeria acuminata (Blackwall, 1833)	5	12	6	7	6	4	11	8	0	6	30	17	GL
Walckenaeria antica (Wider, 1834)	7	3	1	0	0	0	0	1	0	0	0	0	GL
Walckenaeria atrobtibialis (O. P.-Cambridge, 1878)	33	8	58	11	0	0	0	0	0	0	2	0	–
Walckenaeria clavicornis (Emerton, 1882)	1	0	0	0	0	0	0	0	0	0	0	0	O, W, GL
Walckenaeria cuspidata (Blackwall, 1833)	8	2	3	6	2	4	0	1	0	0	0	0	GL
Walckenaeria dysderoides (Wider, 1843)	0	1	0	0	0	0	0	0	1	0	0	0	GL
Walckenaeria kochi (O. P.-Cambridge, 1872)	0	0	0	1	0	0	0	1	0	0	0	0	O, W, GL
Walckenaeria nodosa (O. P.-Cambridge, 1873)	2	1	0	0	0	0	0	0	0	0	0	0	W
Walckenaeria nudipalpis (Westring, 1851)	8	1	8	1	6	1	0	1	0	0	1	0	GL
Walckenaeria unicornis (O. P.-Cambridge, 1861)	3	4	1	2	2	9	7	4	0	3	2	2	–
Walckenaeria vigilax (Blackwall, 1851)	89	52	10	9	42	16	43	12	2	1	7	2	W, GL
Xysticus cristatus (Clerck, 1757)	12	3	0	0	16	2	4	0	2	2	3	2	O
Xysticus erraticus (Blackwall, 1834)	1	0	0	0	0	0	0	0	0	0	0	0	O
Xysticus ulmi (Hahn, 1831)	0	0	0	1	0	0	0	0	0	0	0	0	O, W, LV
Zelotes latrielli (Simon, 1878)	2	0	2	0	0	1	0	0	0	0	0	0	O, GL
Zelotes lutetianus (L. Koch, 1866)	1	0	0	0	0	0	0	0	0	0	0	0	O, GL
Zora spinimana (Sundevall, 1833)	7	0	9	8	1	0	0	0	0	0	1	0	GL
Immature	812	180	598	328	308	140	225	133	268	115	218	108	
Total individuals	6942	2246	3204	1958	4552	1571	2107	1443	3718	1279	2641	1496	

The habitat associations of each species used in the analyses are also given: O, open habitats; F, forested habitats; D, dry habitats; W, wet habitats; GL, ground layer; LV, low vegetation; UV, upper vegetation (shrubs and trees); (–) habitat generalists.

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