

Ground-dwelling spider diversity in rare European oak and yew woodlands and the impact of grazing

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Abstract In Ireland only 2 % of the total land area is native woodland, which tends to be small and fragmented. Killarney National Park in south-west Ireland contains the most extensive semi-natural woodland in the country, and includes oak (*Quercus petraea*) and yew (*Taxus baccata*) woodlands which are internationally protected. Here, over-grazing by large populations of red deer (*Cervus elaphus*) and Asian sika deer (*Cervus nippon*) have lead to changes in overstorey and understorey vegetation species composition and structure. This study presents the first description of ground-dwelling spider fauna in the rare woodlands of Killarney National Park and asked (1) do these rare woodlands support rare or specialist species, (2) does deer grazing have an effect on spider abundance, richness and species composition in the park, (3) what management recommendations can be made for deer in the park? Active ground-dwelling spiders were sampled in the oak and yew woodlands of the park by pitfall trapping within deer-proof exclosures and adjacent grazed controls. Four spider species classified as vulnerable were collected from these woodlands: *Agyreta subtilis* occurred in the oak and yew woodlands but *Saaristoa firma*, *Tapinocyba insecta* and *Walckenaeria dysderoides* were collected only in the oak woodland. Killarney National Park may be important for five species, not typically found in plantation forests, which rely on nationally scarce habitats. Deer grazing was linked with decreased ground-dwelling spider abundance and species richness in the oak woodland by reducing structural diversity of the habitat. Fewer effects of grazing were detected in the yew woodland,

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possibly due to increased culling in the area. Results provide evidence that controlling deer grazing is important for woodland biodiversity in Killarney National Park. Incorporating deer into woodland management in the park is recommended to maintain low grazing levels which will prevent woodland closure and maintain ground vegetation diversity.

Keywords Conservation · Deer · Grazing · Killarney National Park · Spider · Woodland

Introduction

Currently the forest cover of the European continent stands at 45 % of the total land area and 70 % of this is classified as semi-natural woodland (Forest Europe et al. 2011). In contrast, the forest cover of Ireland, which has historically undergone vast deforestation and modification of its natural environment, is just 11 % (737,000 ha) of the total land area (Forest Europe et al. 2011). The majority of this is comprised of exotic conifer plantations (513,000 ha) (Forest Europe et al. 2011) and only 11 % of the total forest cover is semi-natural woodland (82,000 ha), meaning just 2 % of the total land cover is semi-natural woodland (Anon 2007). These remnants of semi-natural woodland tend to be small and fragmented, with approximately 68 % less than 10 ha (Perrin et al. 2008).

Killarney National Park in south-west Ireland has been a designated UNESCO biosphere reserve since 1982 (UNESCO 2001) and contains the most extensive areas of semi-natural woodland in Ireland (1,400 ha) (NPWS 2005). Several areas of internationally important woodland are found in the park, including yew (*Taxus baccata*) and acidophilus sessile oak (*Quercus petraea*). These two woodland types have a very limited distribution across Europe and yew woodland in particular is one of the rarest European woodland types (Perrin et al. 2006). In Ireland, yew covers just 40 ha of the land surface and sessile oak covers 7,300 ha of the land surface (Anon 2007).

The yew woodland of Killarney National Park is the largest of its kind in Ireland (25 ha) and is one of only three pure yew woodlands in Europe. Furthermore it is on an area of karst limestone pavement, making it even more unique. The scarcity of this woodland type means that the yew woodland in Killarney National Park is a priority habitat under Annex I of the EU Habitats Directive (National Parks and Wildlife Service 2008). A prominent feature of this woodland and of yew woodland in general, is the paucity of field layer and shrub vegetation and the lack of regeneration, which is thought to be due to the heavy shade cast by the dense evergreen canopy (Rodwell 1991).

The acidophilus sessile oak woodlands are on Devonian sandstone and these are also included in Annex I of the EU Habitats Directive (National Parks and Wildlife Service 2008) and are considered to be the most natural sessile oak woodlands in Ireland (National Parks and Wildlife Service 2006). These woodlands are characterised by a holly (*Ilex aquifolium*) understory with *Blechnum spicant* prevalent in the field layer and support a wide diversity and abundance of bryophytes, lichens and filmy ferns (Hymenophyllaceae) (Kelly 1981). The vegetation of the oak and yew woodlands has been described in detail by Kelly (1981).

These woodlands support a population of red deer (*Cervus elaphus*) which may have been present in County Kerry since the Neolithic period (Carden et al. 2011, 2012). There is also a population of the more recently introduced Asian sika deer (*Cervus nippon*)

(Carden et al. 2011, 2012). The estimated deer density in the Killarney area is 5–28 animals per km² (Purser et al. 2009). This appears to be average compared to reports from other areas of Ireland, e.g. 5–25 animals per km² in Wicklow and 16 animals per km² from Baronscourt Estate in County Tyrone (Purser et al. 2009), although in general there is little information available on deer densities in Ireland.

Grazing pressure from large ungulates such as deer can have far reaching ecological impacts by reducing the cover and diversity of field layer vegetation and decreasing the survival of tree saplings. This not only changes the species composition of the overstorey but also has a cascading effect on arthropods, including insects, and birds and mammals (Côté et al. 2004). In Killarney it has already been noted that grazing pressure from these large herbivores has significantly altered the woodlands by reducing the diversity of field layer vegetation and inhibiting woodland regeneration (Kelly 2002; Perrin et al. 2006, 2008, 2011).

Fencing to exclude large grazers is often used in areas where grazing intensity is a problem (Hester et al. 2000; Spooner et al. 2002) and large areas of woodland in Killarney National Park have had fences erected to exclude deer. Several long-term studies have been conducted in these exclosures to determine the impact of grazing on vegetation and tree regeneration in these woodlands (Kelly 2002; Perrin et al. 2006, 2011). Other research in the park has investigated the diversity of ground vegetation, birds and small mammals in these rare woodland habitats (Batten 1976; Kelly 1981; Smal and Fairley 1982; Lynch and McCann 2007). However, less attention has been given to other elements of their biodiversity such as arthropods and other invertebrates.

Ground-dwelling spiders are sensitive to changes in structural heterogeneity of their habitat (Uetz 1991; Oxbrough et al. 2005) making them a useful group for studying changes in diversity as a result of habitat disturbance. Consequently they have been used to determine the effects of grazing on invertebrate communities in grasslands and forests (Gibson et al. 1992a, b; Miyashita et al. 2004). Spiders play an important role in the functioning of all ecosystems and form an integral part of food webs as both predators of other arthropods and prey for insectivorous birds and small mammals (Wise 1993; Gunnarsson 1983; Clarke and Grant 1968). Additionally, they are ubiquitous in the ground layer of woodlands, easily caught by pitfall trapping and taxonomically well-known.

