

The influence of open space on ground-dwelling spider assemblages within plantation forests

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Abstract

Sustainable forest management advocates the retention or creation of open space within plantation forests to enhance biodiversity. However, the biodiversity value of these open spaces will depend on the habitat type chosen, as well as open-space size and shape. The present study investigated ground-dwelling spider assemblages in glades, rides and forest roads of various sizes in 12 mature Sitka spruce (*Picea sitchensis*) plantations across Ireland. Spiders were sampled along a transect from the open space into the forest using pitfall traps. Species richness and abundance declined along the open-forest transect with the open-space supporting a unique spider fauna, absent within the forest. Total species richness and richness of species associated with open habitats was significantly greater in the glades. There were few significant linear relationships between species variables and open-space width or area, however roads and rides <15 m wide did not support an open spider fauna due to the influence of the canopy. No such 'threshold' area was found for glades, probably because the glades investigated did not cover a low range of areas. Open-space habitat type is an important determinant of spider assemblage structure, although open spaces' with high shrub cover or unplanted broadleaves did not differ in assemblage structure from those within the plantation. At a large scale the total amount of open space within 200 m of sampling plots was positively correlated with species richness and abundance. Forest management plans should encourage the retention of a range of habitat types in non-linear open space (glades), whereas the biodiversity value of linear open space (rides and roads) will be enhanced if wider than 15 m. © 2006 Elsevier B.V. All rights reserved.

Keywords: Spider assemblages; Open-space size; Plantation; Forest management; Ride; Forest road; Glade

1. Introduction

One of the goals of sustainable forest management is the enhancement of biodiversity within plantation forests (Coillte, 2005). This can include measures to promote plantations as woodland habitats to the benefit of forest specialist species. Such strategies include the promotion of deadwood (Ferris and Humphrey, 1999), longer rotation lengths (Jukes et al., 2001), and the enhancement of field layer vegetation (Oxbrough et al., 2005). However, measures to promote biodiversity must also examine the effect of afforestation on landscapes, which can lead to the loss of habitats supporting rare or specialised species. More specifically, sustainable forest management must address how species that are typical of pre-planting habitats, and cannot survive in a forest environment, can be retained within forests. This is especially important in an Irish context where around 10,000 ha of land is afforested annually (Forest Service, 2004). In

addition to this the Irish government ultimately aims to increase the national forest cover from 10 to 17% (COFORD, 2000).

The Irish *Forest Biodiversity Guidelines* (Forest Service, 2000) state that 15% of the forest area should be incorporated into Areas for Biodiversity Enhancement (ABE), recommending that these areas should comprise approximately 5–10% retained habitats and 5–10% open space in plantations greater than 10 ha. In order for the maximum biodiversity value to be derived from these ABEs, forest managers need to know which areas to target for open space. More specifically, what habitats should be retained to maximise biodiversity value? And, what size and shape should the open space be in order to facilitate the retention of open-space species?

For plants and invertebrates the level of shade in open space within forests is a key factor affecting the species present (Warren, 1989; Sparks and Greatorex-Davies, 1992; Sparks et al., 1996). Shade levels are primarily determined by open-space width, height of surrounding trees and orientation (Warren and Fuller, 1993). Current guidelines vary in the minimum width necessary to promote species associated with open habitats. Often quoted as a 'rule of thumb' is the 1:1 ratio of tree height to

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ride width (Carter, 1989; Warren and Fuller, 1993). However Irish guidelines recommend that forest rides should be 6 m wide, and forest road corridors should be 15 m wide, in order to qualify for inclusion as an Area for Biodiversity Enhancement (Forest Service, 2003). Furthermore, Warren and Fuller (1993) recommend that some forest glades should be at least 0.25 ha in size to encourage biodiversity.

Previous research has examined the influence of orientation and width on diversity of invertebrates within rides and forest roads, with particular interest in the affects on butterflies (Warren, 1989; Greatorex-Davies et al., 1992, 1993; Sparks et al., 1996). Other invertebrate groups examined include Coleoptera and Hemiptera (Greatorex-Davies and Sparks, 1994); and mixed groups of arthropods (Carter, 1989; Mullen et al., 2003). Fewer studies have focused on the biodiversity value of different types of open space (such as forest roads, rides and glades) and of varying open-space size. There is also a need to investigate the influence of open space within forests on different invertebrate taxa, enabling forest management plans to try to reach a consensus on the best way to manage open habitats for a range of invertebrate groups. Spiders are useful as indicators of habitat change as they are primarily affected by changes in habitat structure (Uetz, 1991). Spiders also occupy an important position in terrestrial food webs as both predators and prey and hence have the potential to be used as surrogate indicators of invertebrate diversity (Marc et al., 1999).

The aim of this study was to assess the influence of open space in plantation forests on ground-dwelling spider assemblages by addressing the following questions: firstly, how does open space enhance spider diversity within plantation forests; and secondly, how does the type of open space and its size influence spider diversity within plantation forests?

2. Methodology

2.1. Study areas

Twelve commercially mature Sitka spruce (*Picea sitchensis*) stands of at least 80 ha were sampled within Ireland. The stands

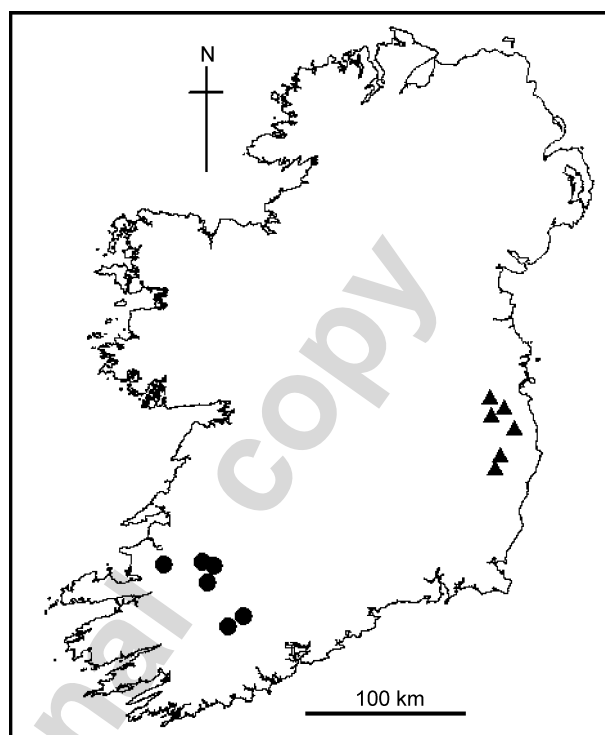


Fig. 1. The distribution of sampling sites across Ireland in the Wicklow (▲) and Cork (●) geographical clusters.

were located in two geographical clusters (Wicklow and Cork) of six sites that were matched for environmental variables such as altitude, soil and geology (Fig. 1). The Wicklow cluster were typically well-drained upland sites on peaty-podzol soils and the unplanted open space in these sites was predominately humid acid-grassland/dry heath (Table 1). The Cork cluster were typically poorly drained sites on peaty soils with modified blanket bog as the predominate habitat type in the unplanted open space. The sites in the Wicklow cluster were generally at higher altitudes than the Cork region, ranging from 296 to 593 m compared to 205–390 m (Table 1). The age of the forest stands and tree height were relatively similar among the regions

Table 1
Configuration of open space sampled and site characteristics

	Forest age	Mean \pm S.E. tree height (m)	Mean \pm S.D. altitude (m)	Soil type	Glade	Ride	Road
Wicklow region							
Athdown	28	14 \pm 1.1	440 \pm 62	Peaty podzol	3 ^a	1	1
Ballinastoe	29	10.5 \pm 1.7	528 \pm 33	Podzol	1	3	1
Ballysmuttan	38	17 \pm 2.0	324 \pm 9	Podzol	3	1	1
Ballycurragh	42	18 \pm 0.6	442 \pm 22	Peaty podzol	3	1	1
Lugg	31	16 \pm 1.2	296 \pm 8	Podzol	3	1	1
Mucklagh	42	18 \pm 3.0	446 \pm 24	Peaty podzol	0	3	2
Cork region							
Carrigagula	43	21 \pm 2.1	223 \pm 5	Peat	2	1	2
Cleanglass	31	14 \pm 1.2	275 \pm 33	Peat	2 ^a	1	2
Glanharee	38	16 \pm 0.6	323 \pm 5	Peat	2	1	2
Knocnagoum	32	14 \pm 1.0	205 \pm 19	Peat	0	3	2
Meetinny	32	13 \pm 1.5	357 \pm 22	Peat	2	2	1
Reanahoun	39	15 \pm 1.7	390 \pm 8	Peat	0	3	2

^a Two plots established in the same glade.

ranging from 28 to 42 years in the Wicklow region and 31 to 43 years in the Cork region whereas tree height ranged from 14 to 18 and 14 to 21 m, respectively.

