

The response of ground-dwelling spiders (Araneae) and hoverflies (Diptera: Syrphidae) to afforestation assessed using within-site tracking

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In many countries throughout the world, the area of plantation forests continues to increase and they now dominate many landscapes. In recent decades, forest cover in Ireland has expanded largely due to commercial afforestation with non-native conifers. This study provides the first within-site assessment of the response of two important arthropod groups to afforestation in agricultural grasslands in Ireland. Five sites were studied 1 year before and 7 years after afforestation using pitfall trapping for active ground-dwelling spiders and Malaise trapping for hoverflies. Both species groups were studied in grassland habitat, and spiders were also sampled in field boundary hedgerow habitat. Afforestation within the study sites had a positive effect on ground-dwelling spider diversity over the first 7 years; total species richness increased in afforested grassland and hedgerow habitats, and forest specialist species richness increased in afforested grassland habitat. This was concurrent with, and most likely influenced by, the increase in habitat structure created by the forest vegetation, litter and deadwood layers and the increase in canopy cover. There was no effect of afforestation on hoverfly species richness over the first 7 years, possibly due to confounding effects of hoverfly movements across landscapes. Spider and hoverfly species compositions were also positively affected by afforestation. These results indicated that afforestation in our study sites, set within a predominantly agricultural landscape, benefitted arthropod diversity by increasing habitat diversity. Hedgerow habitats were also an important contributor to biodiversity in these newly planted forests. Ecologically oriented planning and management of afforestation must consider the influence of habitat quality in forest plantations, including the protection of biodiversity rich habitats and the quality of the land being afforested, to improve the contribution to biodiversity enhancement and conservation.

Introduction

With the expansion of commercial plantation forests (European Commission, 2011), there is growing interest in ecologically sound forest planning and management practices (FAO, 2011). At the beginning of the 20th century, very little of the once extensive natural forest cover in Ireland remained, and <1 per cent of the Irish landscape was forested (Anon, 2008). This lack of forest estate led to government policy and grant-aid in support of afforestation, which has increased forest cover to ~11 per cent in Ireland over the last century (Forest Europe *et al.*, 2011). The current target is to further increase this cover to 14 per cent by 2030, mainly through the establishment of plantation forests (COFORD Council, 2009).

The planting of forest on agricultural land is increasing, and in Ireland in 2010, 95 per cent of afforestation was carried out on agricultural land (Anon, 2010). Changes in forest management practices in recent decades reflect the growing importance of ecological considerations; particularly biodiversity conservation and land owners undertaking afforestation in Ireland must comply with forestry objectives that form part of a legal and

institutional framework. These include not only producing commercial timber but also providing ecosystem services such as climate change mitigation, improving water quality and increasing biodiversity (Anon, 2012). Although afforestation in Ireland consists mainly of non-native tree species, these objectives and initiatives mean that new forests are compliant with the principles of sustainable forest management that aims to manage the world's plantation forests in a way that maintains biodiversity and ecosystem functioning whilst providing forest products and services (United Nations Conference on Environment and Development, 1992; MCPFE, 1993).

Afforestation impacts on biodiversity and the magnitude and direction of the effect is influenced by preceding land use and forest management practices (Hunter, 2000; Carnus *et al.*, 2006). In countries such as Ireland, which have an extensively modified and intensively managed agricultural landscape, native forests have become rare and plantation forestry can benefit landscape biodiversity, particularly when appropriately managed (Hartley, 2002; Berndt *et al.*, 2008; Brockerhoff *et al.*, 2008; Pawson *et al.*, 2008). Changes in biodiversity throughout the forest cycle are well-documented, but in countries undertaking large-scale

afforestation, the change in land use, and its effect on habitats that are already present, means that the effects on biodiversity in recently planted areas are of particular interest.

The processes involved in preparing a site for afforestation such as chemical application, soil drainage and the subsequent changes in vegetation structure and diversity induce changes in species composition (Gittings *et al.*, 2006; Smith *et al.*, 2006) which are followed by further changes in response to the habitat modification resulting from the planting of trees (Oxbrough *et al.*, 2005; Oxbrough *et al.*, 2006b). Therefore, afforestation is likely to have an impact on the biodiversity of agricultural grasslands and hedgerows contained within this habitat. Hedgerows are woody habitats located at field boundaries and are often the only semi-natural habitat present across large tracts of agricultural land (Marshall and Moonen, 2002). Hedgerows provide an important contribution to ecosystem services, through the conservation of native wildlife, habitat connectivity between forest patches, and for insect pollinators and biological control taxa that utilize this habitat (Landis *et al.*, 2000; Le Coeur *et al.*, 2002; Marshall and Moonen, 2002; Benton *et al.*, 2003; Frank and Reichhart, 2004). The effect of afforestation on the biodiversity of ground vegetation, birds and arthropods has been studied by substituting time for space using a chronosequence approach (Pithon *et al.*, 2005; Oxbrough *et al.*, 2006b; Smith *et al.*, 2006). However, there has been no reported within-site tracking to directly monitor the changes in biodiversity following afforestation in agricultural grasslands.

The diversity of ground-dwelling spiders (Araneae) and hoverflies (Diptera: Syrphidae) in afforested sites is important as they play a significant role in the functioning of ecosystem processes, including food webs and pollination (Clarke and Grant, 1968; Sommaggio, 1999; Meyer *et al.*, 2009). Spiders and many hoverfly species are predatory on other arthropods and can contribute to the biological control of pests in agricultural and forest ecosystems (Sommaggio, 1999; Symondson *et al.*, 2002). Additionally, ground-dwelling spiders respond to changes in vegetation structure, which undergo significant changes during the forest cycle (Oxbrough *et al.*, 2005), and hoverflies are useful as indicators of habitat disturbance and quality (Sommaggio, 1999). Spiders and hoverflies are often used as biodiversity indicators due to their well-known habitat associations, the ease of trapping and identification and reliable species lists (Sommaggio, 1999; Pearce and Venier, 2006).

This study is unique as it is the first to examine changes in arthropod diversity following afforestation in agricultural grasslands in the same sites prior to planting and 7 years after planting, as opposed to a chronosequence approach. Specifically, it examined the change in species richness and composition of ground-dwelling spiders and hoverflies in (1) open grassland habitat found in agricultural fields and (2) hedgerow habitat, which is often found at field boundaries for ground-dwelling spiders only.

Materials and methods

Study sites

Five agricultural grassland sites that had previously been used for livestock grazing were studied 1 year before planting (hereafter called pre-planting) in the summer of 2002 and 7 years after planting in the summer of 2010 (hereafter called post-planting). These sites had a wide geographical distribution across Ireland (Figure 1, Table 1), and each site was planted with

coniferous and broadleaf tree species in 2003 including Sitka spruce (*Picea sitchensis* (Bong.) Carrière), ash (*Fraxinus excelsior* L.), maple (*Acer pseudoplatanus* L.), larch (*Larix kaempferi* (Lamb.) Carrière) and alder (*Alnus glutinosa* (L.) Gaertn.) (Table 1).

Spider sampling

Active ground-dwelling spiders were sampled using pitfall traps in six plots at each site. Three of the plots were located in open grassland habitat and three in field boundary hedgerow habitats (hereafter called open and hedgerow plots, respectively). At one study site, four open plots and two hedgerow plots were established. In each open plot, five pitfall traps were placed in a grid arrangement, the four corner traps were spaced 4 m apart and one trap was placed in the centre. In each hedgerow plot, five pitfall traps were placed in a linear arrangement with traps spaced at 2-m intervals.

Plastic cups of ~7 cm diameter and 9 cm high were used as pitfall traps and were dug into the ground so the rim of the cup was slightly below the ground surface. Each trap was filled with ethylene glycol (anti-freeze) to a depth of 3 cm, and drainage slits were cut 1 cm from the top of the cup to prevent flooding. The contents of each pitfall trap were collected every 3 weeks between May and August, to coincide with the main activity period of Irish spiders (Nolan, 2008), resulting in three collections in 2002 and three in 2010 and a total of 62–66 trapping days in each year. This length of trapping is sufficient to detect variation in spider diversity for biodiversity assessments (Oxbrough *et al.*, 2006a; Oxbrough *et al.*, 2007). The plastic cup was placed back in the ground and filled with fresh anti-freeze after each collection. The contents of the traps were transferred to labelled sample bottles and stored in 70 per cent ethanol.

