Can ground-based assessments of forest biodiversity reflect the biological condition of canopy assemblages?

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A B S T R A C T

Biological assessments of forest systems often involve a single ground-invertebrate sampling method that may ignore the biological component of the non-sampled canopy. Pitfall trapping for ground-active arthropods is a widely implemented technique for biological assessment in forested and open habitats. Although much evidence highlights the biases of pitfall trapping, this evidence typically comes from open-habitat crop and grassland systems. In forest systems where much of the biodiversity is found within the above-ground structure, management recommendations based solely on ground sampling may not represent the diversity within the three dimensional forest habitat. We provide evidence from combined ground and canopy sampling of three major forest types within the study region. We use canopy insecticide fogging to compare with more traditional ground-based pitfall trapping, and use spiders as a comparative species-rich biota that is able to colonise most terrestrial habitats and is strongly affected by changes in environmental condition.

We identified 3933 spiders from 109 species from the 18 forest patches sampled. Both types of sampling defined differences in community composition between forest types in a similar manner; hence, either method could be used to evaluate differences or test management regimes in well-replicated experiments of forest type. However, the association in community composition between ground and canopy assemblages at the individual site-based level was weak; we found low correlation between the two data sets indicating that surrogacy between methods was not supported at this level. Furthermore, disparities in spider habitat association, body size, hunting guild and vertical stratification of spider families indicates that where detailed species and family-based information is required, or if inventorying is necessary, then multiple targeted surveys are essential.

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1. Introduction

Biodiversity must be sampled in a way that fits research questions but also meets time and financial budgets. Often these constraints lead to the use of a single survey procedure to derive data with which to draw conclusions that inform policy and management. This leaves questions regarding the consistency of those conclusions if an alternative sampling strategy had been chosen. In complex systems, such as forested landscapes, the three-dimensional structure poses problems for capturing representative samples across vegetation layers (Pinzon et al., 2011). The

importance of forest systems (Ozanne et al., 2003), coupled with the potential of sample bias, means there is a growing need to validate sampling strategies to strengthen management recommendations based on these single survey practices.

Arthropod diversity is frequently used to assess biological condition in applied forest research (Spence et al., 1996; Berndt et al., 2008; Pedley et al., 2014) and more fundamental aspects of ecology, including fragmentation and disturbance (Vasconcelos et al., 2006; Pedley and Dolman, 2014). New DNA barcoding techniques (Yang et al., 2014), which negate the often laborious taxonomy associated with arthropod sampling, are enabling quicker processing times that may proliferate the use of arthropod monitoring (Ji et al., 2013). However, conventional taxonomic and many contemporary DNA barcoding techniques rely on traditional invertebrate collection methods. One of the most commonly employed

sampling techniques for epigaeic arthropods is pitfall trapping. Pitfall trapping provides a passive means of surveying that, once established, can continuously trap active species with only brief visits needed to service traps. Although pitfall trapping has a long history in ecology, its ability to provide non-bias sampling of habitat has been brought into question (Topping and Sunderland, 1992; Lang, 2000). Pitfalls by their nature target active ground-dwelling species, and can underrepresent less mobile, small-bodied species and species typical of higher strata (Greenslade, 1964; Lang, 2000; Standen, 2000). Furthermore, pitfall catches are a representation of animal density, conditional on animal activity; if activity is disproportionally affected by vegetation structure, shading or animal interactions between sites, then catches may not be comparable (Greenslade, 1964; Melbourne, 1999). Where environmental conditions are similar, comparisons across sites are suitable as long as pitfall trap data are used as an index of the density based on activity and not a species inventory of the sampled habitat (Luff and Eyre, 1988; Oxbrough et al., 2006).

Much of the available methodological literature concerning pitfall trap bias comes from crop and grassland studies (e.g. Topping and Sunderland, 1992; Standen, 2000). However, extensive arthropod monitoring of closed-canopy forests has been conducted with ground-based methods (e.g. Docherty and Leather, 1997; Oxbrough et al., 2005; Berndt et al., 2008). Many studies of this nature make comparisons between the arthropod biodiversity of different forest types with inherently different ground, understory and canopy structures (Fuller et al., 2008; Barsoum et al., 2014). Although such studies do not imply that pitfall trapping will reveal the biodiversity related to the entire three-dimensional structure of the forest, there are few studies that can elucidate the non-sampled aboveground component of forest biodiversity in a similar manner to the methodological papers concerning crop and grasslands (but see Pinzon et al., 2011). This problem of the non-sampled biodiversity is perhaps more significant within forest systems as forest canopies contain a large proportion of the total arthropod diversity on Earth (Erwin, 1982; Lowman and Wittman, 1996).

While canopy sampling is considerably more challenging than many ground sampling methods due to the difficulties in accessing tree canopies, ground-based insecticide fogging can negate these access problems. Insecticide fogging of canopy-dwelling species has proven a reliable survey method but has received less consideration in temperate and boreal zones than in tropical regions. Canopy fogging has proven an effective way to sample temperate canopy invertebrates and to measure biodiversity patterns within single species, across temporal dynamics and between forest types (Southwood et al., 2005; Hsieh and Linsenmair, 2012; Pedley et al., 2014). However, fogging is limited by weather conditions, with at least several hours of dry, still weather required for successful sampling. This method may also overlook some species such as aphids or other phloem feeders (Stork and Hammond, 1997), or those within certain life stages, such as within cocoons, retreats or burrows and those attached by silken threads. While these sampling biases will affect inventorying canopy invertebrates in much the same way as pitfall trap biases do for ground-based invertebrates, it is likely that standardised canopy fogging will allow for comparisons to be made across sampled forest sites.

Among the arthropod groups frequently investigated in ecological surveys, spiders provide an effective means of habitat assessment as they are greatly affected by changes in habitat structure (Duffey, 1968; Robinson, 1981) and respond quickly to brief or sudden changes in environmental conditions, such as variations in prey density, pesticides, or pollution (Marc et al., 1999). Spiders are a species rich group and, being one of the top macro-invertebrate predators, have strong influences in food webs (Wise, 1993; Schmitz et al., 2000). Differences in spider community

assemblages within forest types have often been attributed to differences in habitat heterogeneity (Pinzon et al., 2011; Pedley et al., 2014). The assemblage composition of the forest-floor is influenced by light availability, volume and decay stage of debris, moisture and temperature (Ziesche and Roth, 2008); while canopy leaf/needle density and branch architecture has been shown to influence community composition above the ground layer (Gunnarsson, 1992; Halaj et al., 2000). Although some understanding of the factors influencing community composition in these habitats exists, we do not yet know if common sampling techniques differentially interpret community dissimilarities between forest types.