2.2. Open-space configurations

The open space (unplanted areas) was categorised into three types: forest road edges; rides (areas of linear open space separating stands of even aged trees of the same canopy species); and glades (non-linear open space). Digitised aerial photographs were used to identify the open space within each site and to select suitable areas for sampling. Five areas of open space were sampled per site, with at least one from each open-space type where possible (Table 1). However, three sites did not contain any glades and two sites had only one large glade (>6 ha), so in this case, two sampling plots were established within the open space, with plots always separated by a minimum of 100 m (Table 1). A total of 60 plots of open space were sampled comprising 21 glades, 21 rides and 18 roads. The plots were all located on the south facing side (or southwest/west where south facing was not possible) of the open space in a homogenous area of vegetation which was typical of the open space being sampled.

2.3. Spider sampling

Pitfall traps were used to sample the ground-dwelling spider fauna. Pitfalls consisted of a plastic cup, 7 cm in diameter by 9 cm depth. Each trap had several drainage slits pierced approximately 2 cm from the top of the cup and was filled with antifreeze (ethylene glycol) to a depth of 1 cm to act as a killing and preserving agent. The traps were placed in holes dug with a bulb corer so that the rim was flush with the surface of the ground.

Sampling plots consisted of pitfall traps arranged in a transect from the open space into the forest. Each sample point on the transect consisted of three pitfall traps, each set 2 m apart which were arranged perpendicular to the forest edge. Two of these traps were used in the analysis with the third to be used only if traps were lost due to flooding or animal damage. Five sampling points were established on the transect in the following locations: open (centre of the open space); open-boundary (2 m into the open space from tree trunks); boundary (tree trunk); forest-boundary (2 m into the forest from the tree trunk); forest (5 m into the forest interior). The traps were set in May 2004 and were active for nine consecutive weeks, being emptied every 3 weeks. Sampling duration was considered adequate as most spider species are abundant as adults in May and June (Niemelä et al., 1994; Harvey et al., 2002) and ground-dwelling spiders have been successfully compared in forested habitats over a similar duration in previous studies (e.g. Pajunen et al., 1995).

2.4. Environmental variables

The percentage cover of vegetation was recorded in a 1 m² quadrat surrounding two of the pitfall traps in each sample point on the transect in the following structural 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 and litter were also recorded using this scale and litter depth was measured within each quadrat. All cover values were estimated using the Braun–Blanquet scale (Mueller-Dombois and Ellenberg, 1974), which involves giving numerical rankings to a range of percentages (+ = <1% cover; 1 = 1–5%; 2 = 6–25%; 3 = 26–50%; 4 = 51–75%; 5 = 76–100%).

Soil samples were taken from the Open, Boundary and Forest sampling points on the transect using a bulb corer which extracted the top layer of substrate to a depth of 15 cm. Organic content of the soil was obtained by firing dried soil samples in a furnace for 3 h at 550 °C and calculating weight loss on ignition (Grimshaw, 1989). Hemispherical photographs were used to measure canopy openness in the centre of each open space with the percentage of open space calculated from the scanned images using Gap Light Analyser 2.0 software (Frazer et al., 1999).

Within each ride and road open-space plot the distance between tree trunks was measured. Digitised aerial photographs were used to estimate glade area and also estimate the area of open space within 200 m of each plot in the following categories: unplanted, rides (>10 m wide), clearfell, young forestry (pre-canopy closure), broadleaved, undeveloped (areas of crop failure), windthrow, outside (open space outside the plantation), forest road.

2.5. Species identification

Spiders were sorted from the pitfall trap debris and stored in 70% alcohol. The species were identified using a 50× magnification microscope and nomenclature follows Roberts (1993). Difficult species were sent Robert Johnston and Dr. Peter Merrett for verification with voucher specimens retained by the corresponding author at University College Cork. Only adult specimens were identified due to the difficulty in assigning juveniles to species.

3. Data analysis

3.1. Trends along the open-forest transect

Global non-metric multi-dimensional scaling analysis (NMS) was used to examine differences in assemblage structure across the open-forest transect. This ordination method has been successfully used in several studies of invertebrates within forests (Siira-Pietikainen et al., 2001, 2003; Huhta, 2002; Oxbrough et al., 2005). The NMS used mean relative abundance of each species per site, for each location on the open-forest transect. Relative abundance was used rather than absolute abundance data as variation in vegetation structure (as may be present across the open-forest transect) can affect the efficiency of pitfall traps (Melbourne, 1999). The NMS ordination diagram was presented as a joint biplot which uses correlation analyses to relate habitat variables (measured at each transect location) with the NMS ordination axes. The NMS used the Bray–Curtis distance measure and the

following parameter set-up was used: 6 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; 50 runs of the Monte Carlo test.

Indicator Species Analysis was used to determine habitat associations (open-, forest-associated or generalists) of each spider species by their position on the open-forest transect. For a given species this analysis combines the relative abundance and relative frequency within predetermined groups (in this case positions on the transect) to give an indicator value which is tested for significance using a Monte Carlo test. Species with less than five individuals overall were not classified and those with between 5 and 10 individuals were classified using both Indicator Species Analysis and the available literature (Roberts, 1993; McFerran, 1997; van Helsdingen, 1996, 1997; Cawley, 1997; Harvey et al., 2002; Nolan, 2002). Spider families can be classified into guilds determined by their hunting strategy which adds a further dimension to the interpretation of ecological data. Two of the spider families occurred in sufficient numbers to allow such comparisons, the Linyphiidae, which build small sheet webs on or close to the ground and the Lycosidae which are active hunters on the ground. Two-way ANOVA and Tukey post hoc tests with region and transect position as fixed factors were used to assess trends in species variables (total species richness, abundance and richness and relative abundance of habitat specialists, Linyphiids and Lycosids) with plot used as the replicate.

3.2. The influence of open-space type and size

The aforementioned NMS analyses indicated that traps in the centre of the open space supported an open spider fauna so data from these traps were used in following analyses. One-way ANOVA with Tukey post hoc tests was used to examine differences in species richness and abundance among the open-space types (with plot as the replicate). Pearson's correlation analyses were used to examine any linear relationships between species richness and abundance and the following open-space dimensions: glade area; ride/road width (trunk to trunk); ride/road verge width (trunk to road edge). Rides and roads were combined as the above analyses indicated that their species richness, abundance and assemblage structure were similar. Flexible-beta cluster analysis (with $\beta = -0.25$) was used to explore the relationship between spider assemblage structure and open-space types. This analysis allowed the determination of assemblage groups that better describe the similarity between the sampling plots irrespective of a priori groupings such as open-space type or region. Differences in the open space size as well as species and habitat variables among these assemblage groups were then tested using one-way ANOVA. In addition to this the open-space plots were further classified by broad habitat type based on the predominant vegetation cover present (high cover of lower-field layer vegetation or high cover of shrub/deciduous vegetation). Differences in the spider assemblages among these two habitat groupings were examined using NMS and Indicator Species Analysis.

3.3. Large scale influence of open space

Pearson's correlation analyses were used to examine the relationship between species variables and the total amount of open space within 200 m of each plot using the open-space categories described above. The open-space categories were also combined into total unforested open space (road, ride, outside and unplanted) and total open space (all categories). In addition to this one-way ANOVA and Tukey post hoc tests were used to examine the effect of open-space amount in the following groups: <5, 5–10 and >10 on species richness and abundance.

Where the assumptions of normality and homogeneity of variance were not met, data were square root transformed, however if the data still did not conform to the assumptions of ANOVA the Kruskal–Wallis (H) test with a Tukey-type post hoc comparison (Zar, 1996) was used. Proportional data (relative abundance and cover of environmental variables) were arcsin transformed prior to the use of parametric statistics. ANOVA and correlation analyses were carried out in SPSS (SPSS, 2002). Multivariate analyses (NMS and cluster analysis) as well as Indicator Species Analysis were carried out using PC-ORD (McCune and Mefford, 1997).

4. Results

Two of the plots (a glade in Ballysmuttan and a ride in Mucklagh) had a substantial number of traps (33%) disturbed and so were excluded from the analyses. This gave a total of 58 plots used in the analyses: 20 rides, 20 glades and 18 roads. There were a total of 11,872 individual spiders captured in 13 families and 122 species. Of these 2435 were juveniles and so were excluded from the analyses. Twenty-eight species were classified as being associated with open habitats and seven with forested habitats. There were 48 species represented by less than 5 individuals so these were not classified into a habitat association. A full list of species and their habitat association is given in Appendix A. Eighty-seven of the species were from the Linyphiidae family, whereas nine species were from the Lycosidae family. *Monocephalus fuscipes* (Blackwall, 1836), *Lepthyphantes zimmermanni* (Bertkau, 1890) and *Diplocephalus latifrons* (O.P.-Cambridge, 1863) were the most abundant species accounting for 32% of the total adult catch and occurring in 97% of the traps.