Spiders were identified to species level using Roberts (1993), nomenclature follows Platnick (2012) and sub-groups of specialist species that exhibit a preference for open or forest habitats were identified using Nolan (2008).

Hoverfly sampling

Two Malaise traps were placed in each site using a standard sampling procedure, in linear areas that act as flight paths for hoverflies (Speight, 2000). The traps were spaced ~10 m apart in sheltered, un-shaded areas and orientated with the collecting bottles facing south so that they received the maximum amount of sunlight. The collection bottles were filled with 70 per cent ethanol used as a killing agent and a preservative. The contents of each bottle were collected every 3 weeks from May to August, resulting in a total of three collections in 2002 and three in 2010 and a total of 62–68 trapping days at each Malaise trap in each year. After each collection, a new bottle of 70 per cent ethanol was placed back on the trap.

Hoverflies were identified to species level using Stubbs and Falk (1983); van Veen (2004) and Haarto and Kerppola (2007) and species nomenclature follows Speight (2008). Species were separated into sub-groups of open, woody vegetation and water-associated species using the Database of Irish Syrphidae (Speight, 2008). The Database of Irish Syrphidae uses the fuzzy coding system that codes habitats with the numbers 1–3, where 1 indicates the habitat is low preference and 3 indicates the habitat is maximally preferred by the species. Only species that were coded 3 for maximum preference were included in the sub-groups for habitat associated species.

Habitat variables

The habitat surrounding each pitfall trap was surveyed using 1 × 1 m quadrats placed over each trap. The percentage cover of the following variables was recorded as follows: ground vegetation (0–10 cm), lower field layer vegetation (10–50 cm), upper field layer vegetation (50–200 cm), litter and deadwood. The canopy cover in open plots was also recorded from

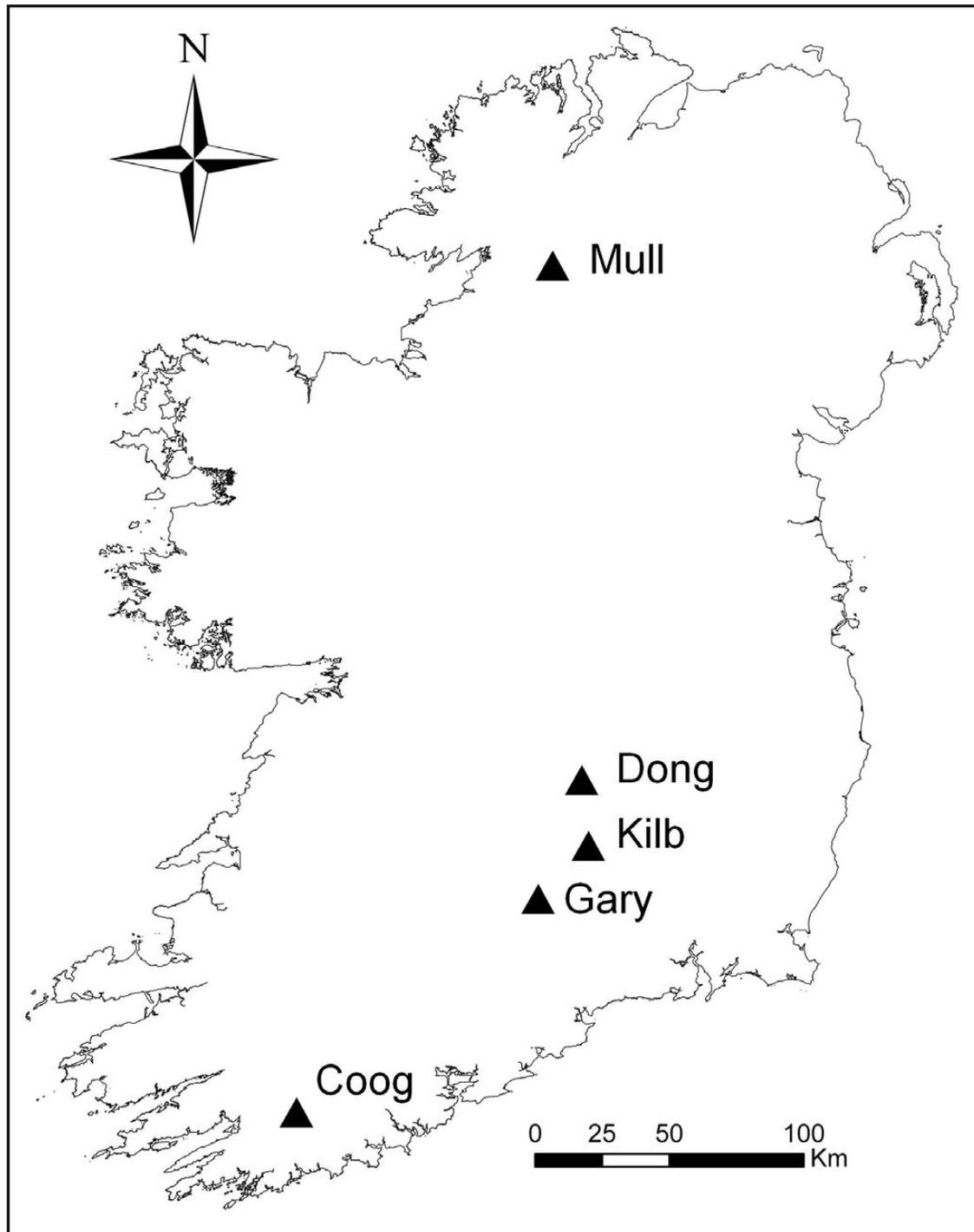


Figure 1 Distribution of study sites in Ireland.

the centre of each pitfall plot using one hemispherical photograph taken at a height of 1.3 m and analysed with GLA 2.0 (Frazer *et al.*, 1999).

The habitat categories defined by Gittings *et al.* (2006), which are based on the Syrph the Net microhabitat categories (Speight *et al.*, 2004), were surveyed within a 100 m radius of the Malaise traps at each site using the DAFOR (dominant, abundant, frequent, occasional, rare) scale. The categories surveyed were as follows: mature trees, immature/understory trees, tall shrubs, low shrubs, tussocks, tall herbs, short herbs, submerged sediment/

debris and water-saturated ground. Conifer and broadleaf trees and shrubs were recorded separately, and the length of streams and rivers within the 100 m radius were also recorded.

Data analysis

Sampling across different years can affect species abundance and richness due to temporal variation; therefore, species with two or fewer individuals

Table 1 Locations and characteristics of the study sites

Site code	Size (ha)	Irish national grid reference	Elevation (m)	Soil type	Tree species planted in 2003 ¹
Coog	6.9	W209559	140	Peaty podzol	Ash (F), Alder (F), Larch (F), Oak (O)
Dong	12.6	S269797	92	Brown earth	Maple (A), Ash (A), Sitka spruce (F), Alder (O)
Gary	16.7	S107353	140	Brown earth	Ash (A), Maple (F)
Kilb	11.4	S295552	237	Brown podzol	Sitka spruce (A), Larch (A)
Mull	23.0	H162712	145	Gley	Sitka spruce (D)

¹DAFOR abundance scale: D = dominant; A = abundant; F = frequent; O = occasional; R = rare.

Alder (*A. glutinosa*), ash (*F. excelsior*), larch (*L. kaempferi*), maple (*A. pseudoplatanus*), oak (*Quercus robur*), Sitka spruce (*P. sitchensis*).

were removed from the spider and hoverfly datasets as they could potentially occur as singletons in both sampling years (Norris, 1999). Data were unavailable for three of the hedgerow spider sampling plots from the pre-planting survey, so these three plots were excluded from the analysis. In the post-planting survey, the hedges had been removed from three of the hedgerow spider sampling plots; therefore, these three plots were also removed from the analysis. The number of spider sampling plots used in the analysis totalled 16 open plots in both the pre-planting and post-planting surveys, 11 hedgerow plots in the pre-planting survey and 9 hedgerow plots in the post-planting survey.