In the current study, we selected three distinctive forest types that were likely to vary in spider composition, semi-natural ash (*Fraxinus excelsior*) forests, semi-natural oak (*Quercus petraea*) forests and Sitka spruce (*Picea sitchensis*) plantations. We did not attempt to directly compare species richness or abundance between canopy and ground trapping, as sampling effort is not consistent between the two methods. Rather, we examined whether there is correspondence between the two methods for defining differences in assemblage structure between the three forest types. For each of the following hypotheses we looked for idiosyncratic and corresponding changes in biodiversity structure across forest types for the ground and canopy sampling techniques. (1) Assemblages sampled in the canopy and the ground differ similarly between the forest stands and forest types. (2) Patterns of hunting guilds (active and web spinners), habitat specialism (woodland and generalist), and body size will be inconsistent across forest types for ground and canopy sampled assemblages. (3) Spider families will show vertical stratification between ground and canopy sampling. Finally, we discuss whether there is possible surrogacy between ground and canopy methods. This is one of the first studies to compare and interpret forest biodiversity obtained from canopy and ground trapped invertebrate assemblages.

2. Methods

Three closed-canopy forests types were sampled across Ireland (Appendix A); six ash (*F. excelsior*) dominated semi-natural woodlands, six oak (*Q. petraea*) dominated semi-natural woodlands and six second-rotation Sitka spruce (*P. sitchensis*) plantations (hereafter referred to as ash forest, oak forest and spruce plantation, respectively). All stands were a minimum of 6 ha in size and 100 m in width. Sitka spruce plantations were selected as they are the dominant species in the Irish forest estate, comprising approximately 60% of the forest cover and are a non-native species (Forest Service, 2007). Ash and oak forests were selected as they are the most common native tree species in Irish semi-natural forests, comprising 22% and 18%, respectively (Higgins et al., 2004), and were expected to have contrasting biodiversity to spruce plantations. The semi-natural forest types considered in this study comprised a mix of tree species, i.e. oak-dominated forests included oak, birch and holly, while ash-dominated forests included ash, oak and hazel. Semi-natural ash and oak forests were at least 150 years old, whereas sampled spruce plantations ranged from mid rotation 20–30 year old closed-canopy stands to 60-year-old commercially mature stands.

2.1. Canopy sampling

Canopy fogging was conducted once at each of the 18 study sites. In each sampled forest stand a fogging plot was established in a representative area of the site in terms of stand structure and vegetation cover. A target tree was selected at the centre of each fogging plot that corresponded to the forest type being

sampled. The fogging plot consists of 16 plastic sheets (1.5 m^2), with a combined area of 24 m^2, arranged around the central tree on the eight cardinal and ordinal compass bearings. Plastic sheets were suspended 1 m above the ground to reduce the risk of contamination by ground-active species not sampled by fogging (Stork and Hammond, 1997). Sampling sheets were separated by 0.5 m from each other and all trees within the fogging plot. The fogging plot was at least 50 m from the forest perimeter to reduce possible edge effects.

Fogging was carried out between April and August in 2008 and 2009. A petrol-driven fogging machine (SwingFog SN50-PE, Swing-Tec Ltd, Germany) was used with a natural pyrethroid (Pybuthrin 33). Pyrethroid insecticide was chosen as it is non-persistent in the environment, with no phytotoxic effects and the levels used by this method are not harmful to mammals (Straw et al., 1996). Each canopy was fogged until fully covered in insecticide (typically 6–9 min duration). Fogging was only carried out in dry, calm conditions (wind-speeds of less than 8 km h^{-1}) and after a dry, calm night to minimise fog dispersion. At each site, sample sheets remained in place for three hours after fogging (Stork and Hammond, 1997), after which the captured invertebrate material was pooled and stored in 70% alcohol.

2.2. Pitfall sampling

Pitfall trapping was conducted for 63 days at each of the 18 study sites. At each site, pitfall traps were used to collect ground-dwelling spiders from three sampling plots. Each sampling plot was 50 m apart and 50 m away from the forest edge and comprised a transect of five pitfall traps spaced 2 m apart. Pitfall traps consisted of a plastic cup 7 cm in diameter and 9 cm in depth. Traps were filled with ethylene glycol (1 cm deep) to act as a killing and preserving agent. All traps were set in mid-May 2007 and left *in situ* for nine weeks with traps serviced every three weeks. There was considerable animal disturbance (>80% trap loss) at two of the spruce study sites sampled during 2007 and so these sites were re-sampled during the same period in 2008 with previous material being discarded. No other trap disturbance was recorded during the study. Catches from each site were pooled across the nine weeks for analyses giving a total of 945 trap days (63 days $\times$ 5 traps $\times$ 3 plots) per site.

2.3. Analysis

Abundance measures for analysis comprise the numbers of individuals per canopy plot and numbers of individuals per pitfall plot (pooled across traps and sampling periods for pitfall traps). All analysis was carried out in the statistical software R v3.1.2 (R Development Core Team, 2012). To visualise the difference in richness and abundance of spiders recorded from the different sampling methods, we calculated individual-based rarefaction curves using the rarecurve function in the vegan package (Oksanen et al., 2010).

Indicator species analysis was conducted separately for the two sampling methods to determine species affinity to forest types. We used the function multipatt in the package indicspecies (De Cáceres et al., 2010) to calculate species indicator values (Dufrêne and Legendre, 1997), and permutation (999) to test the significance.

To visualise the community composition among forest types for each sampling method, we used non-Metric Multidimensional Scaling (NMDS), performed on a matrix of Bray-Curtis dissimilarities of abundance data (square root transformed and Wisconsin double standardization) using the vegan package. Differences in community composition between forest types were tested using the package mvabund (Wang et al., 2012), which allows hypothesis

testing by multivariate implementation of generalised linear models. This method does not confound location with dispersion effects (a change in the mean-variance relationship), which can lead to misleading results and inflation of type-1 and 2 errors (Warton et al., 2012). Using likelihood-ratio-tests (LR) in the summary. manyglm function we tested for significant differences in assemblage composition of spruce and semi-natural ash and oak forests.

We use Procrustes rotation analysis on NMDS scores to explore the degree of congruence between the different biotic datasets obtained by pitfall trapping and fogging (Peres-Neto and Jackson, 2001). We implemented the protest function in the vegan package to test the best fit of two ordinations against a relationship occurring by chance (Peres-Neto and Jackson, 2001); larger correlation coefficients indicate a better concordance between two datasets (perfect concordance when correlation coefficient = 1).