4.1. Trends along the open-forest transect

The majority of the species variables declined across open-forest transect (Table 2), with the open traps supporting significantly more species and individuals and also greater richness and abundance of open-associated species, Linyphiid and Lycosid species. Similarly the open-boundary transect position supported a greater number of species and individuals than the traps at the boundary, forest-boundary and forest positions on the transect for the above-mentioned species variables. Richness and abundance of forest-associated species however exhibited the opposite trend being significantly lower

Table 2
Trends in mean species variables (\pm S.D.) per plot across the open-forest transect

Species variables	Wicklow region (W)					Cork region (C)					ANOVA <i>F</i> and post hoc results	
	O (<i>n</i> = 6)	OB (<i>n</i> = 6)	B (<i>n</i> = 6)	FB (<i>n</i> = 6)	F (<i>n</i> = 6)	O (<i>n</i> = 6)	OB (<i>n</i> = 6)	B (<i>n</i> = 6)	FB (<i>n</i> = 6)	F (<i>n</i> = 6)	Transect position (d.f. = 4,50)	Region (d.f. = 1,50)
Species richness	15.7 (\pm 2.4)	11.8 (\pm 2.0)	10.1 (\pm 1.0)	9.16 (\pm 1.5)	8.98 (\pm 2.0)	14.7 (\pm 1.4)	12.3 (\pm 1.0)	10.7 (\pm 1.1)	9.9 (\pm 1.1)	8.63 (\pm 1.5)	32.0*** [O > OB, B, FB, F] [OB > FB, F]	n.s
Open-associated S ^a	7.05 (\pm 1.53)	2.00 (\pm 0.81)	0.65 (\pm 0.45)	0.66 (\pm 0.27)	0.52 (\pm 0.22)	6.93 (\pm 1.06)	3.17 (\pm 0.81)	1.30 (\pm 0.52)	1.37 (\pm 0.34)	1.00 (\pm 0.31)	115.8*** [O > OB, B, FB, F] [OB > B, FB, F]	20.5*** C > W
Forest-associated S	2.18 (\pm 0.73)	4.03 (\pm 0.45)	4.18 (\pm 0.43)	4.12 (\pm 0.63)	4.37 (\pm 0.50)	2.00 (\pm 0.22)	3.33 (\pm 0.64)	4.13 (\pm 0.85)	3.80 (\pm 0.66)	3.77 (\pm 0.87)	22.5*** [O > OB, B, FB, F]	5.1* W > C
Linyphiidae S	12.3 (\pm 1.84)	10.8 (\pm 1.86)	9.22 (\pm 1.14)	8.29 (\pm 1.49)	8.23 (\pm 1.80)	11.3 (\pm 0.96)	10.3 (\pm 0.99)	9.33 (\pm 1.03)	8.77 (\pm 0.92)	7.57 (\pm 1.36)	15.6*** [O > B, FB, F] [OB > FB, F]	n.s
Lycosidae S	1.65 (\pm 0.86)	0.28 (\pm 0.20)	0.07 (\pm 0.10)	0.18 (\pm 0.15)	0.14 (\pm 0.11)	1.47 (\pm 0.62)	0.43 (\pm 0.37)	0.20 (\pm 0.25)	0.13 (\pm 0.21)	0.10 (\pm 0.11)	25.8*** [O > OB, B, FB, F]	n.s
Berger–Parker dominance	0.34 (\pm 0.08)	0.27 (\pm 0.04)	0.37 (\pm 0.09)	0.36 (\pm 0.05)	0.37 (\pm 0.07)	0.29 (\pm 0.07)	0.29 (\pm 0.04)	0.31 (\pm 0.06)	0.30 (\pm 0.05)	0.39 (\pm 0.05)	n.s	n.s
Abundance	51.2 (\pm 15.1)	31.1 (\pm 12.1)	27.0 (\pm 11.4)	24.2 (\pm 11.3)	24.4 (\pm 10.1)	42.0 (\pm 8.9)	29.8 (\pm 5.4)	30.5 (\pm 5.4)	27.6 (\pm 6.4)	26.3 (\pm 7.9)	9.4*** [O > OB, B, FB, F]	n.s
Open-associated RA ^a	0.55 (\pm 0.16)	0.10 (\pm 0.06)	0.04 (\pm 0.04)	0.03 (\pm 0.02)	0.04 (\pm 0.02)	0.57 (\pm 0.16)	0.26 (\pm 0.06)	0.09 (\pm 0.04)	0.09 (\pm 0.02)	0.06 (\pm 0.02)	100.3*** [O > OB, B, FB, F] [OB > B,FB,F]	25.5*** C > W
Forest-associated RA	0.15 (\pm 0.10)	0.49 (\pm 0.10)	0.62 (\pm 0.09)	0.69 (\pm 0.09)	0.67 (\pm 0.05)	0.13 (\pm 0.02)	0.35 (\pm 0.11)	0.56 (\pm 0.05)	0.54 (\pm 0.08)	0.64 (\pm 0.06)	82.5*** [O > OB, B, FB, F] [OB > B, FB, F]	14.8*** W > C
Linyphiidae RA	0.67 (\pm 0.18)	0.91 (\pm 0.06)	0.95 (\pm 0.03)	0.95 (\pm 0.03)	0.95 (\pm 0.02)	0.80 (\pm 0.04)	0.87 (\pm 0.05)	0.91 (\pm 0.04)	0.90 (\pm 0.03)	0.92 (\pm 0.02)	28.4*** [O > OB, B, FB, F] [OB > B, FB, F] ^b	7.0** W > C ^b
Lycosidae RA	0.23 (\pm 0.15)	0.02 (\pm 0.03)	0	0.01 (\pm 0.01)	0.01 (\pm 0.01)	0.11 (\pm 0.04)	0.02 (\pm 0.02)	0.01 (\pm 0.01)	0.01 (\pm 0.01)	0	32.8*** [O > OB, B, FB, F] [OB > B, FB, F] ^b	n.s ^b

O = open (centre of the open space); OB = open-boundary (2 m into the open space); B = boundary (tree base); FB = forest-boundary (2 m into the forest); F = forest (5 m into the forest). The results of two-way ANOVA and Tukey post hoc tests with region and transect position as fixed factors are shown. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

^a S = species richness; RA = relative abundance.

^b Kruskal–Wallis (*H*) non-parametric ANOVA with Nemenyi Tukey-type comparisons.

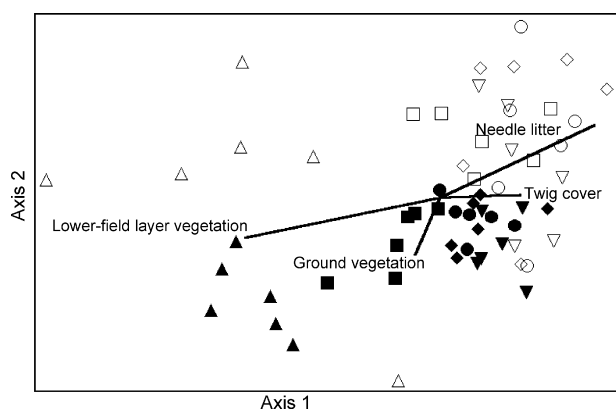


Fig. 2. NMS ordination of spider assemblages (mean relative abundance per site) across the open-forest transect. Closed shapes represent sites in the Wicklow region and open shapes represent sites in the Cork region: (▲, △) = open (centre of the open space); (■, □) = open-boundary (2 m into the open space from the boundary); (◆, ◇) = boundary (tree base); (●, ○) = forest-boundary (2 m into the forest); (▼, ▽) = forest (5 m into the forest). Final stress: 16.32; final instability: 0.0005; axis 1: $r = 0.50$; axis 2: $r = 0.35$. Habitat variables that have a Pearson correlation (r) of >0.1 for both axes are shown.

in the centre of the open space than at any of the other transect positions. Between the regions, the Cork region supported more open-associated species and individuals, whereas the Wicklow region supported more forest-associated species and individuals. The Berger–Parker dominance index did not differ significantly among either the transect positions or the regions and there were no significant interactions between region and transect position for any of the species variables.

The NMS ordination of spider assemblages across the open-forest transect explained 85% of the variation in the species data, with axes 1 and 2 accounting for 50 and 35%, respectively (Fig. 2). Axis 1 represented a separation of the assemblages of spiders along the open-forest transect, with the open traps distinct from those at the boundary, forest-boundary and forest positions. The spider assemblages found at the open-boundary sampling point on the transect represent a transition of assemblages in the centre of the open space to those within the forest. The spider assemblages at the boundary and those within the forest form a

tight cluster of points whereas those in the open space and at the open-boundary exhibit much greater variation across both axes. Axis 2 represents a separation of the Cork and Wicklow sites (with the exception of Mucklagh in the Wicklow region which is more similar to the Cork cluster of sites). Cover of lower-field layer vegetation is associated with the spider assemblages in the open, whereas needle litter and twig cover are associated with spider assemblages within the forest. Cover of ground vegetation was associated with the assemblages at the open-boundary (2 m into the open space) in the Cork region.

4.2. The influence of open-space type and size

The glades supported significantly more species and individuals than the roads and the rides as well as a greater richness of Lycosid species and richness and abundance of the Linyphiid spiders (Table 3). The number of Linyphiid species however did not differ significantly among the open space types. A similar trend was seen with the open-associated species, although only the glades and roads differed significantly. The forest-associated species exhibited the opposite trend, where richness and abundance was significantly greater in the roads than the glades. There were no significant differences in the Berger–Parker dominance index or between the regions for the species variables with the exception of the number of Lycosids sampled, where significantly more individuals were sampled in the Wicklow region. In addition to this, none of the interactions between open-space type and region were significant.

