

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

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20

21 **Abstract**

22 Biological assessments of forest systems often involve a single ground-  
23 invertebrate sampling method that may ignore the biological component of the  
24 non-sampled canopy. Pitfall trapping for ground-active arthropods is a widely  
25 implemented technique for biological assessment in forested and open habitats.  
26 Although much evidence highlights the biases of pitfall trapping, this evidence  
27 typically comes from open-habitat crop and grassland systems. In forest systems  
28 where much of the biodiversity is found within the above-ground structure,  
29 management recommendations based solely on ground sampling may not  
30 represent the diversity within the three dimensional forest habitat. We provide  
31 evidence from combined ground and canopy sampling of three major forest  
32 types within the study region. We use canopy insecticide fogging to compare  
33 with more traditional ground-based pitfall trapping, and use spiders as a  
34 comparative species-rich biota that is able to colonise most terrestrial habitats  
35 and is strongly affected by changes in environmental condition.  
36 We identified 3933 spiders from 109 species from the 18 forest patches sampled.  
37 Both types of sampling defined differences in community composition between  
38 forest types in a similar manner; hence, either method could be used to evaluate  
39 differences or test management regimes in well-replicated experiments of forest  
40 type. However, the association in community composition between ground and  
41 canopy assemblages at the individual site-based level was weak; we found low  
42 correlation between the two data sets indicating that surrogacy between  
43 methods was not supported at this level. Furthermore, disparities in spider  
44 habitat association, body size, hunting guild and vertical stratification of spider  
45 families indicates that where detailed species and family-based information is

46 required, or if inventorying is necessary, then multiple targeted surveys are  
47 essential.

48

49 Keywords: canopy fogging, arachnid, forest management, arthropod, pitfall,  
50 spruce plantation.

51

## 52 **1. Introduction**

53 Biodiversity must be sampled in a way that fits research questions but also  
54 meets time and financial budgets. Often these constraints lead to the use of a  
55 single survey procedure to derive data with which to draw conclusions that  
56 inform policy and management. This leaves questions regarding the consistency  
57 of those conclusions if an alternative sampling strategy had been chosen. In  
58 complex systems, such as forested landscapes, the three-dimensional structure  
59 poses problems for capturing representative samples across vegetation layers  
60 (Pinzon et al. 2011). The importance of forest systems (Ozanne et al. 2003),  
61 coupled with the potential of sample bias, means there is a growing need to  
62 validate sampling strategies to strengthen management recommendations based  
63 on these single survey practices.

64

65 Arthropod diversity is frequently used to assess biological condition in applied  
66 forest research (Spence et al. 1996, Berndt et al. 2008, Pedley et al. 2014) and  
67 more fundamental aspects of ecology, including fragmentation and disturbance  
68 (Vasconcelos et al. 2006, Pedley and Dolman 2014). New DNA barcoding  
69 techniques (Yang et al. 2014), which negate the often laborious taxonomy  
70 associated with arthropod sampling, are enabling quicker processing times that  
71 may proliferate the use of arthropod monitoring (Ji et al. 2013). However,  
72 conventional taxonomic and many contemporary DNA barcoding techniques rely  
73 on traditional invertebrate collection methods. One of the most commonly  
74 employed sampling techniques for epigeic arthropods is pitfall trapping. Pitfall  
75 trapping provides a passive means of surveying that, once established, can

76 continuously trap active species with only brief visits needed to service traps.  
77 Although pitfall trapping has a long history in ecology, its ability to provide non-  
78 bias sampling of habitat has been brought into question (Topping and  
79 Sunderland 1992, Lang 2000). Pitfalls by their nature target active ground-  
80 dwelling species, and can underrepresent less mobile, small-bodied species and  
81 species typical of higher strata (Greenslade 1964, Lang 2000, Standen 2000).  
82 Furthermore, pitfall catches are a representation of animal density, conditional  
83 on animal activity; if activity is disproportionately affected by vegetation  
84 structure, shading or animal interactions between sites, then catches may not be  
85 comparable (Greenslade 1964, Melbourne 1999). Where environmental  
86 conditions are similar, comparisons across sites are suitable as long as pitfall  
87 trap data are used as an index of the density based on activity and not a species  
88 inventory of the sampled habitat (Luff and Eyre 1988, Oxbrough et al. 2006).  
89  
90 Much of the available methodological literature concerning pitfall trap bias  
91 comes from crop and grassland studies (e.g. Topping and Sunderland 1992,  
92 Standen 2000). However, extensive arthropod monitoring of closed-canopy  
93 forests has been conducted with ground-based methods (e.g. Docherty and  
94 Leather 1997, Oxbrough et al. 2005, Berndt et al. 2008). Many studies of this  
95 nature make comparisons between the arthropod biodiversity of different forest  
96 types with inherently different ground, understory and canopy structures (Fuller  
97 et al. 2008, Barsoum et al. 2014). Although such studies do not imply that pitfall  
98 trapping will reveal the biodiversity related to the entire three-dimensional  
99 structure of the forest, there are few studies that can elucidate the non-sampled  
100 aboveground component of forest biodiversity in a similar manner to the

101 methodological papers concerning crop and grasslands (but see Pinzon et al.  
102 2011). This problem of the non-sampled biodiversity is perhaps more significant  
103 within forest systems as forest canopies contain a large proportion of the total  
104 arthropod diversity on Earth (Erwin 1982, Lowman and Wittman 1996).