Species richness and abundance of woodland associated and generalist species were compared among forest types separately for ground and canopy sampling using generalised linear models (GLMs). The appropriate error term for each analysis was selected by patterns in residuals and by examining model dispersion. Differences among forest type means were examined by Tukey pairwise comparisons using the glht function in the multcomp package (Hothorn et al., 2008). Spatial autocorrelation of GLM residuals was examined by Moran's I in the ape package v.3.0-6 (Paradis et al., 2004). In all instances, Moran's I was not significant ($P > 0.05$).

For each sampling site we calculated the abundance-weighted mean values for spider body size. This metric simply multiples spider body-size by the sampled abundance of each species recorded per site and calculates a single community-weighted mean (CWM) per site. Body size for each species was obtained from Roberts (1987, 1996). We tested the average CWM body-size of spiders sampled by pitfall trapping against those sampled by fogging using a Man-Whitney U test. Within each sampling method, differences in CWM body-size between forest types were tested with GLMs as above.

3. Results

We identified 3933 spiders of 109 species from the 18 forest patches sampled. Pitfall trapping, where each of the 15 traps per site was active for 63 days as opposed to a single discrete trapping event per site for fogging, captured a greater overall abundance and richness of spiders (Fig. 1). Pitfall trapping captured 3205 spiders from 87 species whereas fogging captured 728 spiders from 36 species. Analysis of variance showed that species richness of the three forest types was significantly different for pitfall-trapped assemblages ($F_{2,15} = 5.141$, $P = 0.020$; ash mean (±SD) 23.8 ± 4.6, oak mean 25.7 ± 5.7, spruce mean 17.7 ± 2.6), with post hoc tests indicating that only oak and spruce were significantly different (Turkey $P = 0.020$). No differences in species richness were found between forest types for canopy-fogged assemblages (Kruskal–Wallis $\chi^2 = 0.467$, $P > 0.05$; ash mean (±SD) 6.8 ± 2.2, oak mean 6.7 ± 0.5, spruce mean 7.0 ± 2.6). For details of species identification and classification of hunting and habitat guilds see Appendix B.

Fourteen species were common to both trapping methods, 73 species were unique to pitfall trapping (including 22 woodland species) and 22 to fogging (including five woodland species). Of the 87 species in pitfall traps, 16 (18%) species were unique to ash forest, 14 (16%) unique to oak and five (6%) unique to spruce. A larger proportion of species were unique to forest types in the fogged samples, from the 36 species captured, nine (25%) were unique to ash forests, seven (19%) were unique to oak forest and nine (25%) were unique to spruce plantations. Twenty five (29%)
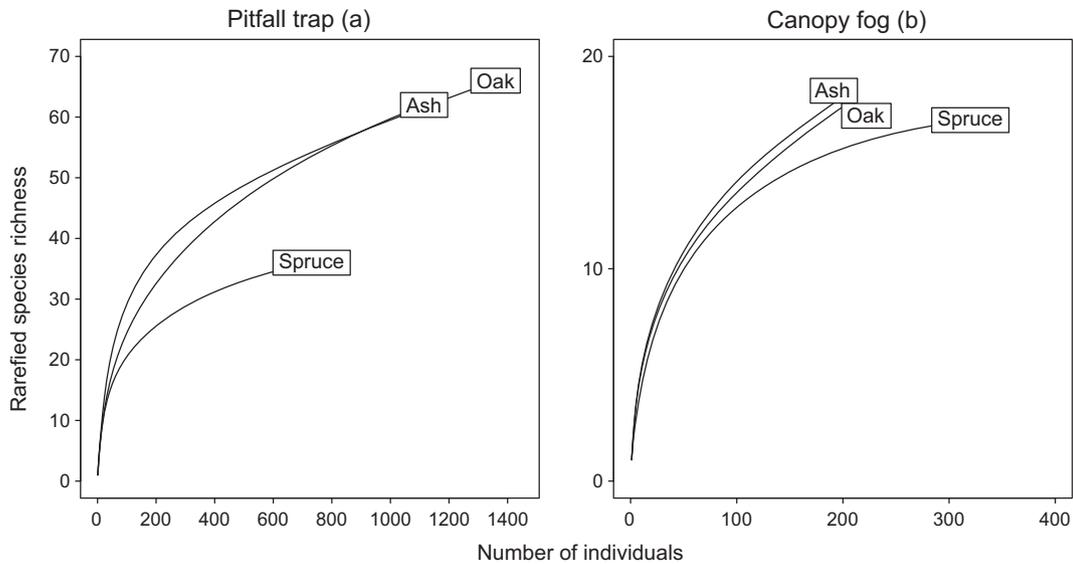
Fig. 1. Individual-based rarefaction curves for (a) pitfall trapped and (b) canopy fogged spider assemblages from three forest types (ash, oak and spruce).

species were common to all forest types sampled by pitfall trapping whereas six species (16%) were common to all fogged forest types.

The woodland-associated Linyphiid, *Lepthyphantes zimmermanni* was the most abundant species recorded in all forest types by pitfall trapping (ash $n = 331$, oak $n = 293$, spruce $n = 140$). For canopy assemblages, ash forests were dominated by the generalist species *Tetragnatha montana* ($n = 66$), oak forests by the woodland species *Neriene peltata* ($n = 64$) and spruce by the woodland species *Pelecopsis nemoralis* ($n = 184$).

Indicator species analysis identified associations for all forest types, although canopy sampled indictors were only identified from ash and spruce (Table 1). All species identified as indicators were web hunters. The highest indicator values for pitfall-trapped species were for habitat generalist whereas those sampled by fogging were both generalist (ash) and woodland associated (spruce).

Significant differences in community composition were found between forest types using both pitfall trapping and fogging methods (Deviance = 360.6, $P = 0.007$; Deviance = 137.4, $P = 0.004$ respectively); however, assemblages sampled with pitfall trapping showed greater separation between forest types (Fig. 2). Compared with spruce, semi-natural forests had significantly different species compositions for both pitfall trapped and fogged assemblages ($P < 0.001$). Although fogged ash and oak forests showed some overlap in NMDS space, assemblages in the two semi-natural forest types were significantly different (LR value = 45.61, $P = 0.002$).

Procrustes tests performed on the NMDS ordinations indicated significant concordance between pitfall trapped and fogged assemblages ($m^2 = 0.77$, correlation coefficient = 0.48, $P = 0.026$); however, this was not sufficiently strong ($m^2 = <50$, correlation coefficient >0.7) to regard robust surrogacy between sampling methods (Heino, 2010).