There was no relationship between total species richness and ride/road verge width however richness of open-associated species was significantly positively correlated with ride/road verge width (Pearson $r = 0.58$, $p = <0.001$, $n = 33$ [3 outliers removed see Fig. 3]). Total abundance and abundance of open-associated species were both significantly positively correlated with ride/road verge width (Pearson $r = 0.47$, $p = 0.008$, $n = 36$ and $r = 0.61$, $p = <0.001$, $n = 33$, respectively) whereas the abundance of forest-associated species was significantly negatively correlated (Pearson $r = -0.52$, $p = <0.008$, $n = 36$). A similar trend was seen between ride/road width

Table 3
Mean (\pm S.E.) species variables per plot among the open-space types within each region

	Wicklow (W)			Cork (C)			ANOVA <i>F</i>	
	Glade ($n = 12$)	Ride ($n = 9$)	Road ($n = 7$)	Glade ($n = 8$)	Ride ($n = 11$)	Road ($n = 11$)	OS type	Region
Total S	18.3 \pm 1.2 a	13.3 \pm 1.4	15 \pm 2.1	16.5 \pm 2.1 a	14.4 \pm 1.1 b	13.6 \pm 1.0 b	3.74*	n.s
Open-associated S	8.92 \pm 0.91 a	6.22 \pm 1.06	5.14 \pm 1.39 b	8.13 \pm 1.36 a	6.82 \pm 0.92	6.18 \pm 0.66 b	4.00*	n.s
Forest-associated S	1.75 \pm 0.35 b	2.11 \pm 0.51	2.86 \pm 0.46 a	1.63 \pm 0.26 b	1.82 \pm 0.26	2.45 \pm 0.39 a	3.20*	n.s
Linyphiidae	13 \pm 0.90	10.9 \pm 1.32	13 \pm 1.18	11.4 \pm 1.39	11.1 \pm 0.70	11.5 \pm 0.78	n.s	n.s
Lycosidae	2.58 \pm 0.42 a	1.0 \pm 0.33 b	1.0 \pm 0.49 b	2.13 \pm 0.58 a	1.45 \pm 0.58 b	1 \pm 0.33 b	4.71*	n.s
Berger–Parker	0.36 \pm 0.04	0.28 \pm 0.02	0.3 \pm 0.07	0.34 \pm 0.06	0.24 \pm 0.03	0.29 \pm 0.05	n.s	n.s
Abundance	75.9 \pm 11.0 a	31.4 \pm 6.7 b	37.9 \pm 9.1 b	49.6 \pm 9.0 a	41 \pm 9.2 b	37.5 \pm 5.7 b	5.50**	n.s
Open-associated RA	0.68 \pm 0.07 a	0.54 \pm 0.07	0.36 \pm 0.11 b	0.67 \pm 0.06 a	0.52 \pm 0.07	0.53 \pm 0.08 b	4.18*	n.s
Forest-associated RA	0.09 \pm 0.04 b	0.14 \pm 0.04	0.26 \pm 0.07 a	0.05 \pm 0.01 b	0.14 \pm 0.03	0.18 \pm 0.06 a	5.19**	n.s
Linyphiidae RA	0.5 \pm 0.07 b	0.76 \pm 0.07 a	0.82 \pm 0.10 aa	0.7 \pm 0.06 b	0.8 \pm 0.06 a	0.87 \pm 0.03 a	7.83***	n.s
Lycosidae RA	0.36 \pm 0.06 a	0.14 \pm 0.06 b	0.14 \pm 0.09 b	0.19 \pm 0.06 a	0.11 \pm 0.05 b	0.05 \pm 0.02 b	5.27**	4.06* [W > C]

Results of two-way ANOVA and Tukey post hoc tests with open-space type (OS) and region as fixed factors are shown. * $p = <0.05$; ** $p = <0.01$; *** $p = <0.001$. Letter a denotes value significantly greater than letter b.

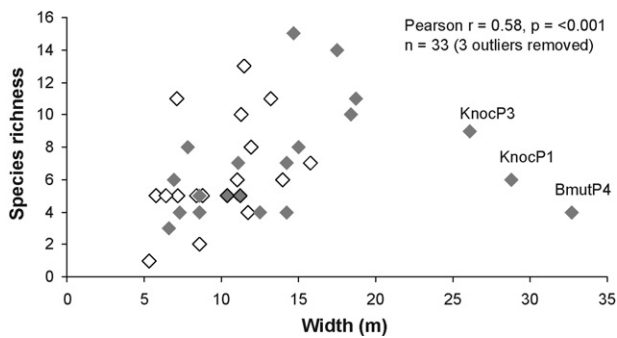


Fig. 3. The relationship between open-associated species richness and ride width (◆) and road verge width (◇). Three outliers were removed from this analysis. These wide rides were atypical of the rides sampled and contained features which may have affected the number of open-associated species present: two plots in Knocnagoum (KnocP3 and P1) were bordered by several rows of planted birch trees and were originally to be planted as forest roads, whereas one plot in Ballysmuttan (BmutP4) was established under a large rowan tree.

and both total abundance and abundance of open-associated species although less significantly so (Pearson $r = 0.38$, $p = 0.03$, $n = 38$ and $r = 0.32$, $p = 0.04$, $n = 38$, respectively). There were no significant correlations between glade area and the species variables and also between the open-space metrics and the richness and abundance of the Linyphiid and Lycosid families and the Berger–Parker dominance index.

The cluster analysis distinguished the spider sampling plots into four assemblage groups (Fig. 4). Cluster Group 1 contains most of the glades, with the plots predominately from the Wicklow region, whereas cluster Group 2 consists mostly of road and rides plots that were all from the Cork region. Cluster Groups 3 and 4 consist mainly of road and ride plots; however in Group 3 these are predominately from the Cork region whereas in Group 4 the majority of plots are from the Wicklow region. Cluster Groups 1 and 2 were initially split from Groups 3 and 4 in the analysis (Fig. 4) suggesting that the assemblages were first distinguished by the degree of canopy openness and second by geographic location (i.e. Group 1 consists of plots which are mainly from Wicklow and Group 2 mainly from Cork).

The mean width of rides and roads as well as glade area was greater in cluster Groups 1 and 2 although these differences were not significant (Table 4). Cluster Groups 1 and 2 were characterised by significantly greater canopy openness than cluster Groups 3 and 4, however the other layers of vegetation did not differ significantly among the cluster groups. In addition to this Cluster Groups 1 and 2 generally supported a greater number of species and individuals Groups 3 and 4, however both the richness of forest-associated species and the abundance of the Linyphiids was significantly lower in Cluster Group 1.

The open-space plots within each cluster group were classified by broad habitat type based on the predominant vegetation cover present, plots being characterised by either high cover of lower-field layer vegetation or high cover of shrub/deciduous vegetation (Table 5). Cluster Groups 1 and 2 do not contain any plots that have a shrub/deciduous cover whereas at least half of the total number of plots in Groups 3 and 4 do. The road/ride widths of cluster Groups 1 and 2 range from 15 to 34 m (Table 5), all of which have lower-field layer cover. In Groups 3 and 4 however the plots with lower-field layer cover have a much smaller range of widths (7–14 m), furthermore, this does not overlap with those in Groups 1 and 2. This would suggest that the roads and rides with lower-field layer cover that are less than 15 m wide support a different assemblage of species than those in Groups 1 and 2 (which are wider than 15 m). Furthermore these plots with lower-field layer cover (<15 m wide) are more similar to those plots under shrub/deciduous cover. All of the glades present in cluster Groups 3 and 4 were under shrub/deciduous cover, with the exception of the very small glade (80 m²) in cluster Group 3.

The spider assemblages within the open-space plots which were characterised by shrub/deciduous cover did not form a distinct group from those with a lower-field layer cover or from those assemblages sampled on the forest interior transect position (Fig. 5). Moreover, the assemblages within the shrub/deciduous open-space plots represented a transition between the forest interior and the lower-field layer cover habitats. Several species had significantly high indicator values in the shrub/deciduous open space, including the forest-associated

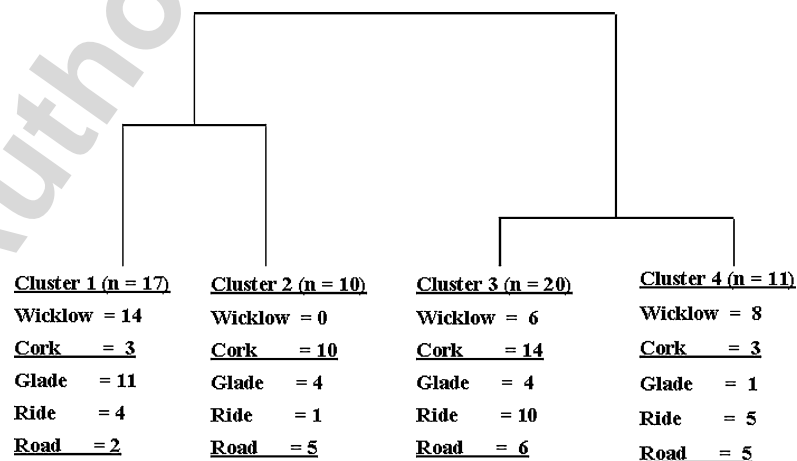


Fig. 4. Cluster analysis dendrogram of the spider assemblages in the open space. The distribution of the plots (n) among each of the open-space types and regions is shown.