In this study we present the first study of ground-dwelling spider diversity in the rare woodland habitats of Killarney National Park. Spider assemblages were sampled in oak and yew woodland in the park and the following research questions were addressed:

1. Do these rare woodlands support rare species or specialist species which are range-restricted or rely on scarce habitats?
2. Does deer grazing have an effect on spider abundance, richness and species composition in the park?
3. What recommendations can be made for managing deer grazing in the park to enhance biodiversity?

Methods

Study sites

One oak woodland and one yew woodland were sampled in the summer of 2011 in Killarney National Park (longitude 9°34', latitude 52°1') (Fig. 1). Derrycunihy wood in the

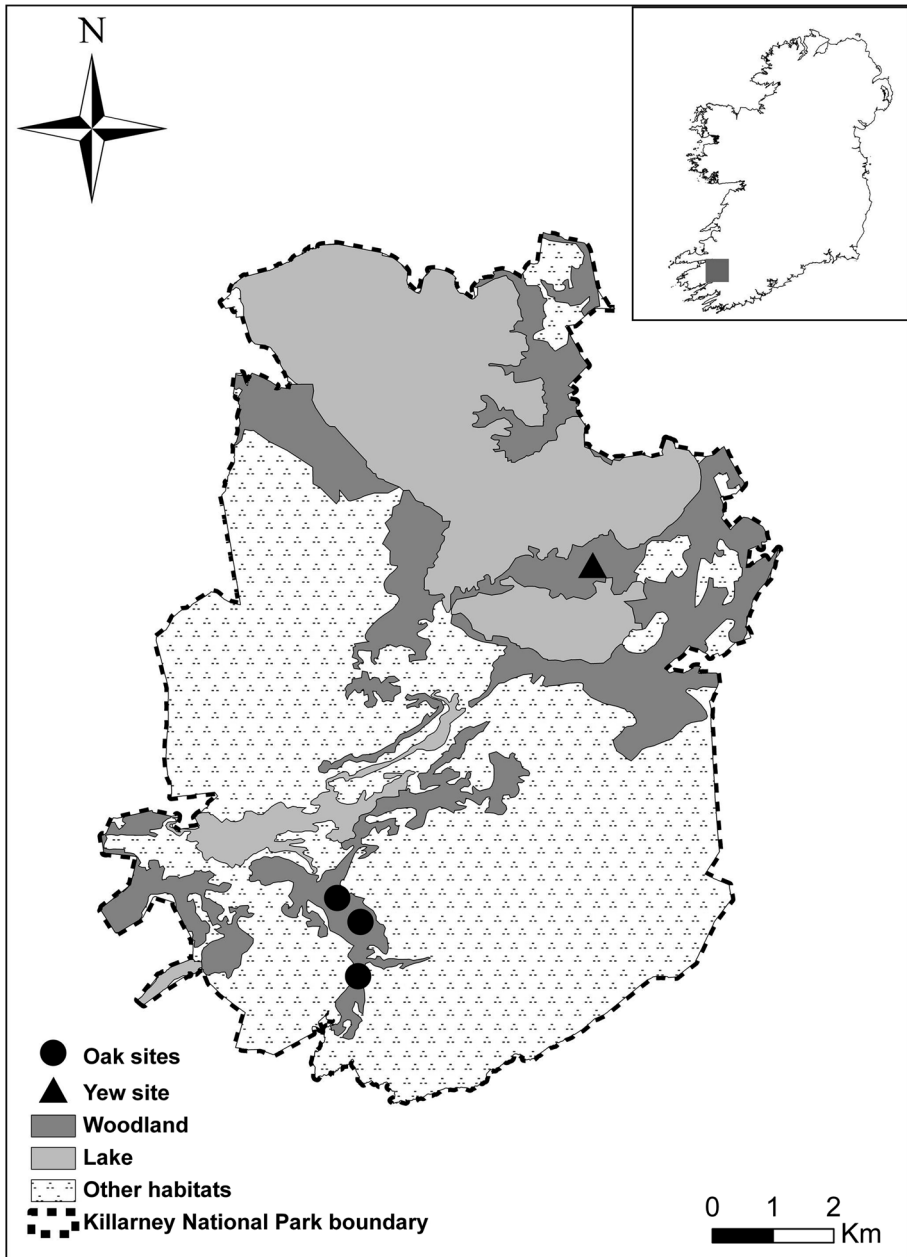


Fig. 1 Location of Killarney National Park in Ireland and the distribution of sampling sites within the Park. Three paired enclosure and control sites in sessile oak woodland (*filled circle*) and one paired enclosure and control site in yew woodland (*filled triangle*)

south of the National Park is acidophilus Atlantic oak woodland and had 11 deer exclosures erected in 2005 with open unfenced areas left between the exclosures to allow movement of deer through the area. Three of these exclosures and an adjacent control area

Table 1 Size and position of enclosure and control sites relative to one another

Site code	Woodland	Position	Enclosure size (ha)	Distance between enclosure and control (m)
DCUN	Derrycunihy	Northern oak enclosure	2.9	109
DCUM	Derrycunihy	Middle oak enclosure	10.9	197
DCUS	Derrycunihy	Southern oak enclosure	15.4	313
MCRO	Reenadinna	Yew enclosure	5.2	630

next to each enclosure were sampled and each paired enclosure and control was labelled with a site code (Table 1). The distance between the central points of each enclosure in the oak woodland was 819 m between DCUN and DCUM, 1,158 m between DCUM and DCUS, and 1,661 m between DCUN and DCUS. Reenadinna wood on the Muckross peninsula is yew woodland on a karst limestone pavement and had one enclosure erected in 2002. This enclosure, which is 5.2 ha in size, and an adjacent control area, collectively labelled MCRO, were sampled (Table 1).

The extent of the yew woodland is much less than that of the oak woodlands and is split into a north and south patch, limited on either side by lakes or geological features (i.e. changing bedrock). Additionally, the southern section of yew woodland was almost entirely fenced with a deer enclosure, meaning only the northern section was available to use as a control area. In contrast, the open unfenced areas adjacent to the enclosures in the oak woodland provided ideal control areas. Thus, the distances between the enclosure and control areas differ between the oak and yew woodlands.

A total of four sites were sampled across the two woodlands and each site consisted of two treatments: an ungrazed enclosure and an adjacent paired grazed control. The study contains a degree of pseudo-replication which could not be avoided, as only these two areas of woodland in Killarney National Park contained enclosures suitable for study.

Spider sampling

Pitfall traps were used to sample the active ground-dwelling spider fauna at the study sites. The traps were plastic cups of approximately 7 cm diameter and 9 cm high which were dug into the ground so the rim was just below the surface. The cups had drainage slits cut 1 cm from the top of the cup to allow water to escape and prevent flooding. Traps were filled to 3 cm with ethylene glycol (anti-freeze) used as a killing agent. Each trap was protected from disturbance by deer and other animals with a 10 × 10 cm wire mesh cage which was held in place by two steel pins. The mesh was made of 2 × 2 cm squares to allow the movement of invertebrates through the cage.