Abundance and richness of woodland associated species were similar in all three forest types for pitfall sampled assemblages (Fig. 3a and e, Appendix C). Fogged spruce assemblages contained significantly more woodland species than semi-natural forests (Fig. 3f); however, only ash forests had significantly lower woodland abundance than spruce (Fig. 3b). The fogged spruce assemblage contained significantly fewer generalist species than ash forests (Fig. 3d) and showed a general trend of reduced generalist abundance. However, it should be noted that richness measures obtained from canopy fogging may be less reliable due to the low abundances caught via this sampling method. Spruce plantations sampled by pitfall traps contained significantly less generalist richness than ash and oak forests (Fig. 3g), and generalist species abundance was significantly higher in oak forests than either spruce or ash forests (Fig. 3c).

Very few species of active hunting spider were recorded in either pitfall assemblages ($n = 10$, mean per sample = 0.8 ± 1.1 SD) or fogged assemblages ($n = 2$, mean per sample = 0.1 ± 0.3 SD). In addition, no active hunting spiders were captured in spruce plantations (Fig. 4). Pitfall assemblages in spruce plantations were confined to two web-hunting families, Linyphidae and Theridiidae;

Table 1

Indicator species identified from the three sampled forest types showing species habitat specialism, hunting guild and associated test statistics.

| Forest type	Sampling method	Family	Species	Habitat association	Hunting guild	Indicator value	P-value
Ash	Pitfall trap	Linyphiidae	*Ceratinella scabrosa*	Generalist	Web	0.831	0.013
	Pitfall trap	Linyphiidae	*Lepthyphantes tenebricola*	Woodland	Web	0.808	0.039
	Canopy fog	Tetragnathidae	*Tetragnatha montana*	Generalist	Web	0.773	0.044
Oak	Pitfall trap	Linyphiidae	*Walckenaeria acuminata*	Generalist	Web	0.850	0.012
	Pitfall trap	Linyphiidae	*Microneta viaria*	Generalist	Web	0.793	0.039
	Pitfall trap	Linyphiidae	*Walckenaeria dysderoides*	Generalist	Web	0.772	0.033
Spruce	Pitfall trap	Linyphiidae	*Centromerus dilutus*	Generalist	Web	0.840	0.015
	Pitfall trap	Linyphiidae	*Diplocephalus latifrons*	Woodland	Web	0.809	0.042
	Pitfall trap	Linyphiidae	*Monocephalus fuscipes*	Woodland	Web	0.727	0.050
	Canopy fog	Linyphiidae	*Pelecopsis nemoralis*	Woodland	Web	0.921	0.006
	Canopy fog	Linyphiidae	*Lepthyphantes obscurus*	Woodland	Web	0.816	0.030
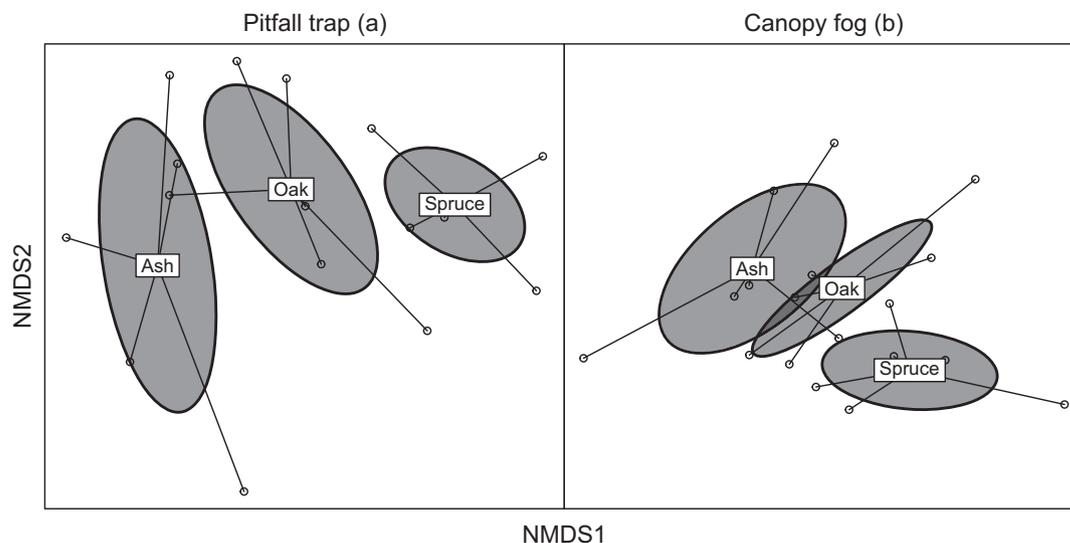
Fig. 2. Non-Metric Multidimensional Scaling (NMDS) ordination comparing the spider assemblage composition of three forest types for (a) pitfall trapping assemblages and (b) canopy fogged assemblages. Stress scores for each ordination are 0.14 and 0.15 respectively. Points are sampled sites with lines connecting to habitat centroids and polygons represent 95% confidence interval of forest type centroids.

fogging assemblages also included web hunters from the family Tetragnathidae (Fig. 4).

CWM body size differed significantly between spiders sampled by pitfall traps and fogging ($U = 90$, $P = 0.022$, pitfall trapping: mean (±SD) 5.1 ± 2.7, range 1.7–13 mm; fogging: mean 3.2 ± 2.3, range 8.2–0.5 mm). In pitfall-trapped assemblages, spider body-size was smaller in spruce than semi-natural forests, although the only significantly difference in CWM spider body size was between oak and spruce ($\chi^2 = 1.62$, $P = 0.011$, ash mean (±SD) 5.6 ± 1.4, oak mean 6.5 ± 3.7, spruce mean 3.1 ± 1.2). No significant differences in body size were found between forest types sampled by fogging (ash mean (±SD) 3.8 ± 3.3, oak mean 2.9 ± 1.5, spruce mean 2.8 ± 2.0).

4. Discussion

To explore possible congruency in biological assessment methods, we evaluated ground-based pitfall trapping compared to canopy insecticide fogging of spiders from three closed-canopy forest types. Both pitfall trapping and canopy fogging separated spider assemblages of managed plantation forest from semi-natural forest types. Both methods indicated that the greatest differences in assemblage composition were between ash and spruce plantations. Despite these broadly similar patterns in composition, congruency between sampling methods was not strongly supported, specifically, procrustes rotation produced low correlation scores. This illustrates that at the broadest scale of forest type (oak, ash and spruce) differences in community composition were consistent between sampling methods, but the between site differences were not consistent enough to allow surrogacy in methods. Therefore, unless surveys are designed to look specifically at broad scale patterns in well-replicated studies, forest assessments of spider community assemblages require separate sampling of forest layers. However, where a single sampling method is implemented a clear statement of the bias is essential.