Table 4
Mean (\pm S.E.) open-space metrics, species and habitat variables among the cluster groups

	Cluster 1 (n = 17)	Cluster 2 (n = 10)	Cluster 3 (n = 20)	Cluster 4 (n = 11)	ANOVA (d.f. = 3,57)	Post hoc
Open-space metrics						
Mean area of glade (m ²)	12991 \pm 4994	8406 \pm 1967	3818 \pm 1798	3083	n.s	
Mean width of ride (m)	16.4 \pm 1.0	28.8	13.3 \pm 1.8	9.0 \pm 1.4	n.s	
Mean width of road (m)	23.6 \pm 3.0	25.2 \pm 3.3	20.5 \pm 1.9	16.6 \pm 3.3	n.s	
Mean width of road verge (m)	9.3 \pm 2.2	11.8 \pm 1.4	9.1 \pm 1.4	9.9 \pm 1.5	n.s	
Species variables						
Species richness	19.1 \pm 0.86	14.4 \pm 1.27	13.6 \pm 0.91	13.3 \pm 1.27	F = 7.59***	1 > 2, 3, 4
Open-associated S	12.0 \pm 0.60	7.8 \pm 0.73	5.9 \pm 0.64	4.9 \pm 0.73	F = 23.10***	1 > 2, 3, 4
Forest-associated S	1.5 \pm 0.19	1.6 \pm 0.27	2.1 \pm 0.27	3.1 \pm 0.49	H = 9.33*	1 < 4
Linyphiidae S	12.9 \pm 0.75	11.1 \pm 0.87	11.2 \pm 0.71	11.9 \pm 1.08	n.s	
Lycosidae S	3.06 \pm 0.29	1.5 \pm 0.27	0.85 \pm 0.37	0.64 \pm 0.31	F = 13.93***	1 > 2, 3, 4
Berger–Parker dominance	0.38 \pm 0.03	0.38 \pm 0.05	0.25 \pm 0.03	0.24 \pm 0.03	F = 5.15**	[1, 2 > 3, 4]
Abundance	80.0 \pm 7.8	46.0 \pm 6.1	29.5 \pm 3.3	28.2 \pm 4.1	F = 22.81***	[1 > 2, 3, 4] [2 > 3, 4]
Open-associated RA	0.84 \pm 0.03	0.72 \pm 0.05	0.45 \pm 0.05	0.40 \pm 0.07	F = 22.43***	[1 > 2, 3, 4] [2 > 3, 4]
Forest-associated RA	0.04 \pm 0.01	0.05 \pm 0.01	0.17 \pm 0.03	0.29 \pm 0.06	H = 22.87***	[1 < 3, 4] [2 < 4]
Linyphiidae RA	0.47 \pm 0.04	0.97 \pm 0.06	1.08 \pm 0.06	1.2 \pm 0.09	F = 28.1***	1 < 2, 3, 4
Lycosidae RA	0.44 \pm 0.04	0.09 \pm 0.02	0.07 \pm 0.03	0.03 \pm 0.02	F = 34.1***	1 > 2, 3, 4
Habitat variables						
Canopy openness (%) ^a	61 \pm 0.04	55 \pm 0.04	37 \pm 0.04	18 \pm 0.04	F = 17.9***	[1, 2 > 3, 4] [3 > 4]
Ground vegetation	0.50 \pm 0.07	0.20 \pm 0.08	0.34 \pm 0.07	0.51 \pm 0.1	n.s	
Lower-field layer vegetation	0.51 \pm 0.08	0.74 \pm 0.05	0.59 \pm 0.07	0.38 \pm 0.1	n.s	
Upper field layer vegetation	0.01 \pm 0.01	0.05 \pm 0.03	0.15 \pm 0.05	0.13 \pm 0.06	n.s	

Results of one-way ANOVA and Tukey-post hoc tests are shown. * <0.05; ** <0.01; *** <0.001.

^a Two data points missing hence ANOVA d.f. = 3,55.

species *Lepthyphantes alacris* (Indicator value = 63%, $p = <0.01$), and the open-associated species' *Bathyphantes nigrinus* (Indicator value = 57%, $p = <0.01$), *Dicymbium tibiale*, *Oedothorax gibbosus* and *Bathyphantes gracilis* (each with Indicator values of 43%, $p = <0.01$). Three species had significantly high indicator values within the forest traps, all of which were associated with forest habitats: *M. fuscipes* (67%, $p = <0.01$), *L. zimmermanni* (65%, $p = <0.01$) and *D. latifrons* (62%, $p = <0.01$).

4.3. Large scale influence of open space

Correlations between the amount of open space (within 200 m of the plots) and species variables revealed several significant relationships, although these were rather weak

(Table 6). The total number of species, and individuals as well as the number of open-associated species and the relative abundance of the Lycosids, were significantly positively correlated with the area of unplanted open space, whereas these variables were significantly negatively correlated with ride area. Forest-associated species abundance and that of the Linyphiids however, showed the opposite trend. There were no significant relationships between the species variables and the any of the following open-space types: road, outside, undeveloped, windthrow, clearfell, broadleaf, total unforested and total open space.

Mean species richness increased with increasing amounts of unplanted open space within 200 m of each plot: <5% open space (13.9 \pm 0.8 S.E.); 5–10% open space (15.5 \pm 0.9 S.E.); >10% open space (17.5 \pm 1.3 S.E.). Furthermore plots which

Table 5
The number of plots and the range of open-space size between the habitat types (shrub/deciduous cover or lower-field layer cover) within each cluster group

Cluster group	Number of plots		Range of open-space size	
	Shrub/deciduous cover	Lower-field layer cover	Shrub/deciduous cover	Lower-field layer cover
Ride/Road plots				
1	0	6	–	15–27 m
2	0	6	–	16–34 m
3	10	6	10–27 m	7–14 m
4	5	5	7–26 m	9–14 m
Glade plots				
1	0	11	–	1105–45211 m ²
2	0	4	–	4166–11753 m ²
3	3	1	1396–6898 m ²	80 m ²
4	1	0	3083 m ²	–

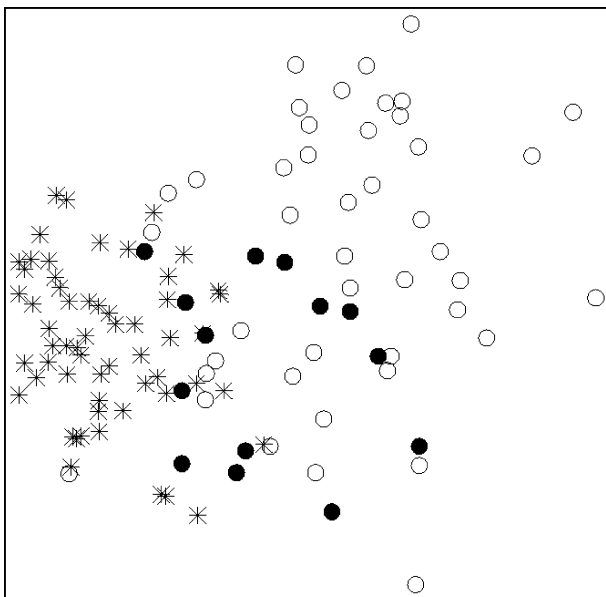


Fig. 5. NMS ordination of spider assemblages in the two types of open-space habitat and adjacent forest traps on the transect: (○) lower-field layer cover open space; (●) shrub/deciduous cover open space; (*) forest traps. Final stress: 16.22; final instability: 0.0001; axis 1: $r^2 = 0.38$; axis 2: $r^2 = 0.22$.

had >10% unplanted open space were significantly greater in mean species richness than those with <5% ($F_{(2,57)} = 3.09$, $p = 0.05$). A similar trend was exhibited between mean richness of open-associated species and unplanted open space: <5% (6.5 ± 0.7 S.E.); 5–10% (8.6 ± 0.9 S.E.); >10% (9.3 ± 1.0 S.E.) where plots with >10% unplanted open space have significantly greater richness than those with <5% ($F_{(2,57)} = 3.39$, $p = 0.04$). There was no significant difference between forest-associated species or species abundance and unplanted open-space amounts; or between the other open-space categories and the species variables.