In each site × treatment combination three plots were placed in areas that were representative of the woodland in terms of ground vegetation, topography and canopy cover. Plots were established a minimum of 50 m apart and a minimum of 50 m from the edge of the woodland. Each plot consisted of five pitfall traps set 2 m apart in a linear arrangement.

The contents of each pitfall trap were collected every three weeks from May to August 2011, resulting in a total of four collections and 84 trapping days, and the plastic cup was placed back in the ground and filled with fresh anti-freeze. There was no trap disturbance during the whole trapping period. The contents of the traps were transferred to labelled sample bottles and stored in 70 % ethanol. Spiders were identified to species level using

Roberts (1993) and nomenclature follows The World Spider Catalog, Version 13.0 (2012). Individual species were categorised as habitat generalist, forest specialist or open habitat specialist based on Harvey et al. (2002) and Nolan (2008) and families were assigned to feeding guilds using (Uetz et al. 1999). Information from Harvey et al. (2002) and Nolan (2008) were also used to identify species which are range-restricted or rely on scarce habitats. Information from Great Britain by Dawson et al. (2008) was used to designate conservation status and identify rare species, e.g. vulnerable, threatened or endangered, as comparable data for a majority of spider species in Ireland are not currently available.

Environmental surveys

Habitat was surveyed within a 1×1 m quadrat placed over each pitfall trap. The percentage cover of bare ground, leaf/needle litter, fine woody debris (<10 cm diameter), coarse woody debris (>10 cm diameter), ground layer vegetation (0–10 cm), lower field layer vegetation (10–50 cm) and upper field layer vegetation (50–200 cm) was recorded. The depth of the leaf/needle litter was also measured and percentage canopy cover was calculated using GLA 2.0 (Frazer et al. 1999) from a hemispherical photograph taken at a height of 1.3 m.

Data analysis

The five pitfall traps and four collections were pooled for each plot and plot level data was used as the sample unit in all analyses. Sørensen dissimilarity index was used to examine the spatial turnover and differences in species richness of the spider species composition among the four study sites (Koleff et al. 2003). The dominance of each spider species were calculated separately for the oak woodland and the yew woodland. This was expressed as a percentage of the total species, based on each species overall abundance weighted by its overall frequency of occurrence among plots, using the method developed by Pinzón and Spence (2010).

Total abundance and species richness were compared between treatments in each woodland type using generalised linear mixed modelling (GLMM). This type of analysis is an extension of linear modelling which controls for the effects of nestedness where plots are nested within sites (Zuur et al. 2009). The Poisson distribution was used with the log link function, except where the data were over-dispersed, in which case the negative binomial distribution was used with the log link function. The fixed effect in the model was treatment and site was used as a random effect. Analyses were carried out separately for each woodland type. The abundance and species richness of forest specialist species and the three most abundant feeding guilds (ground runners, wandering sheet/tangle weavers and space web-builders) were also compared using the same modelling protocol.

A permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) was used to test the effect of grazing on species composition. Prior to analysis the spider species data was Hellinger transformed to reduce the influence of highly abundant species (Legendre and Gallagher 2001). This analysis was carried out separately for each woodland type, using a blocking variable for site and using 4,999 permutations.

The environmental variables measured within the 1×1 m quadrat were averaged across the five quadrats per plot and plot level data was used in all analyses. The variables were compared between treatments with GLMM to control for the effect of plots nested within sites. The Gaussian distribution with identity link function was used, treatment was the fixed effect and site was the random effect. Analyses were carried out separately for

each woodland type. Percentage cover values of variables were arcsine transformed before testing.

All analyses were conducted in R (R Core Team 2012). GLMM was carried out using the MASS package (Ripley et al. 2013) and the glmmADMB package (Fournier et al. 2012; Skaug et al. 2013), and Sørensen dissimilarity index, Hellinger transformations and PERMANOVA were carried out using the vegan package (Oksanen et al. 2012).

Results

Over the sampling period 1,133 adult spiders were collected, belonging to 66 species and 14 families (Table 6 in Appendix). Thirty of these species were classified as forest specialists, six were classified as open habitat specialists and the remaining 30 species were habitat generalists. The most abundant family was Linyphiidae (83 %) and the dominant species was *Tenuiphantes zimmermanni* in both the oak and yew woodlands (Table 2).

Spider fauna of oak woodland

A total of 59 species were captured in the oak woodland and the ten species with the highest dominance values are presented in Table 2. Four main species, *T. zimmermanni*, *Robertus lividus*, *Monocephalus fuscipes* and *Diplocephalus latifrons* dominated the total species assemblage, and, when totalled, comprised 54 % relative to the remaining of the assemblage (Table 2). The dominance values of species not presented in Table 2 each comprised ≤ 3 % of the assemblage and, when totalled, these species comprised only 11 % relative to the remaining of the total assemblage. The majority of species were classified as “least concern” by Dawson et al. (2008) and were widespread, occurring in a range of open and forest habitats. However, one specimen of *Coelotes terrestris* was collected; this species is range-restricted in Britain, occurring only in the south of England, and is associated with coarse woody debris in semi-natural woodland (Harvey et al. 2002). Four of the Linyphiid species collected here, *Agyneta subtilis*, *Saaristoa firma*, *Tapinocyba insecta* and *Walckenaeria dysderoides*, are classified as “vulnerable” in Great Britain (Dawson et al. 2008). Analysis of the species composition among the sites using the Sørensen dissimilarity index revealed that the spatial turnover and species richness were less dissimilar between the middle site, DCUM, compared with the most northern oak site, DCUN, and compared with the most southern oak site, DCUS, whereas DCUN and DCUS exhibited higher levels of dissimilarity (Table 3).

Effects of grazing in oak woodland

GLMM identified significantly greater structural diversity of ground layer habitats in the ungrazed plots compared with the grazed plots, where the cover of litter and lower field layer vegetation was higher. In contrast the grazed plots had significantly greater cover of bare ground (Table 4). GLMM also revealed a significant positive effect of the ungrazed plots compared to grazed plots on the abundance of all species, forest specialist species, space web-builder species and wandering sheet/tangle weaver species (Table 5). Total species richness was also significantly higher in the ungrazed plots compared with grazed plots, which was driven by higher species richness of wandering sheet/tangle weaver spiders. However, despite differences in abundance and species richness between