Pitfall trapping recorded greater species richness in ash and oak assemblages than spruce plantations. This is consistent with previous research showing low species richness of ground-dwelling invertebrates within managed coniferous forest sampled by pitfall trapping (Finch, 2005; Fuller et al., 2008). In contrast, no differences in species richness were detected between forest types

surveyed by fogging. The divergent patterns in ground and canopy richness may provide evidence for stratified biodiversity patterns between forest layers and may relate to comparative differences in the habitat heterogeneity of forest stratums. Although it has been shown that branch composition and leaf density influence arthropod composition (Gunnarsson, 1992; Halaj et al., 2000), it is possible that differences in habitat heterogeneity within the canopies of the three forest types is not as influential to spider richness as heterogeneity at the ground layer. However, it should also be noted that the disparity in patterns of species richness between sampling methods might also be related to the uneven sampling effort between surveys at different forest layers (Pinzon et al., 2011). For example, canopy sampling may not have been comprehensive enough to detect differences in coarse measures such as species richness. Rarefaction for fogging showed that species richness curves for ash and oak were steeper than spruce plantations, indicating that the sampling in these sites was not as complete. Greater sampling effort, i.e. more trees fogged per forest patch, may detect a larger disparity between semi-natural and plantation forests. However, our relative sampling effort is likely to be reasonable and consistent with other studies (see Zheng et al., 2015; Yanoviak et al., 2003) given the logistical difficulties and the labour intensive nature of this method.

4.1. Hunting guilds, habitat specialism and body size representation

Web-hunting Linyphiids dominated the assemblages of both survey methods. Active hunters were represented by very few individuals in semi-natural forest types and there was a total absence of active-hunting species in spruce plantations for both trapping methods (proportion of active hunters: ash 1.8%, oak 0.5%). This is consistent with previous surveys of plantation forest conducted using pitfall trapping in the same region (Oxbrough et al., 2010; Fuller et al., 2014). Barsoum et al. (2014) compared both Irish and English spider assemblages and found forest plantations in Ireland to be dominated by web-hunting Linyphiidae, whereas assemblages in England comprised a mixture of hunting guilds. In North American broad-leaf forests, Larrivée and Buddle (2009) found 21 species of hunting spiders from understory and canopies sampled by beating; while sweep netting by Stratton et al. (1978) found hunting spiders in the understories of three types of North
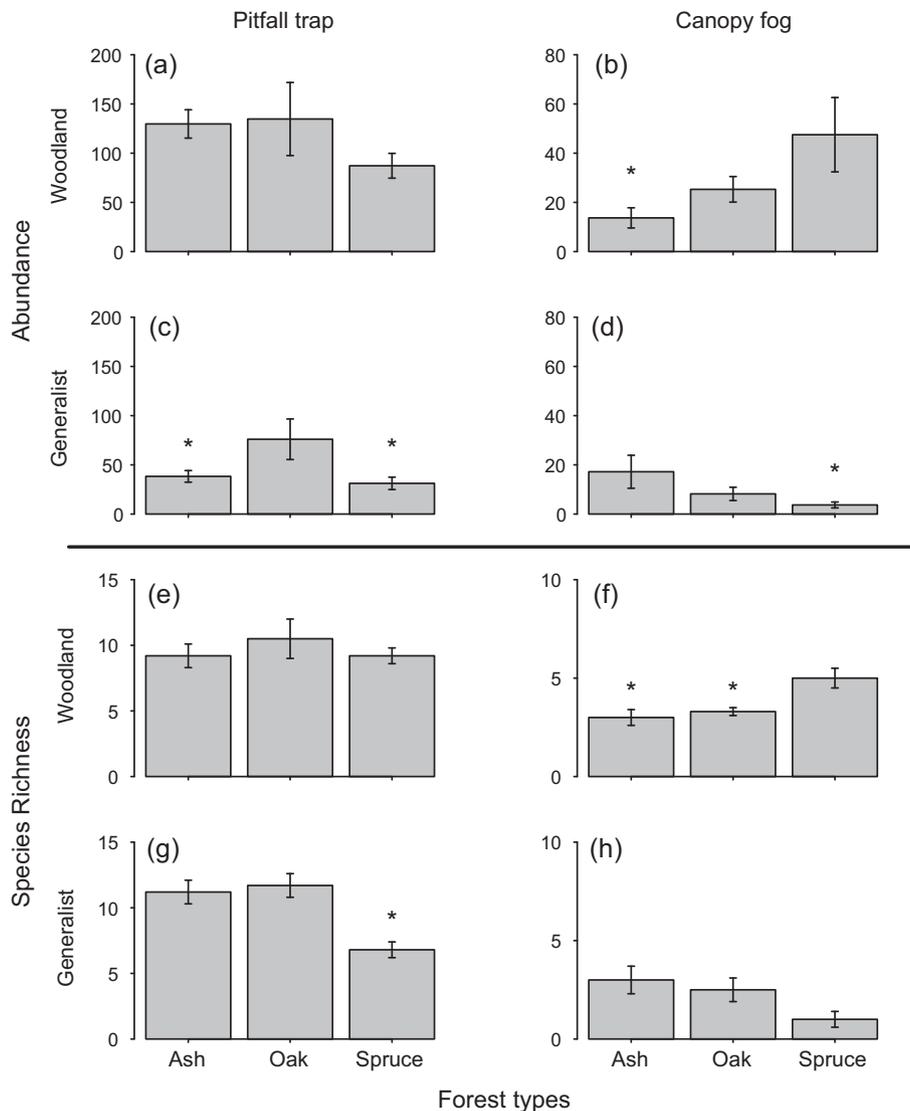
Fig. 3. Mean (±s.e) spider abundance and species richness of woodland and generalist species per forest type for pitfall trapping and canopy fogging. Asterisks indicate significant differences from the forest type with the greatest species richness or abundance in each plot as derived from generalised linear models (Tukey pairwise comparisons *P* < 0.05). See Appendix C for model statistics. Thick central line separates abundance and species richness plots.

American coniferous forest. The paucity of active hunters in the Irish forest fauna may be a result of meteorological conditions favouring smaller species such as the web-hunting Linyphiidae (Entling et al., 2010). This combined with the high dispersal potential of Linyphiidae that are able to balloon as adults over vast distances (Thomas et al., 2003; Bell et al., 2005), may help to explain their dominance in the severely fragmented Irish forest system where less than 1% of the land cover was forested at the end of the 19th century (Forest Service, 2007; Forest Europe et al., 2011).