5. Discussion

This study suggests that open space within forest plantations can support a wide array of spider species that are not present

Table 6
Correlations (Pearson r) between the area of open space within 200 m of the sample plots and species variables ($n = 58$)

Species variable	Open-space type	
	Unplanted (m ²)	Ride (m ²)
Species richness	0.36**	-0.28*
Open-associated species richness	0.35**	-0.31*
Forest-associated species richness	-0.04	-0.01
Linyphiidae S	0.21	-0.15
Lycosidae S	0.24	-0.31*
Berger–Parker dominance	0.20	-0.25
Abundance	0.34**	-0.35**
Open-associated species RA	0.20	-0.31*
Forest-associated species RA	-0.25*	0.30*
Linyphiidae RA	-0.32*	0.25
Lycosidae RA	0.31*	-0.25

* <0.05; ** <0.01.

within the forest. The open space supports a greater number of generalist species as well as providing a suitable refuge for species associated with open habitats. This is consistent with studies of plants (Sparks et al., 1996; Peterken and Francis, 1999; Mullen et al., 2003) and other groups of invertebrates (Carter, 1989). Furthermore, the present study found that plantation forests supported fewer species than the open space. Previous studies have also found that, in terms of invertebrates, mature plantation forests are relatively species poor compared to more open habitats (Day and Carthy, 1988; Butterfield et al., 1995; Oxbrough et al., 2005).

5.1. Trends along the open-forest transect

The spider assemblages at the open-boundary sampling point on the transect represent a transition between the open and forested habitats. This is consistent with other studies which have found an ‘edge effect’ across the open-forest ecotone with the boundary zone being able to support species from both habitat types (Terrel-Nield, 1986; Downie et al., 1996). In the present study, the traps at the open-boundary were under variable amounts of canopy cover depending on the length of branches above a particular trap (personal observation). This created varied vegetation cover at a small scale, where some of the lower-field layer vegetation is shaded out to the benefit of ground vegetation, predominantly more shade tolerant mosses. Spider diversity is positively influenced by vegetation structure, which facilitates greater prey diversity, web attachment points, protection from predators, stable micro-climates and hiding places for active hunters (Uetz, 1991). In the present study the open-boundary ‘transition zone’ supported more species than those in the forest, though not more than those in the open, suggesting that some open-associated species can take advantage of the conditions in the open-boundary area. Downie et al. (1996) also found species with a particular preference for the boundary zone, however there did not appear to be any species which were particularly specialised to the open-boundary within this study.

Spider species richness and abundance declined dramatically once the traps were under the influence of the canopy. The spider assemblages at the boundary (tree base) were indistinguishable in assemblage structure from those 2 and 5 m into the forest but different from those at the open-boundary (only 2 m away). Vegetation structure declined across the open-forest transect with lower-field layer cover associated with the open space and ground vegetation cover associated with the open-boundary. It is well known that vascular plant cover is lower under the canopy (Ferris et al., 2000; Oxbrough et al., 2005). This agrees with the findings of Bedford and Usher (1994) and Downie et al. (1996) which suggest that even at a distance of a few meters the movement of open species into the forest is limited.

5.2. Influence of open-space type and size

The present study found that glades support more species and individuals, as well as a distinct fauna from the rides and

road edges. The non-linear shape of glades means that they have a larger area away from the influence of the forest canopy, probably allowing them to support a greater number of species associated with open habitats. The relationship between area and species richness is well-studied, with larger areas having a greater potential for habitat heterogeneity, less chance of random extinctions and greater likelihood of random immigration affecting the spider population (MacArthur and MacArthur, 1961; Pianka, 1966). This suggests that the glades have a greater potential than roads or rides to retain open species associated with the pre-planting habitat.

Although the number of Linyphiid species did not differ among open-space types, the number of Lycosid species and individuals sampled was greater in the glades. In contrast relative abundance of Linyphiids was greater in the roads and rides. The Lycosids sampled in the present study (i.e. *Pardosa pullata* and *Alopecosa pulverulenta*) are well-known open-associated species (Harvey et al., 2002). These relatively large active hunters may benefit from the greater availability of prey in the structurally diverse open areas especially in terms of larger prey items that may be available. In addition to this the greater vegetation structure may offer greater protection from predators and places to conceal themselves from prey (Uetz, 1991). The smaller Linyphiids, which are known to inhabit both open and forested habitats (e.g. Pajunen et al., 1995; Downie et al., 1996) may be less specific in their habitat requirements: they construct small sheet webs amongst litter and ground vegetation which can capture a range of prey types. This may mean that Linyphiids are able to take advantage of conditions across a range of habitat types whereas Lycosids are somewhat more restricted.

The spider assemblages were also distinct among the geographical clusters in the open space (though not in the traps in the forest interior). The differing environmental characteristics between the Cork and Wicklow sites (poorly drained modified blanket bog and well-drained humid acid-grassland/dry heath, respectively) indicate that habitat type is an important factor in determining the spider fauna of the open space. Furthermore, this suggests that the species present are not just generalist species, but maybe retained from the pre-planting habitat.

The relationship between open-space size and spider diversity was confounded by the influence of the plantation canopy and the habitat type of the open space. Several of the open-space plots were characterised by a heavy shrub layer or deciduous woodland cover, with more forest-associated species and fewer open species. These plots were similar in assemblage structure to the rides and roads which were less than 15 m wide. This suggests that open spaces with a width of less than 15 m wide are not able to support a fauna of spiders associated with typical open habitats. Rides and roads <15 m wide are affected more shaded, which probably leads to vegetation and micro-climatic conditions similar to those of a mature open forest.

It has been recommended that ride width should be between 1 and 1.5 times tree height to provide adequate light conditions for open-associated species (Carter, 1989; Greatorex-Davies, 1989; Warren and Fuller, 1993). In the present study, mean height of mature spruce was 15.3 m (± 4.3 S.D.), giving a ride

width of 15–23 m to support open species. Therefore our results would appear to support the recommended ratio of tree height to width if it is taken as the minimum needed to support an open spider fauna. This also suggests that the inclusion of rides with a width of 6 m as Areas for Biodiversity Enhancement in Irish plantations may be too low for spiders (Forest Service, 2003), whereas the 15 m width recommendation for roads should be taken as a lower limit. Furthermore, as species richness showed no indication of levelling off when compared with road verge width, this would suggest that widening roads above the 15 m standard width will further enhance biodiversity.

One of the goals of sustainable forest management is to emulate natural forest dynamics, and a logical step might be to select areas of retained habitat which contain 'pockets' of deciduous trees or shrubs which may act as a source for forest species. This is important in an Irish context where there is very little natural forest cover: forested land accounts for 10% of the total land area (Forest Service, 2004) in Ireland but natural woodlands constitute <1% (Teagasc, 2005). Hence plantation forests could potentially play an important role in sustaining forest species in Ireland. In the present study these deciduous/shrub open-space areas represented an intermediate habitat between the plantation forest and the lower-field layer-type open space. Furthermore, the lack of specialist species (for instance, forest specialists which are not supported within the plantation), indicates that their potential for adding to plantation biodiversity may be negligible. It should be noted however that in the present study it was unclear whether these areas of 'open space' were retained from the pre-planting habitat or developed as the plantation matured and further research may be required to determine the biodiversity value of such areas.

The glades sampled in this study did not exhibit a similar 'threshold' size as was found for the roads and rides. However, one glade was similar in assemblage structure to the glades that were characterised by deciduous woodland and shrubs, although it was characterised by lower-field layer vegetation. This glade was only 80 m² in area, whereas the next smallest glade in area was 1000 m². This might suggest that this very small glade was under the influence of the forest plantation canopy and so was not large enough to support an open spider fauna. However to identify a threshold area (over which open species can be supported), areas between 80 and 1000 m² will need to be studied, although the 15 m threshold for ride/road width might suggest 225 m² as a minimum area for glades.

5.3. Large-scale influence of open space

The overall amount of unplanted open space within a plantation was positively related to both species richness and abundance. Similarly, Peterken and Francis (1999) found that the number of open-space species supported by woodlands was far greater in large woods, which they attributed to the presence of more open space across the whole wooded area.

Whilst there was a relationship with unplanted open space at a large scale, there was no relationship with non-linear open space at a smaller scale (within each open space). This may suggest that more open space at a larger scale encourages the

movement of individuals among open space. Spiders utilise both aerial (Duffey, 1956) and ground dispersal (Thomas et al., 1990) as a means to colonise habitats, so the amount of open space surrounding the sampling plots will directly affect the ability of open-associated species to disperse within the forested landscape. There was a negative relationship between ride area and spider assemblages. However it is likely that ride area indirectly represents the amount of forested area within 200 m of the sampling points, i.e. the greater the amount of planted forest, the greater potential for more rides.

The Irish *Forest Biodiversity Guidelines* (Forest Service, 2000) recommend that 5–10% of forest plantations larger than 10 ha should be kept as retained open space. However as spider species richness increased with the amount of unplanted open space in the three categories of <5, 5–10 and >10%, this suggests that the number of species which can be supported in areas with 5–10% has not reached a maximum and hence the 5–10% area may not be adequate to support a full suite of species associated with open habitats.