Table 2 The ten dominant species in each of the oak and yew woodlands

	Family	Habitat association	Relative frequency	Relative abundance	Dominance %
Oak					
<i>Tenuiphantes zimmermanni</i>	Linyphiidae	Forest specialist	1	0.15	22
<i>Robertus lividus</i>	Theridiidae	Habitat generalist	0.89	0.10	12
<i>Monocephalus fuscipes</i>	Linyphiidae	Forest specialist	0.94	0.08	11
<i>Diplocephalus latifrons</i>	Linyphiidae	Forest specialist	0.83	0.08	10
<i>Tenuiphantes alacris</i>	Linyphiidae	Forest specialist	0.83	0.06	8
<i>Pirata hygrophilus</i>	Lycosidae	Habitat generalist	0.72	0.06	7
<i>Agyneta subtilis</i>	Linyphiidae	Habitat generalist	0.72	0.06	6
<i>Saaristoa abnormis</i>	Linyphiidae	Habitat generalist	0.78	0.05	5
<i>Microneta viaria</i>	Linyphiidae	Forest specialist	0.89	0.04	5
<i>Agyneta ramose</i>	Linyphiidae	Forest specialist	0.67	0.04	4
Yew					
<i>Tenuiphantes zimmermanni</i>	Linyphiidae	Forest specialist	1	0.60	75
<i>Agyneta subtilis</i>	Linyphiidae	Habitat generalist	0.67	0.13	11
<i>Tenuiphantes alacris</i>	Linyphiidae	Forest specialist	0.67	0.03	3
<i>Saaristoa abnormis</i>	Linyphiidae	Habitat generalist	0.50	0.04	3
<i>Metellina menzei</i>	Tetragnathidae	Habitat generalist	0.67	0.03	2
<i>Neriere peltata</i>	Linyphiidae	Forest specialist	0.67	0.02	2
<i>Linyphia hortensis</i>	Linyphiidae	Forest specialist	0.33	0.03	1
<i>Diplostyla concolor</i>	Linyphiidae	Habitat generalist	0.33	0.02	1
<i>Harpactea hombergi</i>	Dysderidae	Forest specialist	0.33	0.01	0.4
<i>Cyclosa conica</i>	Araneidae	Forest specialist	0.17	0.01	0.2

treatments, PERMANOVA did not identify treatment as a significant factor ($F_{1,16} = 1.39$, $P = 0.17$) affecting species composition.

Spider fauna of yew woodland

A total of 20 species were collected in the yew woodland and the ten most dominant species are presented in Table 2. Dominance was heavily weighted in favour of *T. zimmermanni* and to a lesser extent *Agyneta subtilis* (Table 2), with all other species making up relatively small proportions of the assemblage. The dominance values of species not included in Table 2 each comprised $\leq 0.2\%$ relative to the assemblage and, when totalled, these species only comprised 1% relative to the remaining of the species assemblage. *Agyneta subtilis* is classified as “vulnerable” in Britain (Dawson et al. 2008), but no other species of conservation concern were collected. One specimen of *Philodromus albidus* was collected, this species is widespread in western and central Europe, but is range-restricted in Britain and confined to the south of England and its presence in Ireland was only recently discovered (Harvey et al. 2002; Cawley 2008). In terms of species composition,

Table 3 Sørensen dissimilarity index results from the four study sites (oak sites = DCUN, DCUM and DCUS, yew site = MCRO)

	DCUN	DCUM	DCUS
DCUM	0.3421053		
DCUS	0.4545455	0.3650794	
MCRO	0.6000000	0.6470588	0.6923077

Sørensen dissimilarity index revealed that the spatial turnover and species richness of the yew site was highly dissimilar compared to the three oak sites (Table 3).

Effects of grazing in yew woodland

GLMM revealed that ungrazed plots had significantly higher cover of upper field vegetation compared with grazed plots; however, there was no effect on any of the other habitat variables (Table 4). GLMM also identified significantly higher total species abundance, forest specialist species abundance and wandering sheet/tangle weaver species abundance in grazed plots compared to ungrazed plots, but there was no effect of treatment on species richness (Table 5). Again, as in the oak woodland, PERMANOVA did not identify a significant effect of treatment on species composition ($F_{1,5} = 4.01$, $P = 0.10$).

Discussion

To our knowledge these results provide the first description of the ground-dwelling spider fauna of Killarney National Park and the first insight into ground-dwelling spider diversity in semi-natural oak and yew woodland in Ireland. Furthermore, Killarney National Park provides a unique opportunity to assess the effects of grazing in extremely rare habitat types. However, it must be noted that the results should be interpreted with caution as the results come from only three oak exclosures and only one yew exclosure, meaning that pseudo-replication may be a limitation on the findings (Hurlbert 1984). Nevertheless, due to the nature of grazing studies, it is common for a number of exclosures in only one area of woodland to be sampled (Holt et al. 2013; Melis et al. 2006; Perrin et al. 2006, 2011), meaning that the results from the oak woodland could be interpreted with more confidence.

Spider fauna of oak and yew woodlands

Killarney National Park is one of the few areas in Ireland which has had continuous woodland cover since the last glacial period (Mitchell 1988). Rare and ancient woodlands often support specialised species groups, particularly for vascular plants (Hermy et al. 1999; Peterken and Game 1984). Therefore it might be expected that these woodlands could also support a distinct spider species assemblage including rare or specialist species which might not otherwise be supported in the highly anthropogenically modified landscape of Ireland. However, the dominant species in both the oak and yew woodlands were typical of a forest spider assemblage, associated with many types of broad-leaved and coniferous woodland, and the majority of species collected were of no conservation

Table 4 Mean \pm SE for habitat variables from plots (n) in each woodland type \times treatment combination

	Oak				Yew				
	Ungrazed ($n = 9$)		Grazed ($n = 9$)		Ungrazed ($n = 3$)		Grazed ($n = 3$)		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Bare ground	28.33 \pm 7.11 ^a		45.28 \pm 4.52 ^A		46.39 \pm 7.24		54.72 \pm 1.21		$t_{1,4} = -1.09$
Litter cover	79.35 \pm 3.49 ^A		65.93 \pm 5.11 ^a		54.17 \pm 17.22		55.83 \pm 16.07		$t_{1,4} = -0.02$
Litter depth	1.78 \pm 0.21		1.53 \pm 0.18		0.50 \pm 0		0.92 \pm 0.21		$t_{1,4} = -2.62$
Fine woody debris cover	21.87 \pm 4.62		29.98 \pm 5.36		43.67 \pm 12.61		42.56 \pm 16.50		$t_{1,4} = 0.03$
Coarse woody debris m ³	1.48 \pm 1.42		1.38 \pm 0.48		4.17 \pm 3.37		2.22 \pm 1.11		$t_{1,4} = 0.55$
Ground vegetation cover	76.48 \pm 5.23		62.69 \pm 4.66		92.22 \pm 6.19		81.39 \pm 9.82		$t_{1,4} = 0.65$
Lower field cover	56.48 \pm 10.74 ^A		21.48 \pm 10.72 ^a		1.67 \pm 0.96		3.33 \pm 3.33		$t_{1,4} = -0.48$
Upper field cover	6.85 \pm 3.82		0 \pm 0		5.28 \pm 1.55 ^A		0 \pm 0 ^a		$t_{1,4} = 3.41^*$
Canopy cover	83.33 \pm 1.44		84.00 \pm 1.00		80.00 \pm 5.77		88.33 \pm 1.67		$t_{1,4} = -1.37$

Differences between ungrazed and grazed plots tested with GLMM: * <0.05, ** <0.01

^A is significantly greater than ^a

Table 5 Mean \pm SE for species metrics from plots (n) in each woodland type \times treatment combination