Spider species count data were pooled across the five pitfall traps, and all three collections for each plot and plot level data were used as the sample unit in all analysis. Due to trap losses and different sampling period lengths, the species richness for each plot was standardized by computing individual-based rarefaction curves based on unstandardized abundance data (Gotelli and Colwell, 2001). The number of individuals along the X axis was then standardized and the species richness for each plot extracted. The number of individuals was standardized using the following formula: $ni/Ti \times T$, where ni is the number of individuals at the i th plot, Ti is the number of traps multiplied by the number of trapping days at the i th plot and T is lowest number of traps multiplied by the lowest number of trapping days.

Hoverfly species count data were pooled across the three collections and two Malaise traps per site, and these site totals were used as the sample unit in analyses, making five replicates each in the pre-planting and post-planting surveys. Species richness required standardization due to different sampling period lengths and Malaise trap damage. It has been shown that the log volume of Malaise trap catch and the number of hoverfly species per sample is positively correlated (Gittings *et al.*, Unpublished report); therefore, species richness was standardized to the lowest log catch volume of total catch. This was calculated using the following steps: (1) calculate predicted species richness for each sample, using the regression equation from the regression of species richness on log catch volume, (2) use the following formula to calculate a standardized value for lowest log catch volume: $\text{standardized } y_i = (\text{observed } y_i) / (\text{predicted } y_i) \times (a + b \times c)$, where y_i is the species richness value at site i , a is the intercept and b is the slope from the regression equation of the relationship between observed y and log catch volume, and c is the lowest log catch volume. This was calculated for total, water, open and forest-associated species.

The dominance of each species, expressed as a percentage of the total species, was calculated. This was based on each species overall abundance weighted by its overall frequency of occurrence among plots using the method developed by Pinzón and Spence (2010). The difference in the total species richness of spiders and the identified sub-groups of habitat specialists between pre-planting and post-planting in the open and hedgerow plots was analysed using generalized linear mixed modelling (GLMM). GLMM is an extension of linear modelling, which allows data to be analysed using a mixed model by including a fixed-effects term and a random effects term (Zuur *et al.*, 2009). This type of analysis was used as the plots were

nested within sites. The difference in species richness was calculated as the post-planting value minus the pre-planting value, as each individual plot was sampled both pre-planting and post-planting meaning that plots were paired within sites. The models used the Gaussian distribution and identity link function, with the intercept as the fixed effect and site as the random effect. The difference in the total species richness of hoverflies and the identified sub-groups of habitat specialists between pre-planting and post-planting was also analysed using GLMM. This type of analysis was used as the pre-planting and post-planting samples were nested within sites. The models used the Poisson distribution and log link function, with year (pre-planting or post-planting) as the fixed effect and site as the random effect. The data were checked for normality prior to analyses, and the residuals vs fitted values were plotted to check the fit of each model.

Indicator species analysis (ISA) was used to identify spider and hoverfly species, which were strongly associated with either the pre-planting or post-planting habitat within open plots and hedgerow plots and also to identify species, which were associated with open or hedgerow plots pre-planting and open or hedgerow plots post-planting. This analysis uses species count data to calculate the relative abundance and relative frequency with which a species occurs in *a priori* determined groups. An indicator value percentage is then assigned to each species to indicate which group they are associated with (Dufrene and Legendre, 1997). The analysis was run using 4999 permutations followed by a Monte Carlo test of statistical significance.

Redundancy analysis (RDA) was used to examine the relationship between spider species composition, open and hedgerow plots, pre- and post-planting and the measured habitat variables. This analysis was also used on hoverfly species composition and pre-planting and post-planting habitat variables. This type of analysis tests how much of the variation in species composition can be explained by the constraining variables (ter Braak, 1994). Prior to analysis, the habitat variables were examined for collinearity using Spearman's rho correlations, any which were collinear >0.7 were removed, the variables were scaled so the mean = 0 and SD = 1 and the species data were Hellinger-transformed (Legendre and Gallagher, 2001). Latitude can affect spider species composition in Ireland (Oxbrough *et al.*, 2012), and here longitude also had an effect, therefore partial RDA using latitude and longitude as conditional variables was carried out. Latitude also had an effect on hoverfly species composition and so it was used as a covariable in a partial RDA. Forward selection was used to identify the variables that explained the most variation in species composition among the plots (Blanchet *et al.*, 2008). ANOVA was then used to determine the significance level of the final model and the selected variables. The selected variables used in the final model for spiders were plot type (open or hedgerow), litter cover and canopy cover, and only one variable, understory trees, was selected for the final hoverfly model.

Habitat variables recorded at the spider sampling plots were averaged across the five quadrats, and plot level data were used in analyses. The data were compared between pre-planting and post-planting using paired Wilcoxon tests on arcsine-transformed percentage cover data.

This method was used as plots were paired from the pre-planting and post-planting surveys, and the data were non-normally distributed. Habitat variables recorded for the Malaise traps were in categorical form so were not suitable for statistical analysis among plots. However, the categories were recoded from 1 to 5, with 1 representing rare and 5 representing dominant, and these dummy variables were included in the RDA ordination of hoverfly species composition.

ISA was conducted in PC-ORD (McCune and Mefford, 2011). All other analyses were conducted in R (R Core Team, 2012). GLMM used the nlme package (Pinheiro et al., 2013) and the MASS package (Ripley et al., 2013), RDA used the vegan package (Oksanen et al., 2012) and forward selection used the packfor package (Dray et al., 2012).

Results

The effect of afforestation on habitat characteristics

There was a significant increase in most habitat variables following afforestation in open plots, apart from ground vegetation that decreased (Table 2). There was also a notable but non-significant increase in the cover of lower field layer vegetation in the open plots post-planting. There was a significant increase in litter cover in the hedgerow plots following afforestation, and there were notable but non-significant increases in the cover of the vegetation layers (Table 2).

The effect of afforestation on ground-dwelling spiders

Before planting, a total of 909 adult ground-dwelling spiders from 72 species and 5 families were recorded at study sites. After omitting species with 2 or fewer individuals, a total of 898 adult spiders from 62 species and 5 families were used in the analysis, these species comprised mainly of habitat generalists and more open habitat specialist species were present than forest specialist species (Table 3). The dominant species, which occurred most abundantly and frequently, in open plots was *Erigone atra* Blackwall (24 per cent), an open specialist from the Linyphiidae family

(‘money’ spiders) and in hedgerow plots was *Monocephalus fuscipes* (Blackwall) (18 per cent), a forest specialist from the Linyphiidae family. After planting, a total of 2186 adult spiders from 93 species and 10 families were recorded. After omitting species with 2 or fewer individuals, a total of 2149 adult spiders from 67 species and 5 families were used in the analysis. Again, after planting, the majority of species were habitat generalists and there were more open habitat specialist species present in the assemblage than forest specialist species (Table 3). The dominant species, which occurred most abundantly and frequently, in both open and hedgerow plots following afforestation was *Pardosa amentata* (Clerck) (25 and 37 per cent, respectively), an open specialist from the Lycosidae family (‘wolf’ spiders).

There was a significant increase in total spider species richness in open plots and hedgerow plots post-planting (Table 4). Forest specialist species richness significantly increased in open plots post-planting, but there was no significant difference in hedgerow plots (Table 4). Open specialist species richness was not significantly different post-planting in either the open or hedgerow plots.

ISA identified one habitat generalist species and one open specialist species, which were associated with open plots pre-planting, and 16 species, which were associated with open plots post-planting; these were a mixture of open, forest and habitat generalist species (Table 5). No species recorded were associated with pre-planting hedgerow plots; however, 10 species were associated with hedgerow plots post-planting (Table 5). Additionally, more forest specialist species were highly associated with hedgerow plots compared with open plots in both pre-planting and post-planting surveys (Table 6).