6. Conclusions

Open space within plantation forests supports spider species associated with open habitats and enhances overall plantation diversity. Furthermore, the response of the ground-dwelling spider fauna to open space was similar across both of the regions indicating the generality of these findings. In terms of forest management it is suggested that an absolute

minimum width of 15 m is needed for forest roads and rides to support an open spider fauna. For non-linear open space, a stratified sampling approach that varies glade area may reveal a similar ‘threshold’ size, over which open species are supported. The present study also highlights the need to examine the biodiversity value of a range of habitat types that could potentially be selected as retained habitat but with consideration given to the purpose of the open space. For instance, if the goal is to enhance open species, then management should focus on how the unique and rare species associated with the pre-planting habitat can persist in the plantation. However if the goal is to enhance species associated with natural forests, then management should investigate how best to incorporate or create non-plantation wooded areas in managed forests.

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Appendix A

The number of individuals sampled within each species along the open-forest transect (O = open, OB = open-boundary, B = boundary, FB = forest-boundary, F = forest). The indicator values of species within the (a) open and open-boundary traps, and (b) boundary, forest-boundary and forest traps are shown with associated significance values ($p = <0.05$; $**p = <0.01$; $p = <0.001$). The subsequent habitat associations (H) derived from these values are also shown: O = open, F = forest, G = generalist, U = unclassified. Nomenclature follows Roberts (1993).

	Transect positions	Total	Ind. value		H					
			O, OB	B, FB, B						
Family	O	OB	B	FB	F					
<i>Agroeca proxima</i> (O.P.-Cambridge, 1871)	Clubionidae	5	1	1	0	0	7	11	0	G
<i>Agyneta conigera</i> (O.P.-Cambridge, 1863)	Linyphiidae	0	0	4	5	1	10	0	8	G
<i>Agyneta decora</i> (O.P.-Cambridge, 1871)	Linyphiidae	2	0	0	0	1	3	2	2	U
<i>Agyneta olivacea</i> (Emerton, 1882)	Linyphiidae	30	28	3	3	2	66	30*	3	O
<i>Agyneta ramosa</i> (Jackson, 1912)	Linyphiidae	71	56	19	31	17	194	47	20	G
<i>Agyneta subtilis</i> (O.P.-Cambridge, 1863)	Linyphiidae	142	146	60	59	41	448	60*	27	O
<i>Alopecosa pulverulenta</i> (Clerck, 1757)	Lycosidae	49	1	0	0	0	50	33***	0	O
<i>Antistea elegans</i> (Blackwall, 1841)	Hahnidae	6	0	0	0	0	6	17*	0	O
<i>Aphileta misera</i> (O.P.-Cambridge, 1882)	Linyphiidae	1	0	0	0	0	1	4	0	U
<i>Asthenargus paganus</i> (Simon, 1884)	Linyphiidae	6	26	32	39	42	145	9	57**	F
<i>Bathyphantes gracilis</i> (Blackwall, 1841)	Linyphiidae	78	37	13	5	13	146	72***	6	O
<i>Bathyphantes nigrinus</i> (Westring, 1851)	Linyphiidae	21	7	0	3	0	31	35**	0	O
<i>Bathyphantes parvulus</i> (Westring, 1851)	Linyphiidae	8	1	0	0	3	12	25**	1	O
<i>Centromerita concinna</i> (Thorell, 1875)	Linyphiidae	3	0	0	1	0	4	2	1	U
<i>Centromerus arcanus</i> (O.P.-Cambridge, 1873)	Linyphiidae	0	1	2	0	0	3	2	1	U
<i>Centromerus dilutus</i> (O.P.-Cambridge, 1875)	Linyphiidae	19	45	56	47	37	204	38	52	G
<i>Centromerus prudens</i> (O.P.-Cambridge, 1873)	Linyphiidae	5	4	2	5	3	19	11	14	G
<i>Centromerus sylvaticus</i> (Blackwall, 1841)	Linyphiidae	0	1	0	0	0	1	4	0	U
<i>Ceratinella brevipes</i> (Westring, 1851)	Linyphiidae	11	8	7	2	4	32	26	10	G
<i>Ceratinella brevis</i> (Wider, 1834)	Linyphiidae	0	1	0	0	0	1	4	0	U
<i>Clubiona reclusa</i> (O.P.-Cambridge, 1863)	Clubionidae	8	1	0	0	0	9	25**	0	G

Appendix A (Continued)

	Transect positions					Total	Ind. value		H	
	Family	O	OB	B	FB		F	O, OB		B, FB, B
<i>Clubiona trivialis</i> (C.L. Koch, 1843)	Clubionidae	1	0	0	0	0	1	4	0	U
<i>Cnephalocotes obscurus</i> (Simon, 1884)	Linyphiidae	2	0	0	1	0	3	6	1	U
<i>Cryphoea sylvicola</i> (C.L. Koch, 1834)	Agelenidae	0	0	1	0	0	1	0	3	U
<i>Dicymbium nigrum</i> (Blackwall, 1834)	Linyphiidae	11	0	1	0	0	12	8	0	G
<i>Dicymbium tibiale</i> (Blackwall, 1836)	Linyphiidae	67	11	5	3	2	88	68***	2	O
<i>Diplocephalus latifrons</i> (O.P.-Cambridge, 1863)	Linyphiidae	52	127	215	217	332	943	21	74***	F
<i>Diplocephalus permixtus</i> (O.P.-Cambridge, 1871)	Linyphiidae	3	2	0	0	1	6	11	0	G
<i>Diplostylor concolor</i> (Wider, 1834)	Linyphiidae	0	0	1	1	1	3	0	8	U
<i>Dismodicus bifrons</i> (Blackwall, 1841)	Linyphiidae	30	6	3	3	1	43	54***	3	O
<i>Drassodes cupreus</i> (Blackwall, 1834)	Gnaphosidae	2	0	1	0	0	3	1	2	U
<i>Enoplognatha ovata</i> (Clerck, 1757)	Therididae	2	0	0	0	0	2	4	0	U
<i>Erigone atra</i> (Blackwall, 1833)	Linyphiidae	10	0	0	0	0	10	13	0	O
<i>Erigone dentipalpis</i> (Wider, 1843)	Linyphiidae	20	0	1	0	0	21	12	0	O
<i>Erigonella hiemalis</i> (Blackwall, 1841)	Linyphiidae	11	7	1	1	0	20	34**	1	O
<i>Ero cambridgei</i> (Kulczynski, 1911)	Mimetidae	2	0	0	0	0	2	8	0	U
<i>Ero furcata</i> (Villers, 1789)	Mimetidae	0	1	0	0	0	1	4	0	U
<i>Gonatium rubens</i> (Blackwall, 1833)	Linyphiidae	1	1	0	0	0	2	8	0	U
<i>Gongyliellum latebricola</i> (O.P.-Cambridge, 1871)	Linyphiidae	0	1	1	0	0	2	1	2	U
<i>Gongyliellum vivum</i> (O.P.-Cambridge, 1875)	Linyphiidae	38	36	25	17	18	134	48	26	G
<i>Gongylidum rufipes</i> (Linnaeus, 1758)	Linyphiidae	1	0	0	0	0	1	4	0	U
<i>Hahnia nava</i> (Blackwall, 1841)	Hahnidae	1	0	1	0	0	2	1	2	U
<i>Haplodrassus signifier</i> (C.L. Koch, 1839)	Gnaphosidae	5	1	1	0	2	9	8	2	G
<i>Hilaira excisa</i> (O.P.-Cambridge, 1871)	Linyphiidae	2	0	0	0	0	2	8	0	U
<i>Hypomma cornutum</i> (Blackwall, 1833)	Linyphiidae	0	0	1	0	0	1	0	3	U
<i>Lepthyphantes alacris</i> (Blackwall, 1853)	Linyphiidae	110	153	103	96	122	584	49	47	G
<i>Lepthyphantes cristatus</i> (Menge, 1866)	Linyphiidae	10	0	0	0	0	10	21**	0	O
<i>Lepthyphantes ericaeus</i> (Blackwall, 1853)	Linyphiidae	37	39	44	23	13	156	48	39	G
<i>Lepthyphantes flavipes</i> (Blackwall, 1854)	Linyphiidae	5	70	169	102	49	395	14	46	F
<i>Lepthyphantes mingei</i> (Kulczynski, 1887)	Linyphiidae	15	13	5	4	7	44	29	8	G
<i>Lepthyphantes obscurus</i> (Blackwall, 1841)	Linyphiidae	5	12	12	13	6	48	18	32	G
<i>Lepthyphantes pallidus</i> (O.P.-Cambridge, 1871)	Linyphiidae	1	2	3	0	1	7	7	4	G
<i>Lepthyphantes tenebricola</i> (Wider, 1834)	Linyphiidae	32	39	27	31	42	171	21	25	G
<i>Lepthyphantes tenuis</i> (Blackwall, 1852)	Linyphiidae	12	5	8	3	3	31	20	9	G
<i>Lepthyphantes zimmermanni</i> (Bertkau, 1890)	Linyphiidae	97	196	204	216	227	940	38	62**	F
<i>Leptorhoptrum robustum</i> (Westring, 1851)	Linyphiidae	0	0	3	7	0	10	0	6	G
<i>Lophomma punctatum</i> (Blackwall, 1841)	Linyphiidae	3	1	0	0	0	4	13	0	U
<i>Macrargus rufus</i> (Wider, 1834)	Linyphiidae	0	0	2	0	0	2	0	3	U
<i>Maro minutus</i> (O.P.-Cambridge, 1906)	Linyphiidae	10	43	46	37	22	158	27	30	G
<i>Maso sundervalli</i> (Westring, 1851)	Linyphiidae	24	6	1	0	1	32	49***	0	O
<i>Meioneta saxatilis</i> (Blackwall, 1844)	Linyphiidae	61	8	0	1	1	71	31***	0	O
<i>Meta mingei</i> (Blackwall, 1869)	Tetragnathidae	7	4	0	1	1	13	31**	1	O
<i>Meta merianae</i> (Scopli, 1763)	Tetragnathidae	0	1	0	0	0	1	4	0	U
<i>Meta segmentata</i> (Clerck, 1757)	Tetragnathidae	0	2	0	1	0	3	2	1	U
<i>Metopobactrus prominulus</i> (O.P.-Cambridge, 1872)	Linyphiidae	8	1	0	0	0	9	21**	0	G
<i>Micaria pulicaria</i> (Sundevall, 1832)	Clubionidae	0	0	0	1	0	1	0	3	U
<i>Micrargus herbigradus</i> (Blackwall, 1854)	Linyphiidae	16	9	7	8	7	47	30	19	G
<i>Microlinyphia pusilla</i> (Sundevall, 1830)	Linyphiidae	2	0	0	0	0	2	8	0	U
<i>Microneta viaria</i> (Blackwall, 1841)	Linyphiidae	0	1	0	2	0	3	2	1	U
<i>Monocephalus castaneipes</i> (Simon, 1884)	Linyphiidae	0	0	2	3	0	5	0	14	U
<i>Monocephalus fuscipes</i> (Blackwall, 1836)	Linyphiidae	66	242	341	302	232	1183	30	69***	F
<i>Neon reticulatus</i> (Blackwall, 1853)	Salticidae	1	0	0	0	0	1	4	0	U
<i>Nereine clathrata</i> (Sundevall, 1830)	Linyphiidae	3	2	0	0	0	5	13	0	U
<i>Neriere montana</i> (Clerck, 1757)	Linyphiidae	0	0	0	0	1	1	0	3	U
<i>Neriere peltata</i> (Wider, 1834)	Linyphiidae	3	6	3	3	3	18	17	8	G
<i>Nesticus cellulanus</i> (Clerck, 1757)	Nesticidae	0	0	0	1	0	1	0	3	U
<i>Oedothorax fuscus</i> (Blackwall, 1834)	Linyphiidae	1	0	0	0	0	1	4	0	U
<i>Oedothorax gibbosus</i> (Blackwall, 1841)	Linyphiidae	96	7	7	1	1	112	56***	1	O
<i>Oedothorax retusus</i> (Blackwall, 1851)	Linyphiidae	8	0	0	0	0	8	13	0	G
<i>Oxyptila trux</i> (Blackwall, 1846)	Thomisidae	36	9	0	3	0	48	57***	1	O
<i>Pachygnatha clercki</i> (Sundevall, 1823)	Tetragnathidae	5	1	1	0	0	7	19*	0	G
<i>Pachygnatha degeeri</i> (Sundevall, 1830)	Tetragnathidae	47	1	0	0	0	48	25**	0	O
<i>Pardosa amentata</i> (Clerck, 1757)	Lycosidae	10	1	1	1	0	13	23*	1	O
<i>Pardosa nigriceps</i> (Thorell, 1856)	Lycosidae	52	4	2	0	0	58	45***	0	O
<i>Pardosa palustris</i> (Linnaeus, 1758)	Lycosidae	1	0	0	0	0	1	4	0	U