	Oak				Yew				
	Ungrazed ($n = 9$)		Grazed ($n = 9$)		Ungrazed ($n = 3$)		Grazed ($n = 3$)		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Abundance									
All species	66.33 \pm 6.65 ^A		37.11 \pm 3.92 ^a		25.33 \pm 3.84 ^a		42.00 \pm 4.93 ^A		$t_{1,4} = -3.24^{**}$
Forest specialists	39.22 \pm 5.43 ^A		22.11 \pm 2.42 ^a		13.33 \pm 3.38 ^a		32.33 \pm 4.91 ^A		$t_{1,4} = -3.94^{***}$
Ground runners	6.22 \pm 2.97		3.00 \pm 0.75		0.33 \pm 0.33		0.67 \pm 0.33		$t_{1,4} = -0.57$
Space web-builders	8.00 \pm 1.59 ^A		2.00 \pm 0.53 ^a		0.33 \pm 0.33		0.33 \pm 0.33		$t_{1,4} = 0$
Wandering sheet/tangle weavers	50.44 \pm 6.97 ^A		30.67 \pm 3.35 ^a		22.00 \pm 4.36 ^a		40.00 \pm 4.62 ^A		$t_{1,4} = -3.40^{***}$
Species richness									
All species	17.44 \pm 1.48 ^A		13.67 \pm 1.53 ^a		7.00 \pm 0.58		7.00 \pm 1.00		$t_{1,4} = 0$
Forest specialists	8.44 \pm 0.65		7.11 \pm 0.63		3.00 \pm 0		2.33 \pm 0.67		$t_{1,4} = 0.50$
Ground runners	1.78 \pm 0.28		2.11 \pm 0.45		0.33 \pm 0.33		0.67 \pm 0.33		$t_{1,4} = -0.57$
Space web-builders	1.11 \pm 0.11		0.78 \pm 0.15		0.33 \pm 0.33		0.33 \pm 0.33		$t_{1,4} = 0$
Wandering sheet/tangle weavers	13.44 \pm 1.22 ^A		9.56 \pm 0.94 ^a		4.67 \pm 0.33		5.33 \pm 0.88		$t_{1,4} = -0.37$

Differences between ungrazed and grazed plots tested with GLMM: * <0.05, ** <0.01, *** <0.001

^A is significantly greater than ^a

concern (Table 6 in Appendix) (Oxbrough et al. 2006, 2010; Nolan 2008). It should be noted, however, that Killarney National Park supports a range of spider species across its woodlands with dissimilarity between the oak and yew woodlands and between the oak sites.

There is little research on the biodiversity of yew woodlands; however, it generally supports low understory vegetation cover and species richness (Rodwell 1991; Devaney et al. in press). In terms of ground-dwelling spiders, the yew woodland in Killarney National Park also appears to support low species richness and, although this is a rare habitat, few rare species. Similar results have been found for insects in ash forests in Britain (Newton and Humphrey 1997) and for spiders in Ireland (Oxbrough et al. 2005) which was attributed to lack of habitat structure and a shallow litter layer. This explanation may also be applicable in the yew woodland where there was little cover of lower field layer vegetation, due to the karstic outcropping, shallow soils and dense canopy, as well as a shallow litter layer. In contrast the oak woodland, with its broadleaf deciduous canopy, provided lighter conditions with well-developed ground layer vegetation and greater litter cover, which is known to benefit spider abundance and diversity, as well as influence spider species composition (Stevenson and Dindal 1982; Uetz 1979, 1991; Gunnarsson 1996).

Although the majority of species collected in this study commonly occur in many types of broad-leaved and coniferous woodland in Ireland, a number of species are of interest from a conservation perspective. *Coelotes terrestris* is range-restricted in Britain and known to be threatened by the lack of coarse woody debris and loss of semi-natural woodland in Britain and Ireland (Harvey et al. 2002; Sweeney et al. 2010). *Philodromus albidus* was only recently discovered in Ireland (Cawley 2008) and is range-restricted in Britain (Harvey et al. 2002; Jones 1992). The closure of woodland is detrimental to this species and management to prevent woodland closure can utilise light grazing by large mammals such as deer (Harvey et al. 2002). *Tapinocyba insecta* is classed as vulnerable in Britain (Dawson et al. 2008) and thought to have undergone long-term decline due to loss of ancient semi-natural broadleaved woodland in both Britain and Ireland (Harvey et al. 2002; Nolan 2008). *Saaristoa firma*, *A. subtilis*, and *W. dysderoides* are classed as vulnerable in Britain, but able to utilise a variety of habitats present in Ireland and their presence in Killarney National Park is probably of less significance than that of *C. terrestris*, *P. albidus* and *T. insecta* which are more specialised in their ecological requirements. The lack of ancient semi-natural woodland in Ireland suggests Killarney National Park may provide an important and nationally scarce habitat for these species.

Effects of grazing

Grazing may be having an effect on spiders in Killarney National Park by indirectly reducing the abundance and species richness of ground-dwelling spiders, including forest specialists, space web-builders and wandering sheet/tangle weavers in the oak woodland. The Linyphiidae were the most abundant family in these woodlands and these spiders are particularly sensitive to the effects of grazing due to their dependence on vegetation structure (Dennis et al. 1998). Decreases in spider abundance are likely to have an indirect negative effect on higher trophic levels such as birds and insectivorous mammals through reduced prey abundance (Gibson et al. 1992a, b; Evans et al. 2006).

Studies show that greater vegetation cover and structure within grazing exclosures benefits spider abundance and species richness as well other invertebrate species groups such as Lepidoptera, Hymenoptera, Diptera and Coleoptera (Gibson et al. 1992a, b; Baines

et al. 1994; Mysterud et al. 2010). This is most likely mediated through changes in litter and lower field layer vegetation affecting the available habitat area, associated prey, web-attachment points and shelter from predators (Stevenson and Dindal 1982; Uetz 1979, 1991; Gunnarsson 1996).

It is unclear why there was higher abundance observed in grazed plots in the yew woodland, as there was significantly greater cover of upper field vegetation in the ungrazed plots and no difference in other habitat variables which may have an influence on spider abundance. However the lack of a difference in species richness indicates that overall ground-dwelling spider diversity did not differ between the two treatments. A qualitative assessment of the large herbivore impacts in the oak and yew plots [using the 'woodland grazing toolbox' (Forestry Commission Scotland 2013)] indicated that grazing levels were low in the yew woodland control plot and high or very high in the oak woodland control plots (Newman et al. in press), which could explain the differences in abundance and richness. This may be due to the management effort to reduce deer numbers in the yew woodland area (Peter O'Toole, personal communication). It must also be noted that the lack of replication in the yew woodland could mean we were unable to detect any effects of grazing.

The lack of an effect on species composition is surprising given the known influence of habitat structure on ground-dwelling spiders and the documented impact of deer grazing on biodiversity (Mitchell and Kirby 1990; Perrin et al. 2011). However, whilst abundance was strongly affected by grazing, particularly in the oak woodland, there were fewer significant effects on species richness. It is possible that the extra species found in the ungrazed plots were not enough to produce a significant effect on species composition.