Partial RDA of the selected variables produced a significant model ($F_{3,46} = 2.82, P = 0.005$), which explained 6 per cent of the variation in species composition. The covariable latitude explained a further 2 per cent of the variation ($F_{1,49} = 2.91, P \leq 0.0001$) and longitude also explained 2 per cent of the variation ($F_{1,49} = 2.64, P \leq 0.0001$). Three axes were recommended for plotting the partial RDA, and the first two axes that represent 5 per cent of

Table 2 Median \pm interquartile range of habitat variables (percent cover) from open and hedgerow spider sampling plots pre- and post-planting

	Pre-planting	Post-planting	Wilcox test
Open plots			
Ground vegetation	34.25 \pm 52.73	1.25 \pm 31.50	$W_{15} = 113, P = 0.02$
Lower field layer	35.25 \pm 40	57 \pm 49.88	$W_{15} = 62, P = 0.78$
Upper field layer	8.75 \pm 36.75	34 \pm 70.88	$W_{15} = 29, P = 0.046$
Bare soil	0 \pm 0	15.50 \pm 11.25	$W_{15} = 4, P = 0.001$
Litter cover	0 \pm 0	3.50 \pm 28.38	$W_{15} = 0, P = 0.006$
Deadwood	0 \pm 0	0.5 \pm 0	$W_{15} = 0, P = 0.0002$
Canopy cover	0 \pm 0	78.50 \pm 45.50	$W_{15} = 0, P = 0.0005$
Hedgerow plots			
Ground vegetation	33.50 \pm 26	21 \pm 27.50	$W_8 = 38, P = 0.07$
Lower field layer	25.50 \pm 7.50	73 \pm 54	$W_8 = 6, P = 0.05$
Upper field layer	57.50 \pm 29	15.50 \pm 44	$W_8 = 38, P = 0.07$
Bare soil	30.50 \pm 47.50	15.50 \pm 21	$W_8 = 30, P = 0.43$
Litter cover	0 \pm 0	3.50 \pm 66	$W_8 = 0, P = 0.04$
Deadwood	9 \pm 12	0.50 \pm 3	$W_8 = 23, P = 1$

Comparison between pre- and post-planting made using paired Wilcox tests. Statistically significant results are highlighted in bold.

Table 3 The total number of individuals, families, species and species of habitat associated sub-groups collected during the pre-planting and post-planting surveys

	Pre-planting before omitting species with ≤ 2 individuals	Pre-planting after omitting species with ≤ 2 individuals	Post-planting before omitting species with ≤ 2 individuals	Post-planting after omitting species with ≤ 2 individuals
Spiders				
Total abundance	909	898	2186	2149
Total families	5	5	10	5
Total species	72	62	93	67
Habitat generalists	–	39	–	42
Open specialists	–	14	–	15
Forest specialists	–	9	–	10
Hoverflies				
Total abundance	1211	1196	617	600
Total species	52	42	63	50
Habitat generalist	–	2	–	2
Water associated	–	20	–	20
Open associated	–	11	–	13
Woody vegetation associated	–	15	–	20

Table 4 Mean \pm standard error of ground-dwelling spider and hoverfly species richness pre- and post-planting

	Pre-planting	Post-planting	GLMM
Spiders open plots			
All species	8.00 \pm 0.97	14.38 \pm 1.19	$t_{11} = 2.98, P = 0.01$
Open specialists	2.90 \pm 0.33	3.86 \pm 0.60	$t_{11} = 0.93, P = 0.37$
Forest specialists	0.74 \pm 0.17	2.29 \pm 0.36	$t_{11} = 3.81, P = 0.003$
Spiders hedgerow plots			
All species	6.94 \pm 1.29	12.66 \pm 1.28	$t_5 = 5.29, P = 0.003$
Open specialists	1.53 \pm 0.36	2.78 \pm 0.55	$t_5 = 1.51, P = 0.19$
Forest specialists	1.67 \pm 0.34	2.23 \pm 0.37	$t_5 = 1.41, P = 0.22$
Hoverflies			
All species	12.17 \pm 0.89	14.23 \pm 0.91	$t_4 = 3.12, P = 0.15$
Water associated	3.30 \pm 0.42	3.16 \pm 0.20	$t_4 = 0.45, P = 0.54$
Open associated	4.63 \pm 1.05	6.03 \pm 0.72	$t_4 = 1.29, P = 0.32$
Woody vegetation associated	5.05 \pm 0.63	5.71 \pm 0.52	$t_4 = 0.20, P = 0.68$

Comparison between pre- and post-planting made using GLMM. Statistically significant results are highlighted in bold.

the variation are presented in Figure 2. Canopy cover explained 2 per cent of the variation in species composition ($F_{3,46} = 2.91, P \leq 0.0001$), litter cover explained 2 per cent of the variation ($F_{3,46} = 2.90, P \leq 0.0001$) and plot type (open or hedgerow) explained 2 per cent of the variation ($F_{3,46} = 2.65, P = 0.0004$). In the pre-planting survey, the species composition of open plots was different to the hedgerow plots, but post-planting the species composition among open and hedgerow plots became similar (Figure 2).

The effect of afforestation on hoverflies

Before planting, a total of 1211 adult hoverflies from 52 species were recorded. After omitting species with 2 or fewer individuals, 1196 hoverflies from 42 species were used in the analysis. Of these species, 11 were open habitat associated, 15 were woody

vegetation associated, 20 were water associated and 2 were habitat generalists. The dominant species was *Platycheirus clypeatus* (Meigen) (33 per cent), a water-associated species. After planting, a total of 617 adult hoverflies from 63 species were recorded. After omitting species with 2 or fewer individuals, 600 hoverflies from 50 species were used in the analysis. Of these species, 13 were open associated, 20 were woody vegetation associated, 20 were water associated and 2 were habitat generalists. The dominant species was *Rhingia campestris* Meigen (11 per cent), which is associated with cattle farming in Ireland and across much of Europe, as the larvae feed in cow dung, although adults of this species are often found at forest edges.

Afforestation did not impact on total species richness or species richness of the sub-groups of open, water- and woody vegetation-associated species (Table 4). ISA identified five species,

Table 5 Indicator species analysis of ground-dwelling spider within open plots pre-planting vs post-planting and within hedgerow plots pre-planting vs post-planting

Species	Habitat association	Open		Hedgerow	
		Pre-planting	Post-planting	Pre-planting	Post-planting
<i>B. nigrinus</i>	Shade associated	0	31*	3	49*
<i>D. latifrons</i>	Forest specialist	0	38*	4	58*
<i>Dismodicus bifrons</i>	Habitat generalist	0	53**	0	33*
<i>Pachygnatha clercki</i>	Habitat generalist	1	48*	1	31*
<i>P. amentata</i>	Open specialist	9	58*	3	61*
<i>R. lividus</i>	Habitat generalist	1	58**	0	53**
<i>W. acuminata</i>	Habitat generalist	1	57**	2	49*
<i>Erigone dentipalpis</i>	Open specialist	43*	0	-	-
<i>L. punctatum</i>	Habitat generalist	1	51**	-	-
<i>M. fuscipes</i>	Forest specialist	0	56**	-	-
<i>Nerienne clathrata</i>	Habitat generalist	0	38*	-	-
<i>Oedothorax fuscus</i>	Habitat generalist	46*	6	-	-
<i>P. ericaeus</i>	Habitat generalist	0	46*	-	-
<i>P. latitans</i>	Open specialist	0	31*	-	-
<i>P. juncea</i>	Open specialist	1	48**	-	-
<i>P. pumila</i>	Open specialist	2	47*	-	-
<i>Saaristoa abnormis</i>	Habitat generalist	0	56***	-	-
<i>T. zimmermanni</i>	Forest specialist	5	63**	-	-
<i>Centromerus sylvaticus</i>	Shade associated	-	-	0	33*
<i>O. gibbosus</i>	Habitat generalist	-	-	0	54**
<i>P. pullata</i>	Open specialist	-	-	0	32*

Numbers represent indicator value percentages.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

which preferred the post-planting habitat and were a mixture of open, water- and woody vegetation-associated species (Table 7). Partial RDA of the selected variables produced a significant model ($F_{1,7} = 2.82$, $P = 0.008$) and explained 10 per cent of the variation in species composition, which was due to only one variable: the presence of understory trees post-planting. The covariable latitude explained a further 6 per cent of the variation ($F_{1,7} = 2.05$, $P = 0.01$).