It might be expected that older forests would accumulate more forest specialists and hence old growth and/or semi-natural forests would contain a greater diversity of specialists than relatively young plantations (Niemelä, 1997; Fuller et al., 2008). However, pitfall trapping indicates no significant difference in specialist woodland species abundance or richness between forest types. Moreover, fogging shows more woodland species abundance and richness in spruce than in natural forest and the majority of indicator species of spruce were woodland associated whereas most indicators of semi-natural forests were generalists. Pawson et al. (2008) found that mature exotic plantation forests were able to support native forest beetles and compared to other non-native

habitats, such as pasture and clearfell forestry sites, beetle composition in these mature plantations was most similar to native forest. This gradient of landscape suitability was also proposed by Brockerhoff et al. (2008) who suggest that plantation forest could provide useful habitat where pre-plantation areas are non-natural habitat. In the Irish context, plantation forest is not replacing semi-natural forested and it is unlikely the woodland specialists identified in the current study would be found in open habitat in the region (Oxbrough et al., 2006, 2007). Therefore, given that semi-natural forest in the Irish landscape is scarce (1% of total land cover), these areas of plantation maybe important for the canopy fauna, providing essential habitat in an predominantly open landscape. The disparity between ground and canopy results for woodland associated species highlights the need for greater sampling coverage in forest assessments.

While we show that pitfall catches provided a larger CWM body-size than fogging, this is not unexpected given the bias of pitfall trapping to select for larger species (Lang, 2000), which are typically more active. Interestingly, we were able to detect a significant difference in body size between forest types from ground samples, differences that were not detected from canopy
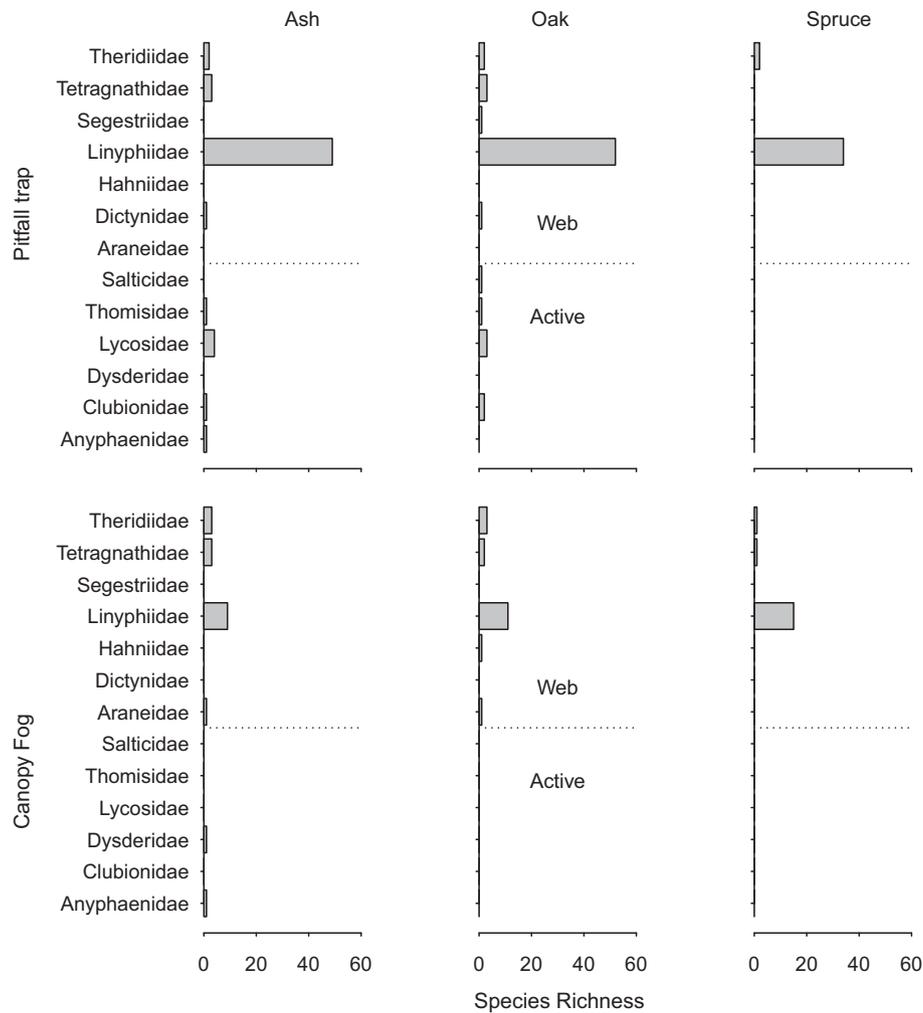
Fig. 4. Total species richness per spider family recorded in three forest types (ash, oak and spruce). Spiders sampled by pitfall trapping are shown in the top three plots, those sampled by canopy fogging are shown in the bottom three plots. Families in each plot are split (dotted line) by those families that exhibit a web-hunting (Web) strategy and those with an active-hunting (Active) strategy.

samples. From ground samples, spider body-size tended to be smaller in spruce plantations than oak and ash forests. This is an interesting finding and may result from different moisture and light regimes and would require targeted investigation to confirm the underlying drivers. Previous studies have indicated moisture and climate as potential drivers of body size variation (Wagner et al., 2003; Entling et al., 2010). Wagner et al. (2003) demonstrated a reduction in average body size and a change in dominant foraging mode (active to web), and suggested a moisture gradient could be driving stratification in their study of forest spider at various litter depths. At a European scale Entling et al. (2010) looked at size-climate relationships across European spider assemblages and concluded body size decreases from warm/dry to cool/moist climates.

4.2. Vertical stratification

While we show stratification of spider families between forest layers, it was not simply that active ground-hunting families such as Lycosidae and Clubionidae dominated the ground catches because all sampling was dominated by small web spinners. Very few studies have attempted to look at both canopy and ground dwelling spider assemblages (but see Docherty and Leather, 1997; Pinzon et al., 2011, 2013) as vertical stratification of spider

guilds in forests is difficult to study given the very different survey strategies required, which can lead to sampling designs that are not comparable. Most studies concerning vertical stratification in temperate and boreal forests have looked at discrete elements, focusing on canopy–understory stratification (Larrivée and Buddle, 2009; Aikens and Buddle, 2012) or different litter layers (Wagner et al., 2003) where vertical stratification and shifts in family dominance have been reported.