Although there was an initial increase in lower field vegetation cover as a result of deer exclusion this may not last. As understory vegetation increases in cover ground flora diversity can decline due to competitive plant species such as *Luzula sylvatica*, bramble (*Rubus fruticosus*) and ivy (*Hedera helix*) outcompeting woodland specialists (Newman et al. in press; Perrin et al. 2011). Therefore long-term deer exclusions in the oak woodland may lead to a decline in vegetation diversity and, thus, a decline in spider diversity. A low level of grazing has been recommended to benefit woodland specialist ground vegetation (Perrin et al. 2011) and light grazing to prevent woodland closure may benefit species such as *P. albidus*.

The woodland grazing toolbox categorises grazing levels by qualitatively assessing impacts on ground disturbance, bark stripping and vegetation (Forestry Commission Scotland 2013). In terms of vegetation structure, light grazing is defined as palatable species in the sward layer only very lightly grazed with the sward generally >10 cm tall (Forestry Commission Scotland 2013). Ground-dwelling spiders positively responded to the greater cover of lower field vegetation (10–50 cm high) in the ungrazed oak plots, suggesting that light grazing to prevent woodland closure whilst maintaining a sward height of >10 cm will be of benefit.

Deer are an integral part of many natural woodland ecosystems and if they are managed appropriately they could be a useful tool in woodland management (Mitchell and Kirby 1990; Kirby et al. 1994; Stewart 2001; Hester et al. 2000). Therefore if the conservation objective is to increase biodiversity in these woodlands permanent deer grazing exclusions may not be necessary or even desirable. A more appropriate system could include deer as part of a management plan for biodiversity rather than use exclusion zones. However, it must be noted that these exclusions have only been in place for five years and the temporal and spatial effects of grazing in forest ecosystems requires further investigation to determine the long-term effects on spider diversity.

Conclusions

The majority of ground-dwelling spider species collected in these rare oak and yew woodlands were typical of Irish forests. However, in the context of Ireland's highly modified landscape, Killarney National Park may provide important habitat for a number of vulnerable and range-restricted species which are threatened by the decline of semi-natural woodland. This research also found that deer grazing may reduce the abundance and species richness of ground-dwelling spiders in the oak woodland of Killarney National Park, mediated through reductions in litter and vegetation structure which spiders rely on. We suggest future conservation efforts should consider incorporating lower densities of deer [e.g. 2–3 animals per km² rather than the current estimate of 5–28 animals per km² in the Killarney area (Purser et al. 2009)] into a woodland management plan which maintains a light level of grazing, as defined by the woodland grazing toolbox (Forestry Commission Scotland 2013).

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Appendix

See Table 6.

Table 6 Species list of ground-dwelling spiders caught in the oak and yew woodlands of Killarney National Park, including habitat association (generalist = habitat generalist, open = open habitat specialist, shaded = under litter, bark and stones in open and forest habitats, forest = forest specialist), conservation status based on Dawson et al. 2008 (DD = data deficient, LC = least concern, VU = vulnerable) and the number of individuals (*n*) caught in each woodland type

Family	Species	Habitat association	Conservation status	Oak (<i>n</i>)	Yew (<i>n</i>)
Amaurobiidae	<i>Amourobium fenestralis</i>	Forest	LC	2	0
	<i>Coelotes terrestris</i>	Forest	LC	1	0
Anyphaenidae	<i>Anyphaena accentuata</i>	Forest	LC	2	0
Araneidae	<i>Cyclosa conica</i>	Forest	LC	1	2
Dictynidae	<i>Cryphoeca silvicola</i>	Shaded	LC	1	0
Dysderidae	<i>Harpactea hombergi</i>	Shaded	LC	2	2
Hahniidae	<i>Hahnia helveola</i>	Shaded	LC	1	0
Linyphiidae	<i>Agyneta cauta</i>	Generalist	LC	12	0
	<i>Agyneta ramosa</i>	Forest	LC	37	1
	<i>Agyneta subtilis</i>	Generalist	VU	55	26
	<i>Asthenargus paganus</i>	Forest	LC	1	0
	<i>Bathyphantes nigrinus</i>	Shaded	LC	2	0
	<i>Centromerus dilutus</i>	Shaded	LC	1	0
	<i>Centromerus prudens</i>	Open	LC	2	0
	<i>Dicymbium tibiale</i>	Shaded	LC	10	0

Table 6 continued

Family	Species	Habitat association	Conservation status	Oak (n)	Yew (n)
	<i>Diplocephalus latifrons</i>	Forest	LC	74	0
	<i>Diplocephalus picinus</i>	Forest	LC	10	0
	<i>Diplostyla concolor</i>	Generalist	LC	5	5
	<i>Hypomma cornutum</i>	Shaded	LC	1	0
	<i>Leptorhoptrum robustum</i>	Generalist	LC	0	1
	<i>Linyphia hortensis</i>	Forest	LC	26	6
	<i>Maso sundevalli</i>	Generalist	LC	1	0
	<i>Meioneta saxatilis</i>	Generalist	LC	1	0
	<i>Micrargus herbigradus</i>	Generalist	LC	0	1
	<i>Microneta viaria</i>	Forest	LC	34	0
	<i>Minyriolus pusillus</i>	Forest	LC	4	0
	<i>Monocephalus fuscipes</i>	Forest	LC	77	0
	<i>Neriere clathrata</i>	Generalist	LC	5	1
	<i>Neriere peltata</i>	Generalist	LC	2	5
	<i>Obscuriphantes obscurus</i>	Forest	LC	1	0
	<i>Pallidiphantes pallidus</i>	Generalist	LC	7	0
	<i>Pocadicnemis pumila</i>	Generalist	LC	3	0
	<i>Porrhomma campbelli</i>	Generalist	LC	0	1
	<i>Porrhomma montanum</i>	Shaded	LC	2	0
	<i>Saaristoa abnormis</i>	Generalist	LC	42	9
	<i>Saaristoa firma</i>	Generalist	VU	1	0
	<i>Tapinocyba insecta</i>	Forest	VU	1	0
	<i>Tapinocyba pallens</i>	Forest	LC	1	0
	<i>Tenuiphantes alacris</i>	Forest	LC	59	8
	<i>Tenuiphantes cristatus</i>	Shaded	LC	2	0
	<i>Tenuiphantes flavipes</i>	Forest	LC	77	0
	<i>Tenuiphantes zimmermanni</i>	Forest	LC	139	122
	<i>Tiso vagans</i>	Generalist	LC	3	0
	<i>Walckenaeria acuminata</i>	Generalist	LC	17	0
	<i>Walckenaeria atrotibialis</i>	Generalist	LC	5	0
	<i>Walckenaeria cuspidata</i>	Generalist	LC	3	0
	<i>Walckenaeria dysderoides</i>	Shaded	VU	3	0
	<i>Walckenaeria nudipalpis</i>	Generalist	LC	4	0
Lycosidae	<i>Pardosa amentata</i>	Open	LC	1	0
	<i>Pardosa lugubris</i>	Forest	DD	7	0
	<i>Pardosa nigriceps</i>	Open	LC	2	0
	<i>Pirata hygrophilus</i>	Generalist	LC	60	0
	<i>Pirata piraticus</i>	Open	LC	1	0
	<i>Trochosa terricola</i>	Open	LC	4	0