Discussion

Effect of afforestation on ground-dwelling spiders

Increased total spider species richness in open and hedgerow plots and the change in spider species composition were concurrent with changes in habitat and likely to be a result of the increased shade provided by canopy cover and the increased ground layer structure provided by vegetation and litter cover, from the planted trees. Structural complexity created by vegetation and litter cover increases the habitat for spider diversity, as they increase web-attachment points, prey abundance and shelter from predators (Gunnarsson, 1983; Greenstone, 1984; Uetz, 1991; Gunnarsson, 1996; Dennis *et al.*, 1998; Castro and Wise, 2009). The sites also retained the open specialist spider fauna of the grassland habitat and continued to support high abundances of these species in the open plots, although the ecology of the dominant species differed. Prior to afforestation, *E. atra* was dominant, this is a pioneer species commonly found in intensively farmed

Table 6 Indicator species analysis of ground-dwelling spiders within open vs hedgerow plots pre-planting and within open vs hedgerow plots post-planting

Species	Habitat association	Pre-planting		Post-planting	
		Open	Hedge	Open	Hedge
<i>B. gracilis</i>	Habitat generalist	62*	11	-	-
<i>M. fuscipes</i>	Forest specialist	0	55**	15	65*
<i>O. fuscus</i>	Habitat generalist	45*	2	-	-
<i>P. pullata</i>	Open specialist	60*	0	-	-
<i>E. atra</i>	Open specialist	-	-	61*	0
<i>E. hiemalis</i>	Forest specialist	-	-	0	44*
<i>O. retusus</i>	Habitat generalist	-	-	51*	1

Numbers represent indicator value percentages.

* $P < 0.05$, ** $P < 0.01$.

grasslands (Downie *et al.*, 2000; Cole *et al.*, 2003). After afforestation, *P. amentata* was the dominant species, which is usually found in the litter layer of humid open habitats (Alderweireldt and Maelfait, 1987; Nolan, 2008). This change in species richness, composition and dominance reflects the initial changes in habitat caused by afforestation. The conversion of grassland to forest habitat was also concurrent with the cessation of livestock

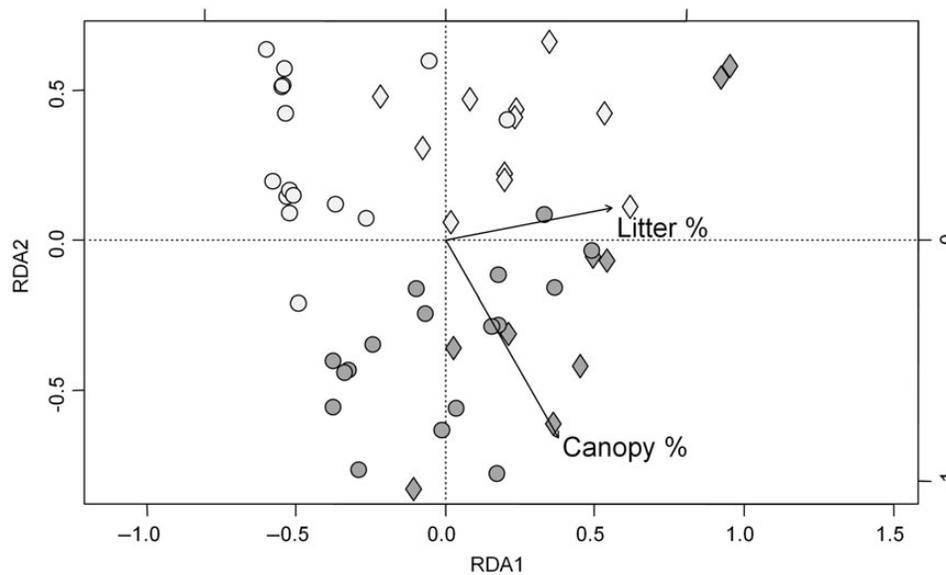


Figure 2 Partial RDA of ground-dwelling spider species composition. Axis 1: $R^2 = 0.03$, $F_{1,46} = 4.18$, $P = 0.0002$. Axis 2: $R^2 = 0.02$, $F_{1,46} = 2.86$, $P = 0.0002$. Open circles represent open plots pre-planting, closed circles represent open plots post-planting, open diamonds represent hedgerow plots pre-planting, closed diamonds represent hedgerow plots post-planting.

Table 7 Indicator species analysis of hoverfly species pre-planting vs post-planting

		Pre-planting	Post-planting
<i>E. pertinax</i>	Water associated	0	60*
<i>E. luniger</i>	Open associated	0	50*
<i>H. hybridus</i>	Water associated	0	60*
<i>M. lasiophthalma</i>	Woody vegetation associated	0	50*
<i>P. peltatus</i>	Water associated	1	62*
<i>X. sylvarum</i>	Woody vegetation associated	0	50*

Numbers represent indicator value percentages.

* $P < 0.05$.

grazing, this is known to reduce ground disturbance and allow the structural diversity of field layer vegetation to increase, which benefits some spider species (Dennis *et al.*, 1998; Oxbrough *et al.*, 2006b). Therefore, it is possible that the release from grazing pressure could also be influencing ground-dwelling spider species in these sites.

Increased shade and litter cover from the planted trees is also likely to have positively influenced forest specialist species richness as well as the structural changes in the vegetation layers where ground vegetation decreased and lower field layer vegetation increased. The shade provided by planted trees during the early stages of canopy development can provide adequate shelter, even before complete canopy closure, to stabilize the microclimate and increase the suitability of these sites for forest specialist species (Pollard, 1968; McIver *et al.*, 1992; Oxbrough *et al.*, 2006b).

Prior to afforestation, the hedgerows plots supported a different species composition than open habitat plots with high

abundance of forest specialist species such as *M. fuscipes*. This finding supports the theory of the importance of field margin hedgerows (Oxbrough *et al.*, 2006b) as a refuge for forest specialist species in predominantly agricultural landscapes. Hedgerows provide important landscape connectivity across small and fragmented forest areas and are an important factor in the capacity of these forests to support biodiversity (Joyce *et al.*, 1999; Hinsley and Bellamy, 2000; Holland and Fahrig, 2000; Pithon *et al.*, 2005).

There were few spider species associated with open or hedgerow plots pre-planting indicating that the species present prior to planting persisted within the early post-planting habitat. The additional species present post-afforestation included generalist species, which can occur in a variety of open and forested habitats and are less important when considering the value of a habitat for species diversity. However, a number of other species of interest were present. Two of the species that preferred the open plots post-planting require damp open habitats: *Lophomma punctatum* (Blackwall) is found among litter and low vegetation in wetland habitats and *Pirata latitans* (Blackwall) occurs in open marsh and fen habitats (van Helsdingen, 1996; van Helsdingen, 1998; Nolan, 2008). The vegetation and moisture requirements of these species may mean that initial stages of afforestation in these sites provide suitable habitat; however, they are unlikely to persist once the forest canopy closes as light, moisture and ground vegetation diversity will decrease (Anderson *et al.*, 1969; Hill, 1979; Avon *et al.*, 2010). Three forest specialist species, *Diplocephalus latifrons* (O.P.-Cambridge), *M. fuscipes* and *Tenuiphantes zimmermanni* Bertkau, and one shade-associated species *Bathypantes nigrinus* (Westring), which are typically found in the litter layer in woodland habitats (Roberts, 1993; Harvey *et al.*, 2002; Nolan, 2008), were associated with the open plots post-planting indicating their increased suitability for species requiring forest habitats. Hedgerow plots shared seven species with open plots that were related to the changes in habitat post-planting, including *B. nigrinus* and *D. latifrons*. However, *M. fuscipes* and *Erigonella*

hiemalis (Blackwall) still showed a higher affinity with hedgerows in the afforested sites compared with the open plots, indicating that hedgerows continued to provide important habitat during the first 7 years post-planting and should be retained in afforestation.