Appendix A (Continued)

	Transect positions					Total	Ind. value		H	
	Family	O	OB	B	FB		F	O, OB		B, FB, B
<i>Pardosa pullata</i> (Clerck, 1757)	Lycosidae	521	7	0	3	0	531	62***	0	O
<i>Pelecopsis nemoralis</i> (Blackwall, 1841)	Linyphiidae	2	5	4	3	2	16	16	7	G
<i>Pelecopsis parallela</i> (Wider, 1834)	Linyphiidae	2	1	0	0	1	4	6	1	U
<i>Pepnocranium ludicrum</i> (O.P.-Cambridge, 1861)	Linyphiidae	4	0	0	0	0	4	13*	0	U
<i>Pholcomma gibbum</i> (Westring, 1851)	Linyphiidae	3	2	0	0	0	5	13*	0	U
<i>Pirata piraticus</i> (Clerck, 1757)	Lycosidae	17	2	0	1	1	21	27***	0	O
<i>Pirata uliginosus</i> (Thorell, 1856)	Lycosidae	45	3	3	1	1	53	32*	2	O
<i>Pocadicnemis juncea</i> (Lockett, Millidge, 1853)	Linyphiidae	9	2	0	0	0	11	29**	0	O
<i>Pocadicnemis pumila</i> (Blackwall, 1841)	Linyphiidae	300	59	19	9	3	390	80***	4	O
<i>Poecilonea globosa</i> (Blackwall, 1841)	Linyphiidae	0	5	0	0	1	6	15*	0	G
<i>Porrhomma campbelli</i> (O.P.-Cambridge, 1894)	Linyphiidae	1	0	0	1	0	2	3	1	U
<i>Porrhomma convexum</i> (Westring, 1861)	Linyphiidae	1	0	0	0	0	1	4	0	U
<i>Porrhomma pallidum</i> (Jackson, 1913)	Linyphiidae	5	30	38	39	42	154	16	61*	F
<i>Porrhomma pygmaeum</i> (Blackwall, 1834)	Linyphiidae	0	3	0	1	1	5	5	2	U
<i>Robertus arundineti</i> (O.P.-Cambridge, 1871)	Therididae	1	0	0	0	0	1	4	0	U
<i>Robertus lividus</i> (Blackwall, 1836)	Therididae	68	71	59	69	74	341	43	49	G
<i>Saaristoa abnormis</i> (Blackwall, 1841)	Linyphiidae	32	39	57	50	65	243	32	65**	F
<i>Saaristoa firma</i> (O.P.-Cambridge, 1905)	Linyphiidae	3	4	3	2	6	18	15	8	G
<i>Silometopus elegans</i> (O.P.-Cambridge, 1872)	Linyphiidae	41	2	1	0	2	46	32**	0	O
<i>Tapinocyba pallens</i> (O.P.-Cambridge, 1872)	Linyphiidae	3	6	8	8	2	27	7	20	G
<i>Tapinocyba praecox</i> (O.P.-Cambridge, 1873)	Linyphiidae	0	1	0	0	0	1	4	0	U
<i>Taranucnus setosus</i> (Simon, 1884)	Linyphiidae	6	1	1	1	0	9	16	1	G
<i>Theonoe minutissima</i> (O.P.-Cambridge, 1879)	Therididae	7	28	33	24	13	105	24	36	G
<i>Theridion pallens</i> (Blackwall, 1834)	Therididae	0	0	2	0	0	2	0	3	U
<i>Tiso vegans</i> (Blackwall, 1834)	Linyphiidae	34	12	2	0	0	48	12	0	G
<i>Trochosa spinipalpis</i> (O.P.-Cambridge, 1895)	Lycosidae	0	1	0	0	0	1	4	0	U
<i>Trochosa terricola</i> (Thorell, 1836)	Lycosidae	27	25	3	3	6	64	28	10	G
<i>Walckenaeria acuminata</i> (Blackwall, 1833)	Linyphiidae	21	22	24	14	19	100	38	39	G
<i>Walckenaeria antica</i> (Wider, 1834)	Linyphiidae	1	0	0	0	0	1	4	0	U
<i>Walckenaeria atrotibialis</i> (O. P.-Cambridge, 1878)	Linyphiidae	5	4	4	0	0	13	7	1	G
<i>Walckenaeria cuspidata</i> (Blackwall, 1833)	Linyphiidae	12	8	8	5	2	35	24	11	G
<i>Walckenaeria dysderoides</i> (Wider, 1843)	Linyphiidae	4	21	26	15	14	80	8	17	G
<i>Walckenaeria nodosa</i> (O.P.-Cambridge, 1873)	Linyphiidae	1	0	0	0	0	1	4	0	U
<i>Walckenaeria nudipalpis</i> (Westring, 1851)	Linyphiidae	10	2	9	5	5	31	11	20	G
<i>Walckenaeria vigilax</i> (Blackwall, 1851)	Linyphiidae	66	28	4	4	1	103	70***	3	O
<i>Xysticus cristatus</i> (Clerck, 1757)	Thomisidae	4	0	0	0	0	4	8	0	U
<i>Zora spinimana</i> (Sundevall, 1833)	Zoridae	3	0	1	0	0	4	6	1	U
Total		2769	1829	1757	1561	1521	9437			

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