Although all samples were dominated by Linyphiidae in the current study, pitfall traps did contain five active hunting families in comparison to just two recorded from fogging. Of these families, only Anyphaenidae was recorded from both ground and canopy sampling, indicating strong family stratification of assemblages. In sampled canopies, web-hunters from the families Theridiidae and Tetragnathidae are also abundant. The only non-Linyphiidae species caught in moderate abundance in the pitfall traps was the Theridiidae, *Robertus lividus*, a ground-dwelling habitat generalist. The majority of spiders identified in the indicator analysis in both the canopy and the ground belonged to the same guild: web-hunting species of Linyphiidae, with *T. montana*, a dominant spider in ash canopies, the only exception. Differential representation of spider families between methods in the current study and the large number of species unique to each method (pitfall n = 73, fogging n = 22) indicates strong stratification. This stratification

illustrates the need to incorporate multiple sampling methods across various forest strata if a more complete understanding of the forest fauna is required. This corresponds to the findings from North American spruce where a strong difference in assemblage composition was recorded between forest layers (Pinzon et al., 2011, 2013).

5. Conclusions

Our study set out to examine the correspondence between pitfall trapping and canopy fogging sampling methods for defining differences in spider assemblage structure in several forest types. Our findings show that if fine detailed species and family based information (e.g. habitat association, hunting guild, body size) is required, then separate targeted surveys are needed, as results were not consistent between methods. Furthermore, many species were unique to a single survey methods, so if management priorities are to maintain or increase diversity, then monitoring of both ground and canopy fauna needs to be undertaken. Comparisons using solely species incidence obtained by either survey method should be avoided. This coarse metric reduces data complexity, can be highly susceptible to sampling effort and can be misleading in habitats that contain numerous non-specialist species such as ecotones, disturbed and small-fragmented habitats (Downie et al., 1996; Niemelä, 1997).

Associations of community composition between the ground and canopy assemblages were not strong enough to allow surrogacy at the individual site level. Weak correlations between site community compositions imply forest assessments need to include both ground and canopy sampling to provide information on these discrete spider assemblages. In studies where a single sampling method is implemented clear statements of the sampling bias should be incorporated. Although our sampling and analyses indicate discrete ground and canopy assemblages, we were able to define and separate the different forest types using either survey method. Both surveys found the greatest community composition differences between ash and spruce. The fact that both survey methods produced similar outcomes for the broad scale (forest type) community analysis, suggests that either method may be suitable for testing management differences based on spider community assemblages in well-replicated experiments within similar ecosystems. However, it must be emphasized that only the broad variations in composition between forest types are similar, and not the actual compositions as indicated by the weak site-based correlation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.10.006.

References

Aikens, K.R., Buddle, C.M., 2012. Small-scale heterogeneity in temperate forest canopy arthropods: stratification of spider and beetle assemblages. Can. Entomol. 144, 526–537.

Barsoum, N., Fuller, L., Ashwood, F., Reed, K., Bonnet-Lebrun, A.S., Leung, F., 2014. Ground-dwelling spider (Araneae) and carabid beetle (Coleoptera: Carabidae) community assemblages in mixed and monoculture stands of oak (*Quercus robur* L./*Quercus petraea* (Matt.) Liebl.) and Scots pine (*Pinus sylvestris* L.). For. Ecol. Manage. 321, 29–41.

Bell, J.R., Bohan, D.A., Shaw, E.M., Weyman, G.S., 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. Bull. Entomol. Res. 95, 69–114.

Berndt, L.A., Brockerhoff, E.G., 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.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17, 925–951.

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684.

Docherty, M., Leather, S.R., 1997. Structure and abundance of arachnid communities in Scots and lodgepole pine plantations. For. Ecol. Manage. 95, 197–207.

Downie, I.S., Coulson, J.C., Butterfield, J.E.L., 1996. Distribution and dynamics of surface-dwelling spiders across a pasture-plantation ecotone. Ecography 19, 29–40.

Duffey, E., 1968. An ecological analysis of spider fauna of sand dunes. J. Anim. Ecol. 37, 641–674.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Entling, W., Schmidt-Entling, M.H., Bacher, S., Brandl, R., Nentwig, W., 2010. Body size-climate relationships of European spiders. J. Biogeogr. 37, 477–485.

Erwin, T.L., 1982. Tropical forests their richness in Coleoptera and other Arthropod species. Coleopts. Bull. 36, 74–75.

Finch, O.D., 2005. Evaluation of mature conifer plantations as secondary habitat for epigeic forest arthropods (Coleoptera: Carabidae; Araneae). For. Ecol. Manage. 204, 21–34.

Forest Europe, UNECE, and FAO, 2011. State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe. Oslo.

Forest Service, 2007. National Forest Inventory: Republic of Ireland Results. Department of Agriculture, Fisheries and Food, Wexford, Ireland.

Fuller, R.J., Oliver, T.H., Leather, S.R., 2008. Forest management effects on carabid beetle communities in coniferous and broadleaved forests: implications for conservation. Insect Conserv. Divers. 1, 242–252.

Fuller, L., Newman, M., Irwin, S., Kelly, T., O'Halloran, J., 2014. Ground-dwelling spider diversity in rare European oak and yew woodlands and the impact of grazing. Biodivers. Conserv. 23, 1911–1929.

Greenslade, P.J.M., 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). J. Anim. Ecol. 33, 301–310.

Gunnarsson, B., 1992. Fractal dimension of plants and body size distribution in spiders. Funct. Ecol. 6, 636–641.

Halaj, J., Ross, D.W., Moldenke, A.R., 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos 90, 139–152.

Heino, J., 2010. Are indicator groups and cross-taxon congruence useful for predicting biodiversity in aquatic ecosystems? Ecol. Ind. 10, 112–117.

Higgins, G.T., Martin, J.R., Perrin, P.M., 2004. National Survey of Native Woodland in Ireland. Dept. of the Environment, Heritage and Local Government.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical J. 50, 346–363.

Hsieh, Y.L., Linsenmair, K.E., 2012. Seasonal dynamics of arboreal spider diversity in a temperate forest. Ecol. Evol. 2, 768–777.

Ji, Y., Ashton, L., Pedley, S.M., et al., 2013. Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding. Ecol. Lett. 16, 1245–1257.

Lang, A., 2000. The pitfalls of pitfalls: a comparison of pitfall trap catches and absolute density estimates of epigeal invertebrate predators in arable land. Anzeiger Fur Schadlingskunde – J. Pest Sci. 73, 99–106.

Larrivée, M., Buddle, C.M., 2009. Diversity of canopy and understorey spiders in north-temperate hardwood forests. Agric. For. Entomol. 11, 225–237.

Lowman, M.D., Wittman, P.K., 1996. Forest canopies: methods, hypotheses, and future directions. Annu. Rev. Ecol. Syst. 27, 55–81.