The effect of afforestation on hoverflies

The difference in hoverfly species composition following afforestation was associated with increased tree cover, although there was a mixture of open, woody vegetation and water-associated species both prior to and following afforestation. Prior to afforestation, the dominant species was *P. clypeatus*, which is associated with water habitats provided by undrained land and wet ditches and could explain its dominance here, where three out of the five sites contained streams and water-saturated ground (Speight, 2008). The streams were still present post-afforestation; however, surface water habitats, which are important for many hoverfly species, can be affected by forestry practices such as land drainage, which is used to prepare land for afforestation and often results in the reduction and quality of these habitats (Gittings et al., 2006; Smith et al., 2006). The prevalence of *R. campestris* after afforestation reflects the surrounding environment of farmland used for grazing, as the larvae of this species feed almost exclusively on cow dung in Ireland (Speight, 2008), although adults of this species also forage at the edges of broadleaf woodland (Stubbs and Falk, 1983). Therefore, planting native broadleaf trees in agricultural land is likely to benefit this species.

There were no species of hoverfly associated with the pre-planting habitat suggesting that, similar to the effect seen for ground-dwelling spiders, these species were not lost post-afforestation and that new species were present in the assemblage. *Eristalis pertinax* (Scopoli), *Helophilus hybridus* Loew and *P. peltatus* (Meigen) occur in wet habitats including wetlands, seasonally flooded grassland, river banks and water-filled ditches. *H. hybridus* in particular prefers tall herb vegetation along rivers and streams, and *P. peltatus* can occur in the open habitat of young plantations, and where humid open areas occur around plantation forests. These species are negatively affected by land drainage, which can accompany afforestation; therefore, provision for wet habitats in afforestation sites is important. *Xylota sylvorum* (L.) is an anthropophobic species, which is strongly associated with broadleaf forests and is not found in cultivated areas, conifer plantations or the standard farmland landscape of green fields plus hedges in Ireland. The presence of this species here may reflect the mixture of tree species planted on the sites, which included broadleaf species, and indicates the importance of planting native tree species for biodiversity conservation. *Melangyna lasiophthalma* (Zetterstedt) and *Eupeodes luniger* (Meigen) occur in a variety of open and forest habitats. The generalist nature of these two species means they are unlikely to require specific habitat management.

At this early stage in the forest cycle, there were large gaps in the canopy meaning the habitat could still be suitable for open-associated species, which could explain the lack of an effect on species richness. However, we would expect the species richness of woody vegetation-associated species to increase after planting. Previous research in grassland sites found that 5 years after afforestation with Sitka spruce, the diversity of hoverfly species associated with open habitats decreased and the diversity of woody vegetation-associated species increased (Smith et al., 2006). The

mixture of open, woody vegetation and water-associated species both pre- and post-planting in this study may be related to the confounding effect of adult hoverfly movements across landscapes, where migratory and foraging movement can result in species being recorded outside of their primary habitat (Castella et al., 1994; Branquart and Hemptinne, 2000; Gittings et al., 2006). Four of the five study sites had forested areas within 1 km before afforestation meaning that woody vegetation-associated species from these areas could have been recorded whilst foraging or passing through grassland habitats. Furthermore, both local habitat factors and landscape factors influence hoverfly species composition, and hoverfly feeding guilds also respond to land use at differing spatial scales (Meyer et al., 2009). Local factors, particularly site management, which affect vegetation height and the species richness of flowering plants, influence hoverflies in grasslands, whilst road length and forest area are important landscape factors (Sjödin et al., 2008; Meyer et al., 2009). Therefore, differences in site management, the availability of flowering plants and the area of forest in the surrounding landscape can all hoverfly species composition.

Long-term monitoring

Long-term monitoring can present difficulties when trying to control for variation over the course of the study (Gardner, 2010). The sites used in the current study were privately owned, and management was not homogenous across sites, particularly in relation to planted tree species. In the present study, 7 years into the forest cycle, the canopy was still quite open and well-developed understorey vegetation was present in both coniferous and broadleaf areas. It has been shown that prior to canopy closure, when there are fewer structural differences between the habitat of different canopy tree species, the ground vegetation, spider and hoverfly species assemblages are similar between conifer and broadleaf plantation forests and resemble that of the pre-planting habitat (Oxbrough et al., 2005; Smith et al., 2005; French et al., 2008). After canopy closure, there is a change in ground vegetation, microclimate and light levels, which can differ between broadleaf and coniferous forests and greatly influences species richness and composition (Wallace and Good, 1995; Humphrey et al., 1999; Oxbrough et al., 2005; Smith et al., 2005; French et al., 2008). Therefore, the differences in planted tree species are less likely to affect spider and hoverfly species in the early stages of the forest cycle studied here compared with later stages, where they may present confounding effects in future studies of these sites. Additionally, before-after-control-impact (BACI) design experiments can be difficult to implement, and it was not possible to establish control sites in this study, meaning that this research represents a before-after-impact study. Therefore, the lack of control sites should be considered before making generalizations from these results. Despite this, our results are similar to what we would expect based on findings from previous studies of afforestation in Ireland. For example, the differences in ground-dwelling spider species richness are the same as those found by Oxbrough et al., (2006a) in their study of afforestation using the chronosequence method. Furthermore, the response of species composition to afforestation and higher abundance of spider species such as *M. fuscipes*, *Palliduphantes ericaeus*, *Pocadicnemis pumila*, *Robertus lividus* and *Walckenaeria acuminata* and hoverfly species such as *R. campestris* and *M. lasiophthalma* in the planted plots mirror

the results of chronosequence studies on spiders (Oxbrough *et al.*, 2006b) and hoverflies (Smith *et al.*, 2006). This lends support to our results and means that our findings are likely to be due to afforestation rather than another factor associated with temporal variation.

Implications of afforestation

Protecting and incorporating habitats, such as hedgerows, which enhance biodiversity will contribute to the objectives of sustainable forest management (Gittings *et al.*, 2006; Oxbrough *et al.*, 2006a; Smith *et al.*, 2008). The species of tree selected for planting may influence the biodiversity value of afforested areas, particularly in plantation forests of exotic conifer species, as when canopy closure occurs the species richness of ground-dwelling spiders and hoverflies has been shown to decrease due to the loss of open specialist species (Gittings *et al.*, 2006; Oxbrough *et al.*, 2006a). It is important that afforestation plans consider not only the area and type of habitats but also their quality and that forest management considers factors related to increased species diversity at all stages of the forest cycle. The current study examines spider and hoverfly diversity 7 years after afforestation, and it is likely that as the forests mature there will be further impacts on spider and hoverfly species in these sites due to changes in light, microclimate and vegetation (Humphrey *et al.*, 1999; Ferris *et al.*, 2000; Smith *et al.*, 2005). Further monitoring is required throughout the forest cycle to fully understand the impact of afforestation on the diversity of these taxa.

The biodiversity benefits of planting forests on agricultural land could also make an important contribution to ecosystem services through the biological control of crop pests and the pollination of arable crops and wildflowers in nearby fields. Forested areas and hedgerows support diverse and abundant populations of predatory arthropods such as spiders and hoverflies, which can disperse into crop fields and may be useful in the biological control of crop pests (Peng *et al.*, 1993; Kajak, 2007; Bennewicz, 2011). Furthermore, hoverflies may be the second most important pollinators after wild bees (Larson *et al.*, 2001) and can contribute to enhanced pollination services (Fontaine *et al.*, 2006; Albrecht *et al.*, 2012; Jauker *et al.*, 2012).

Main conclusions

Within the first 7 years of afforestation, the habitat of agricultural grassland sites changed to provide a mosaic of open and shaded areas with increased structural variation created by litter and vegetation cover. These sites became suitable for a wider range of ground-dwelling spider species with differing ecological requirements. The habitat change did not impact on hoverfly species in the same way due to their migratory behaviour and their response to landscape scale factors, which can mask the effect of site level changes. However, in general afforestation in these sites increased the diversity of habitats and available niches, which afforded these areas the opportunity to increase arthropod biodiversity at both the site and landscape level. The retention of hedgerow habitats was also an important contributor to biodiversity in these forests. Within-site assessment of the effect of afforestation had not been researched in Ireland until now. In this context, the results of this study provide an important step in understanding the impact of afforestation and provide evidence of the biodiversity

benefits and ecosystem services conferred by afforestation in agricultural grassland habitats, where the majority of planned afforestation is likely to take place.