Table 6 continued

Family	Species	Habitat association	Conservation status	Oak (n)	Yew (n)
Mimetidae	<i>Ero furcata</i>	Generalist	LC	0	2
Philodromidae	<i>Philodromus albidus</i>	Forest	LC	0	1
Segestriidae	<i>Segestria senoculata</i>	Generalist	LC	6	1
Tetragnathidae	<i>Metellina mendei</i>	Generalist	LC	4	6
	<i>Pachygnatha clercki</i>	Generalist	LC	2	0
	<i>Pachygnatha degeeri</i>	Generalist	LC	4	0
	<i>Pachygnatha listeri</i>	Forest	LC	3	0
Theridiidae	<i>Anelosimus vittatus</i>	Generalist	LC	0	1
	<i>Pholcomma gibbum</i>	Generalist	LC	0	1
	<i>Robertus lividus</i>	Generalist	LC	89	0
Thomisidae	<i>Diaea dorsata</i>	Forest	LC	1	0
	<i>Ozyptila trux</i>	Generalist	LC	7	0
Total abundance				931	202
Total species richness				59	20

References

- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Anon (2007) National Forest Inventory: Republic of Ireland Results. Government of Ireland
- Baines D, Sage RB, Baines MM (1994) The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *J Appl Ecol* 31:776–783
- Batten LA (1976) Bird communities of some Killarney woodlands. *Proc Royal Ir Acad B* 76:285–313
- Carden RF, Carlin CM, Marnell F, McElholm D, Hetherington J, Gammell MP (2011) Distribution and range expansion of deer in Ireland. *Mamm Rev* 41:313–325
- Carden RF, McDevitt AD, Zachos FE, Woodman PC, O'Toole P, Rose H, Monaghan NT, Campana MG, Bradley DG, Edwards CJ (2012) Phylogeographic, ancient DNA, fossil and morphometric analyses reveal ancient and modern introductions of a large mammal: the complex case of red deer (*Cervus elaphus*) in Ireland. *Quatern Sci Rev* 42:74–84
- Cawley M (2008) More records for uncommon spiders (Araneae), including four species new to Ireland. *Bull Ir Biogeogr Soc* 32:69–83
- Clarke RD, Grant PR (1968) An experimental study of the role of spiders as predators in a forest litter community. Part 1. *Ecology* 49(6):1152–1154
- Core Team R (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM (2004) Ecological impacts of deer over-abundance. *Annu Rev Ecol Evol Syst* 35:113–147
- Dawson I, Harvey P, Russell-Smith T (2008) A national status review: the draft results. *Spider Rec Scheme News* 112:18–24
- Dennis P, Young M, 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
- Devaney JL, Jansen MAK, Whelan PM (in press) Spatial patterns of natural regeneration in stands of English yew (*Taxus baccata* L.); Negative neighbourhood effects. *For Ecol Manag* [Available online 31 July 2013]
- Evans DM, Redpath SM, Evans SA, Elston DA, Gardner CJ, Dennis P, Pakeman RJ (2006) Low intensity, mixed livestock grazing improves the breeding abundance of a common insectivorous passerine. *Biol Lett* 2:636–638

- Forest Europe, UNECE, FAO (2011) State of Europe's Forests 2011. United Nations Economic Commission for Europe
- Forestry Commission Scotland (2013) The woodland grazing toolbox. <http://www.forestry.gov.uk/forestry/INFD-82TLHE>. Accessed 24/9/2013
- Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder M, Nielsen A, Sibert J (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim Methods Softw* 27:233–249
- Frazer G, Canham C, 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, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York
- Gibson CWD, Brown VK, Losito L, McGavin GC (1992a) The response of invertebrate assemblages to grazing. *Ecography* 15(2):166–176
- Gibson CWD, Hamblen C, Brown VK (1992b) Changes in spider (Araneae) assemblages in relation to succession and grazing management. *J Appl Ecol* 29(1):132–142
- Gunnarsson B (1983) Winter mortality of spruce-living spiders: effect of spider interactions and bird predation. *Oikos* 40(2):226–233. doi:10.2307/3544586
- Gunnarsson B (1996) Bird predation and vegetation structure affecting spruce-living arthropods in a temperate forest. *J Anim Ecol* 65:389–397
- Harvey PR, Nellist DR, Telfer MG (2002) Provisional Atlas of British Spiders (Arachnida, Araneae). Natural Environment Research Council, Biological Records Centre, Cambridge
- Hermý M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson JE (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biol Conserv* 91:9–22
- Hester AJ, Edenius L, Buttenschön RM, Kuiters AT (2000) Interactions between forests and herbivores: the role of controlled grazing experiments. *Forestry* 73(4):381–391. doi:10.1093/forestry/73.4.381
- Holt CA, Fuller RJ, Dolman PM (2013) Exclusion of deer affects responses of birds to woodland regeneration in winter and summer. *Ibis*. doi:10.1111/ibi.12096
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54(2):187–211
- Jones D (1992) *Philodromus albidus* Kulczynski in Hampshire. *Newslett Br Arachnol Soc* 64:7
- Kelly DL (1981) The native forest vegetation of Killarney, South-West Ireland: an ecological account. *J Ecol* 69(2):437–472
- Kelly DL (2002) The regeneration of *Quercus petraea* (sessile oak) in southwest Ireland: a 25-year experimental study. *For Ecol Manage* 166(1–3):207–226. doi:10.1016/s0378-1127(01)00670-3
- Kirby KJ, Mitchell FJG, Hester AJ (1994) A role for large herbivores (deer and domestic stock) in nature conservation management in British semi-natural woods. *Arboricult J* 18(4):381–399
- Koleff P, Gaston KJ, Lennon JK (2003) Measuring beta diversity for presence–absence data. *J Anim Ecol* 72:367–382
- Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129(2):271–280. doi:10.1007/s004420100716
- Lynch Á, McCann Y (2007) The diet of the pine marten (*Martes martes*) in Killarney National Park. *Biol Environ* 107(2):67–76. doi:10.3318/bioe.2007.107.2.67
- Melis C, Buset A, Aarrestad P-A, Hanssen O, Meisingset EL, Andersen R, Moksnes A, Røskaft E (2006) Impact of red deer *Cervus elaphus* grazing on bilberry *Vaccinium myrtillus* and composition of ground beetle (Coleoptera, Carabidae) assemblage. *Biodivers Conserv* 15(6):2049–2059
- Mitchell FJG (1988) The vegetational history of the Killarney oakwoods, SW Ireland: evidence from fine spatial resolution pollen analysis. *J Ecol* 76(2):415–436. doi:10.2307/2260603
- Mitchell FJG, Kirby KJ (1990) The impact of large herbivores on the conservation of semi-natural woods in the British uplands. *Forestry* 63(4):333–353. doi:10.1093/forestry/63.4.333
- Miyashita T, Takada M, Shimazaki A (2004) Indirect effects of herbivory by deer reduce abundance and species richness of web spiders. *Ecoscience* 11(1):74–79
- Mysterud A, Aaserud R, Hansen LO, Åkra K, Olberg S, Austrheim G (2010) Large herbivore grazing and invertebrates in an alpine ecosystem. *Basic Appl Ecol* 11:320–328
- National Parks and Wildlife Service (2006) Site synopsis: Killarney National Park, Macgillycuddy's Reeks and Caragh River Catchment. Department of the Environment, Heritage & Local Government
- National Parks and Wildlife Service (2008) The Status of EU Protected Habitats and Species in Ireland. Department of the Environment, Heritage and Local Government, Ireland