Luff, M.L., Eyre, M.D., 1988. Soil-surface activity of weevils (Coleoptera: Curculionoidea) in grassland. Pedobiologia 32, 39–46.

Marc, P., Canard, A., Ysnel, F., 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agric. Ecosyst. Environ. 74, 229–273.

Melbourne, B.A., 1999. Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. Aust. J. Ecol. 24, 228–239.

Niemelä, J., 1997. Invertebrates and boreal forest management. Conserv. Biol. 11, 601–610.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., et al., 2010. Vegan: Community Ecology Package. R package Version 1.17-2. <http://CRAN.Rproject.org/package = vegan>.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. For. Ecol. Manage. 212, 171–183.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006. The initial effects of afforestation on the ground-dwelling spider fauna of Irish peatlands and grasslands. For. Ecol. Manage. 237, 478–491.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2007. Biodiversity of the ground-dwelling spider fauna of afforestation habitats. Agric. Ecosyst. Environ. 120, 433–441.

Oxbrough, A., Irwin, S., Kelly, T.C., O'Halloran, J., 2010. Ground-dwelling invertebrates in reforested conifer plantations. For. Ecol. Manage. 259, 2111–2121.

Ozanne, C.M.P., Anhuf, D., Boulter, S.L., Keller, M., Kitching, R.L., Korner, C., Meinzer, F.C., Mitchell, A.W., Nakashizuka, T., Dias, P.L.S., Stork, N.E., Wright, S.J., Yoshimura, M., 2003. Biodiversity meets the atmosphere: a global view of forest canopies. Science 301, 183–186.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290.

Pawson, S.M., Brockerhoff, E.G., Meenken, E.D., 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.

Pedley, S.M., Dolman, P.M., 2014. Multi-taxa trait and functional responses to physical disturbance. J. Anim. Ecol. 83, 1542–1552.

Pedley, S.M., Martin, R.D., Oxbrough, A., Irwin, S., Kelly, T.C., O'Halloran, J., 2014. Commercial spruce plantations support a limited canopy fauna: evidence from a multi taxa comparison of native and plantation forests. For. Ecol. Manage. 314, 172–182.

Peres-Neto, P.R., Jackson, D.A., 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. Oecologia 129, 169–178.

Pinzon, J., Spence, J.R., Langor, D.W., 2011. Spider assemblages in the overstory, understory, and ground layers of managed stands in the western boreal mixedwood forest of Canada. Environ. Entomol. 40, 797–808.

Pinzon, J., Spence, J.R., Langor, D.W., 2013. Diversity, species richness, and abundance of spiders (Araneae) in different strata of boreal white spruce stands. Can. Entomol. 145, 61–76.

R Development Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, M.J., 1987. The Spiders of Great Britain and Ireland. Harley Books, Colchester.

Roberts, M.J., 1996. Spiders of Britain and Northern Europe. HarperCollins Publishers Ltd, London.

Robinson, J.V., 1981. The effect of architectural variation in habitat on a spider community – an experimental field-study. Ecology 62, 73–80.

Schmitz, O.J., Hamback, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. Am. Nat. 155, 141–153.

Southwood, T.R.E., Wint, G.R.W., Kennedy, C.E.J., Greenwood, S.R., 2005. The composition of the arthropod fauna of the canopies of some species of oak (*Quercus*). Eur. J. Entomol. 102, 65–72.

Spence, J.R., Langor, D.W., Niemelä, J., Cárcamo, H.A., Currie, C.R., 1996. Northern forestry and carabids: the case for concern about old-growth species. Ann. Zool. Fenn. 33, 173–184.

Standen, V., 2000. The adequacy of collecting techniques for estimating species richness of grassland invertebrates. J. Appl. Ecol. 37, 884–893.

Stork, N.E., Hammond, P.M., 1997. Sampling arthropods from tree crowns by fogging with knockdown insecticides: lessons from studies of oak tree beetle assemblages in Richmond Park (UK). In: Stork, N.E., Adis, J., Didham, R.K. (Eds.), Canopy Arthropods. Chapman and Hall, London, pp. 3–26.

Stratton, G.E., Uetz, G.W., Dillery, D.G., 1978. A comparison of the spiders of three coniferous tree species. J. Arachnol. 6, 219–226.

Straw, N.A., Fielding, N.J., Waters, A., 1996. Phytotoxicity of insecticides used to control aphids on Sitka spruce, *Picea sitchensis* (Bong) Carr. Crop Prot. 15, 451–459.

Thomas, C.F.G., Brain, P., Jepson, P.C., 2003. Aerial activity of linyphiid spiders: modelling dispersal distances from meteorology and behaviour. J. Appl. Ecol. 40, 912–927.

Topping, C.J., Sunderland, K.D., 1992. Limitations to the use of pitfall traps in ecological-studies exemplified by a study of spiders in a field of winter-wheat. J. Appl. Ecol. 29, 485–491.

Vasconcelos, H.L., Vilhena, J.M.S., Magnusson, W.E., Albernaz, A., 2006. Long-term effects of forest fragmentation on Amazonian ant communities. J. Biogeogr. 33, 1348–1356.

Wagner, J.D., Toft, S., Wise, D.H., 2003. Spatial stratification in litter depth by forest-floor spiders. J. Arachnol. 31, 28–39.

Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. Mvabund – an R package for model-based analysis of multivariate abundance data. Methods Ecol. Evol. 3, 471–474.

Warton, D.I., Wright, S.T., Wang, Y., 2012. Distance-based multivariate analyses confound location and dispersion effects. Methods Ecol. Evol. 3, 89–101.

Wise, D.H., 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge, UK.

Yang, C.X., Wang, X.Y., Miller, J.A., de Blecourt, M., Ji, Y.Q., Yang, C.Y., Harrison, R.D., Yu, D.W., 2014. Using metabarcoding to ask if easily collected soil and leaf-litter samples can be used as a general biodiversity indicator. Ecol. Ind. 46, 379–389.

Yanoviak, S.P., Nadkarni, N.M., Gering, J.C., 2003. Arthropods in epiphytes: a diversity component that is not effectively sampled by canopy fogging. Biodivers. Conserv. 12, 731–741.

Zheng, G., Li, S.Q., Yang, X.D., 2015. Spider diversity in canopies of Xishuangbanna rainforest (China) indicates an alarming juggernaut effect of rubber plantations. For. Ecol. Manage. 338, 200–207.

Ziesche, T.M., Roth, M., 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: What makes the difference, tree species or microhabitat? For. Ecol. Manage. 255, 738–752.