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Conflict of interest statement

None declared

References

- Albrecht, M., Schmid, T., Hautier, Y. and Müller, C. 2012 Diverse pollinator communities enhance plant reproductive success. *P. R. Soc. B.* **7**, 4845–4852.
- Alderweireldt, M. and Maelfait, J.P. 1987 *Life Cycle, Habitat Choice and Distribution of Pardosa amentata (Clerck, 1757) in Belgium (Araneae: Lycosidae)*. Xème Colloque Européen d'Arachnologie Rennes, 7–15. pp.
- Anderson, R.C., Loucks, O.L. and Swain, A.M. 1969 Herbaceous Response to Canopy Cover, Light Intensity, and Throughfall Precipitation in Coniferous Forests. *Ecology*. **50**, 255–263.
- Anon. 2008 *Irish Forests - A Brief History*. Department of Agriculture, Food and Marine, Government of Ireland.
- Anon. 2010 *Afforestation Statistics*. Department of Agriculture, Food and Marine, Government of Ireland.
- Anon. 2012 *Afforestation Scheme*. Department of Agriculture, Food and Marine, Government of Ireland.
- Avon, C., Bergès, L., Dumas, Y. and Dupouey, J.-L. 2010 Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. *For. Ecol. Manag.* **259**, 1546–1555.
- Bennewicz, J. 2011 Aphidivorous hoverflies (Diptera: Syrphidae) at field boundaries and woodland edges in an agricultural landscape. *Pol. J. Ecol.* **80**, 129–149.
- Benton, T.G., Vickery, J.A. and Wilson, J.D. 2003 Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18**, 182–188.
- Berndt, L., Brockerhoff, E. and Jactel, H. 2008 Relevance of exotic pine plantations as a surrogate habitat for ground beetles (Carabidae) where native forest is rare. *Biodivers. Conserv.* **17**, 1171–1185.
- Blanchet, F.G., Legendre, P. and Borcard, D. 2008 Forward selection of explanatory variables. *Ecology*. **89**, 2623–2632.
- Branquart, E. and Hemptinne, J.-L. 2000 Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). *Ecography*. **23**, 732–742.
- Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C.P. and Sayer, J. 2008 Plantation forests and biodiversity: oxymoron or opportunity? *Biodivers. Conserv.* **17**, 925–951.
- Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K. and Walters, B. 2006 Planted forests and biodiversity. *J. Forest.* **104**, 65–77.

- Castella, E., Speight, M.C.D., Obrdlik, P., Schneider, E. and Lavery, T. 1994 A methodological approach to the use of terrestrial invertebrates for the assessment of alluvial wetlands. *Wetlands Ecol. Manag.* **3**, 17–36.
- Castro, A. and Wise, D.H. 2009 Influence of fine woody debris on spider diversity and community structure in forest leaf litter. *Biodivers. Conserv.* **18**, 3705–3731.
- Clarke, R.D. and Grant, P.R. 1968 An experimental study of the role of spiders as predators in a forest litter community. *Part 1. Ecology.* **49**, 1152–1154.
- COFORD Council. 2009 *Forestry 2030*. Department of Food, Agriculture and the Marine.
- Cole, L. et al. 2003 Comparing the effects of farming practices on ground beetle (Coleoptera: Carabidae) and spider (Araneae) assemblages of Scottish farmland. *Biodivers. Conserv.* **14**, 441–460.
- Dennis, P., Young, M. and Gordon, I. 1998 Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecol. Entomol.* **23**, 253–264.
- Downie, I.S. et al. 2000 Modelling populations of *Erigone atra* and *E. dentipalpis* (Araneae: Linyphiidae) across an agricultural gradient in Scotland. *Agric. Ecosyst. Environ.* **80**, 15–28.
- Dray, S., Legendre, P. and Blanchet, F.G. 2012 *Packfor: Forward Selection with permutation* (Canoco p.46). http://r-forge.r-project.org/R/?Group_id=195 (accessed on 20 June, 2013).
- Dufrene, M. and Legendre, P. 1997 Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* **67**, 345–366.
- European Commission. 2011 *Forestry in the EU and the World – A statistical portrait*. Publications Office of the European Union.
- FAO. 2011 *The European Forest Sector Outlook Study II: 2010–2030*. United Nations Environment Programme.
- Ferris, R., Peace, A.J., Humphrey, J.W. and Broome, A.C. 2000 Relationships between vegetation, site type and stand structure in coniferous plantations in Britain. *For. Ecol. Manag.* **136**, 35–51.
- Fontaine, C., Dajoz, I., Meriguet, J. and Loreau, M. 2006 Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biol.* **4**, e1.
- Forest Europe, UNECE, FAO. 2011 *State of Europe's Forests 2011*. United Nations Economic Commission for Europe.
- Frank, T. and Reichhart, B. 2004 Staphylinidae and Carabidae overwintering in wheat and sown wildflower areas of different age. *Bull. Entomol. Res.* **94**, 209–217.
- Frazer, G., Canham, C. and Lertzman, K. 1999 *Gap Light Analyzer (GLA), Version 2.0: Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs, Users Manual and Program Documentation*. Simon Fraser University and the Institute of Ecosystem Studies.
- French, L.J., Smith, G.F., Kelly, D.L., Mitchell, F.J.G., O'Donoghue, S., Iremonger, S.F. and McKee, A-M. 2008 Ground flora communities in temperate oceanic plantation forests and the influence of silvicultural, geographic and edaphic factors. *For. Ecol. Manag.* **255**, 476–494.
- Gardner, T. 2010 *Monitoring Forest Biodiversity: Improving Conservation through Ecologically-Responsible Management*. Earthscan.
- Gittings, T., O'Halloran, J., Kelly, T. and Giller, P. 2006 The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. *For. Ecol. Manag.* **237**, 290–300.
- Gotelli, N.J. and Colwell, R.K. 2001 Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391.
- Greenstone, M.H. 1984 Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. *Oecologia.* **62**, 299–304.
- Gunnarsson, B. 1983 Winter mortality of spruce-living spiders: effect of spider interactions and bird predation. *Oikos.* **40**, 226–233.
- Gunnarsson, B. 1996 Bird predation and vegetation structure affecting spruce-living arthropods in a temperate forest. *J. Anim. Ecol.* **65**, 389–397.
- Haarto, A. and Kerppola, S. 2007 *Suomen kukkakärpaset ja lähialueiden lajeja [Finnish hoverflies and some species in adjacent countries]*. Otavan Kirjapaino Oy.
- Hartley, M.J. 2002 Rationale and methods for conserving biodiversity in plantation forests. *For. Ecol. Manag.* **155**, 81–95.
- Harvey, P.R., Nellist, D.R. and Telfer, M.G. 2002 *Provisional Atlas of British Spiders (Arachnida, Araneae)*. Biological Records Centre, Natural Environment Research Council.
- Hill, M.O. 1979 The development of a flora in even-aged plantations. In *The Ecology of Even-Aged Forest Plantations*. Ford, E.D., Malcolm, D.C. and Atterson, J. (eds). Institute of Terrestrial Ecology, pp. 175–192.
- Hinsley, S.A. and Bellamy, P.E. 2000 The influence of hedge structure, management and landscape context on the value of hedgerows to birds: A review. *J. Environ. Manag.* **60**, 33–49.
- Holland, J. and Fahrig, L. 2000 Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. *Agric. Ecosyst. Environ.* **78**, 115–122.
- Humphrey, J.W., Hawes, C., Peace, A.J., Ferris-Kaan, R. and Jukes, M.R. 1999 Relationships between insect diversity and habitat characteristics in plantation forests. *For. Ecol. Manag.* **113**, 11–21.
- Hunter, M.L. 2000 *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press.
- Jauker, F., Bondarenko, B., Becker, H.C. and Steffan-Dewenter, I. 2012 Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agric. For. Entomol.* **14**, 81–87.
- Joyce, K.A., Holland, J.M. and Doncaster, C.P. 1999 Influences of hedgerow intersections and gaps on the movement of carabid beetles. *Bull. Entomol. Res.* **89**, 523–531.
- Kajak, A. 2007 Effects of forested strips on spider assemblages in adjacent cereal fields: dispersal activity of spiders. *Pol. J. Ecol.* **55**, 691–704.
- Landis, D.A., Wratten, S.D. and Gurr, G.M. 2000 Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* **45**, 175–201.
- Larson, B.M.H., Kevan, P.G. and Inouye, D.W. 2001 Flies and flowers: taxonomic diversity of anthophiles and pollinators. *Can. Entomologist.* **133**, 439–465.
- Le Coeur, D., Baudry, J., Burel, F. and Thenail, C. 2002 Why and how we should study field boundary biodiversity in an agrarian landscape context. *Agric. Ecosyst. Environ.* **89**, 23–40.
- Legendre, P. and Gallagher, E. 2001 Ecologically meaningful transformations for ordination of species data. *Oecologia.* **129**, 271–280.
- Marshall, E.J.P. and Mooney, A.C. 2002 Field margins in northern Europe: their functions and interactions with agriculture. *Agric. Ecosyst. Environ.* **89**, 5–21.
- McCune, B. and Mefford, M.J. 2011 *PC ORD. Multivariate Analysis of Ecological Data. Version 6*. MjM Software.
- McIver, J.D., Parsons, G.L. and Moldenke, A.R. 1992 Litter spider succession after clear-cutting in a western coniferous forest. *Can. J. Forest Res.* **22**, 984–992.
- MCPFE. 1993 *Second Ministerial Conference on the Protection of Forests in Europe*.
- Meyer, B., Jauker, F. and Steffan-Dewenter, I. 2009 Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl. Ecol.* **10**, 178–186.
- Nolan, M. 2008 *Database of Irish Spiders (Araneae)*. Irish Wildlife Manuals. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government.