- Newman M, Mitchell FJG, Kelly DL (in press) Exclusion of large herbivores: long-term changes within the plant community. For *Ecol Manag*. [Available online 6 October 2013]. doi:[10.1016/j.foreco.2013.09.010](https://doi.org/10.1016/j.foreco.2013.09.010)
- Newton A, Humphrey J (1997) Forest management for biodiversity: perspectives on the policy context and current initiatives. In: Fleming V, Newton A, Vickery J, Usher M (eds) *Biodiversity in Scotland: status, trends and initiatives*. Scottish National Heritage Council, Edinburgh
- Nolan M (2008) Database of Irish Spiders (Araneae). Irish Wildlife Manuals. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin
- NPWS (2005) Management Plan for Killarney National Park 2005–2009. Government of Ireland
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Hendry M, Stevens H, Wagner H (2012) *Vegan: Community Ecology Package*. CRAN
- Oxbrough AG, Gittings T, O'Halloran J, Giller PS, Smith GF (2005) Structural indicators of spider communities across the forest plantation cycle. For *Ecol Manag* 212(1–3):171–183. doi:[10.1016/j.foreco.2005.03.040](https://doi.org/10.1016/j.foreco.2005.03.040)
- Oxbrough AG, Gittings T, O'Halloran J, Giller PS, Kelly TC (2006) The influence of open space on ground-dwelling spider assemblages within plantation forests. For *Ecol Manag* 237(1–3):404–417. doi:[10.1016/j.foreco.2006.09.063](https://doi.org/10.1016/j.foreco.2006.09.063)
- Oxbrough A, Irwin S, Kelly T, O'Halloran J (2010) Ground-dwelling invertebrates in reforested conifer plantations. For *Ecol Manag* 259:2111–2121
- Perrin PM, Kelly DL, Mitchell FJG (2006) Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: natural regeneration and stand dynamics. For *Ecol Manag* 236(2–3):356–367. doi:[10.1016/j.foreco.2006.09.025](https://doi.org/10.1016/j.foreco.2006.09.025)
- Perrin P, Martin J, Barron S, O'Neill F, McNutt K, Delaney A (2008) National Survey of Native Woodlands 2003–2008. National Parks and Wildlife Service, Dublin
- Perrin PM, Mitchell FJG, Kelly DL (2011) Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: changes in ground flora and species diversity. For *Ecol Manag* 262(12):2328–2337. doi:[10.1016/j.foreco.2011.08.028](https://doi.org/10.1016/j.foreco.2011.08.028)
- Peterken GF, Game M (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *J Ecol* 72:155–182
- Pinzón J, Spence J (2010) Bark-dwelling spider assemblages (Araneae) in the boreal forest: dominance, diversity, composition and life-histories. *J Insect Conserv* 14(5):439–458. doi:[10.1007/s10841-010-9273-7](https://doi.org/10.1007/s10841-010-9273-7)
- Purser P, Wilson F, Carden R (2009) Deer and forestry in Ireland. A review of current status and management requirements. Woodlands of Ireland, Dublin
- Ripley B, Venables B, Hornik K, Gebhardt A, Firth D (2013) Package 'MASS'. Version 7.3-29. CRAN
- Roberts MJ (1993) *The spiders of Great Britain and Ireland*. Harley Books, Colchester
- Rodwell JS (1991) *British plant Communities. Woodlands and scrub, vol 1*. Cambridge University Press, Cambridge
- Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B (2013) Generalized Linear Mixed Models using AD Model Builder. R package version 0.7.7. <http://glmmadmb.r-forge.r-project.org>. Accessed 1 Sept 2013
- Smal CM, Fairley JS (1982) The dynamics and regulation of small rodent populations in the woodland ecosystems of Killarney, Ireland. *J Zool* 196(1):1–30. doi:[10.1111/j.1469-7998.1982.tb03491.x](https://doi.org/10.1111/j.1469-7998.1982.tb03491.x)
- Spooner P, Lunt I, Robinson W (2002) Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. *Ecol Manag Restor* 3(2):117–126. doi:[10.1046/j.1442-8903.2002.00103.x](https://doi.org/10.1046/j.1442-8903.2002.00103.x)
- Stevenson BG, Dindal DL (1982) Effect of leaf shape on forest litter spiders: community organization and microhabitat selection of immature *Enoplognatha Ovata* (Clerck) (Theridiidae). *J Arachnol* 10(2):165–178
- Stewart AJA (2001) The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. *Forestry* 74(3):259–270. doi:[10.1093/forestry/74.3.259](https://doi.org/10.1093/forestry/74.3.259)
- Sweeney OFM, Martin RD, Irwin S, Kelly TC, O'Halloran J, Wilson MW, McEvoy PM (2010) A lack of large-diameter logs and snags characterises dead wood patterns in Irish forests. For *Ecol Manag* 259(10):2056–2064. doi:[10.1016/j.foreco.2010.02.016](https://doi.org/10.1016/j.foreco.2010.02.016)
- The World Spider Catalog, Version 13.0 (2012) The American Museum of Natural History. Last accessed: 10th January 2012. URL: <http://research.amnh.org/iz/spiders/catalog/INTRO1.html>
- Uetz G (1979) The influence of variation in litter habitats on spider communities. *Oecologia* 40:29–42
- Uetz G (1991) Habitat structure and spider foraging. In: Bell S, McCoy E, Mushinsky H (eds) *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, London

- Uetz GW, Halaj J, Cady AB (1999) Guild structure of spiders in major crops. *J Arachnol* 27(1):270–280. doi:[10.2307/3705998](https://doi.org/10.2307/3705998)
- UNESCO (2001) Biosphere Reserve Information. Ireland. Killarney. UNESCO. <http://www.unesco.org/mabdb/br/brdir/directory/biores.asp?mode=all&code=IRE+02>. Accessed 28th March 2013
- Wise DH (1993) Spiders in ecological webs. Cambridge University Press, Cambridge
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York