- Norris, K.C. 1999 Quantifying change through time in spider assemblages: sampling methods, indices and sources of error. *J. Insect Conserv.* **3**, 309–325.
- Oksanen, J. et al. 2012 *Vegan: Community Ecology Package*. <http://CRAN.R-project.org/package=vegan> (accessed on 20 June, 2013).
- Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S. and Smith, G.F. 2005 Structural indicators of spider communities across the forest plantation cycle. *For. Ecol. Manag.* **212**, 171–183.
- Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S. and Kelly, T.C. 2006a The influence of open space on ground-dwelling spider assemblages within plantation forests. *For. Ecol. Manag.* **237**, 404–417.
- Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S. and Kelly, T.C. 2006b The initial effects of afforestation on the ground-dwelling spider fauna of Irish peatlands and grasslands. *For. Ecol. Manag.* **237**, 478–491.
- Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S. and Kelly, T.C. 2007 Biodiversity of the ground-dwelling spider fauna of afforestation habitats. *Agric. Ecosyst. Environ.* **120**, 433–441.
- Oxbrough, A., French, V., Irwin, S., Kelly, T.C., Smiddy, P. and O'Halloran, J. 2012 Can mixed species stands enhance arthropod diversity in plantation forests? *For. Ecol. Manag.* **270**, 11–18.
- Pawson, S.M., Brockerhoff, E.G., Meenken, E.D. and Didham, R.K. 2008 Non-native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. *Biodivers. Conserv.* **17**, 1127–1148.
- Pearce, J.L. and Venier, L.A. 2006 The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. *Ecol. Indicators*. **6**, 780–793.
- Peng, R.K., Incoll, L.D., Sutton, S.L., Wright, C. and Chadwick, A. 1993 Diversity of airborne arthropods in a silvoarable agroforestry system. *J. Appl. Ecol.* **30**, 551–562.
- Pinheiro, J., Bates, D., DebRoy, S. and Sarkar, D. 2013 *Package 'nlme'*. <http://cran.r-project.org/web/packages/nlme/nlme.pdf> (accessed on 20 June, 2013).
- Pinzón, J. and Spence, J. 2010 Bark-dwelling spider assemblages (Araneae) in the boreal forest: dominance, diversity, composition and life-histories. *J. Insect Conserv.* **14**, 439–458.
- Pithon, J.A., Moles, R. and O'Halloran, J. 2005 The influence of coniferous afforestation on lowland farmland bird communities in Ireland: different seasons and landscape contexts. *Landscape Urban Plan.* **71**, 91–103.
- Platnick, N.I. 2012 *The World Spider Catalog, Version 13.0*. The American Museum of Natural History.
- Pollard, E. 1968 Hedges. IV. a comparison between the Carabidae of a hedge and field site and those of a woodland glade. *J. Appl. Ecol.* **5**, 649–657.
- R Core Team. 2012 *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Ripley, B., Venables, B., Hornik, K., Gebhardt, A. and Firth, D. 2013 *Package 'MASS'*. <http://cran.r-project.org/web/packages/MASS/MASS.pdf> (accessed on 20 June, 2013).
- Roberts, M.J. 1993 *The Spiders of Great Britain and Ireland*. Harley Books.
- Sjödin, N.E., Bengtsson, J. and Ekblom, B. 2008 The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *J. Appl. Ecol.* **45**, 763–772.
- Smith, G.F., Gittings, T., Wilson, M., French, L.J., Oxbrough, A. and O'Donoghue, S. et al. 2005 Assessment of Biodiversity at Different Stages of the Forest Cycle. *Bioforest Final Report*. Environmental Protection Agency (EPA) and the Council for Forest Research and Development (COFORD).
- Smith, G.F., Gittings, T., Wilson, M., Oxbrough, A., Iremonger, S. and O'Donoghue, S. et al. 2006 Biodiversity Assessment of Afforestation Sites. *Bioforest Final Report*. Environmental Protection Agency (EPA) and the Council for Forest Research and Development (COFORD).
- Smith, G.F., Gittings, T., Wilson, M., French, L., Oxbrough, A. and O'Donoghue, S. et al. 2008 Identifying practical indicators of biodiversity for stand-level management of plantation forests. *Biodivers. Conserv.* **17**, 991–1015.
- Sommaggio, D. 1999 Syrphidae: can they be used as environmental bioindicators? *Agric. Ecosyst. Environ.* **74**, 343–356.
- Speight, M.C.D. 2000 *Syrph the Net: a Database of Biological Information about European Syrphidae (Diptera) and its Use in Relation to Conservation of Biodiversity. Biodiversity: the Irish Dimension*. The Royal Irish Academy, 156–171 pp.
- Speight, M.C.D. 2008 *Database of Irish Syrphidae (Diptera)*. Irish Wildlife Manuals. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government.
- Speight, M.C.D., Castella, E., Sarthou, J.-P. and Monteil, C. 2004 *The Database of European Syrphidae*. Syrph the Net Publications.
- Stubbs, A.E. and Falk, S.J. 1983 *British Hoverflies: An Illustrated Identification Guide*. British Entomological and Natural History Society.
- Symondson, W.O.C., Sunderland, K.D. and Greenstone, M.H. 2002 Can generalist predators be effective biocontrol agents? *Annu. Rev. Entomol.* **47**, 561–594.
- ter Braak, C.J.F. 1994 Canonical community ordination. Part 1: basic theory and linear methods. *Ecoscience*. **1**, 127–140.
- Uetz, G. 1991 Habitat structure and spider foraging. In *Habitat Structure: The Physical Arrangement of Objects in Space*. Bell, S., McCoy, E. and Mushinsky, H. (eds). Chapman and Hall.
- United Nations Conference on Environment and Development. 1992 Agenda 21, the Rio Declaration on Environment and Development, the Statement of Forest Principles, the United Nations Framework Convention on Climate Change and the United Nations Convention on Biological Diversity.
- van Helsdingen, P.J. 1996 The spider fauna of some Irish floodplains. *The Irish Naturalists' Journal*. **25**, 285–293.
- van Helsdingen, P.J. 1998 The spider fauna of Scragh Bog in Co Westmeath, Ireland (Arachnida: Araneae). *Zoologische Verhandlungen*. **323**, 407–415.
- van Veen, M.P. 2004 *Hoverflies of Northwest Europe*. KNNV Publishing.
- Wallace, H.L. and Good, J.E.G. 1995 Effects of afforestation on upland plant communities and implications for vegetation management. *For. Ecol. Manag.* **79**, 29–46.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. and Smith, G.M. 2009 *Mixed Effects Models and Extensions in Ecology with R*. Springer Science + Business Media, LLC.