105

106 While canopy sampling is considerably more challenging than many ground  
107 sampling methods due to the difficulties in accessing tree canopies, ground-  
108 based insecticide fogging can negate these access problems. Insecticide fogging  
109 of canopy-dwelling species has proven a reliable survey method but has received  
110 less consideration in temperate and boreal zones than in tropical regions.

111 Canopy fogging has proven an effective way to sample temperate canopy  
112 invertebrates and to measure biodiversity patterns within single species, across  
113 temporal dynamics and between forest types (Southwood et al. 2005, Hsieh and  
114 Linsenmair 2012, Pedley et al. 2014). However, fogging is limited by weather  
115 conditions, with at least several hours of dry, still weather required for  
116 successful sampling. This method may also overlook some species such as aphids  
117 or other phloem feeders (Stork and Hammond 1997), or those within certain life  
118 stages, such as within cocoons, retreats or burrows and those attached by silken  
119 threads. While these sampling biases will affect inventorying canopy  
120 invertebrates in much the same way as pitfall trap biases do for ground-based  
121 invertebrates, it is likely that standardised canopy fogging will allow for  
122 comparisons to be made across sampled forest sites.

123

124 Among the arthropod groups frequently investigated in ecological surveys,  
125 spiders provide an effective means of habitat assessment as they are greatly

126 affected by changes in habitat structure (Duffey 1968, Robinson 1981) and  
127 respond quickly to brief or sudden changes in environmental conditions, such as  
128 variations in prey density, pesticides, or pollution (Marc et al. 1999). Spiders are  
129 a species rich group and, being one of the top macro-invertebrate predators,  
130 have strong influences in food webs (Wise 1993, Schmitz et al. 2000). Differences  
131 in spider community assemblages within forest types have often been attributed  
132 to differences in habitat heterogeneity (Pinzon et al. 2011, Pedley et al. 2014).  
133 The assemblage composition of the forest-floor is influenced by light availability,  
134 volume and decay stage of debris, moisture and temperature (Ziesche and Roth  
135 2008); while canopy leaf/needle density and branch architecture has been  
136 shown to influence community composition above the ground layer (Gunnarsson  
137 1992, Halaj et al. 2000). Although some understanding of the factors influencing  
138 community composition in these habitats exists, we do not yet know if common  
139 sampling techniques differentially interpret community dissimilarities between  
140 forest types.

141

142 In the current study, we selected three distinctive forest types that were likely to  
143 vary in spider composition, semi-natural ash (*Fraxinus excelsior*) forests, semi-  
144 natural oak (*Quercus petraea*) forests and Sitka spruce (*Picea sitchensis*)  
145 plantations. We did not attempt to directly compare species richness or  
146 abundance between canopy and ground trapping, as sampling effort is not  
147 consistent between the two methods. Rather, we examined whether there is  
148 correspondence between the two methods for defining differences in  
149 assemblage structure between the three forest types. For each of the following  
150 hypotheses we looked for idiosyncratic and corresponding changes in

151 biodiversity structure across forest types for the ground and canopy sampling  
152 techniques. 1) Assemblages sampled in the canopy and the ground differ  
153 similarly between the forest stands and forest types. 2) Patterns of hunting  
154 guilds (active and web spinners), habitat specialism (woodland and generalist),  
155 and body size will be inconsistent across forest types for ground and canopy  
156 sampled assemblages. 3) Spider families will show vertical stratification between  
157 ground and canopy sampling. Finally, we discuss whether there is possible  
158 surrogacy between ground and canopy methods. This is one of the first studies to  
159 compare and interpret forest biodiversity obtained from canopy and ground  
160 trapped invertebrate assemblages.



161 **2. Methods**

162 Three closed-canopy forests types were sampled across Ireland (Appendix A);  
163 six ash (*Fraxinus excelsior*) dominated semi-natural woodlands , six oak (*Quercus*  
164 *petraea*) dominated semi-natural woodlands and six second-rotation Sitka  
165 spruce (*Picea sitchensis*) plantations (hereafter referred to as ash forest, oak  
166 forest and spruce plantation, respectively). All stands were a minimum of 6 ha in  
167 size and 100 m in width. Sitka spruce plantations were selected as they are the  
168 dominant species in the Irish forest estate, comprising approximately 60% of the  
169 forest cover and are a non-native species (Forest Service 2007). Ash and oak  
170 forests were selected as they are the most common native tree species in Irish  
171 semi-natural forests, comprising 22% and 18%, respectively (Higgins et al.  
172 2004), and were expected to have contrasting biodiversity to spruce plantations.  
173 The semi-natural forest types considered in this study comprised a mix of tree  
174 species, i.e. oak-dominated forests included oak, birch and holly, while ash-  
175 dominated forests included ash, oak and hazel. Semi-natural ash and oak forests  
176 were at least 150 years old, whereas sampled spruce plantations ranged from  
177 mid rotation 20-30 year old closed-canopy stands to 60-year-old commercially  
178 mature stands.

179

180 **2.1 Canopy sampling**

181 Canopy fogging was conducted once at each of the 18 study sites. In each  
182 sampled forest stand a fogging plot was established in a representative area of  
183 the site in terms of stand structure and vegetation cover. A target tree was  
184 selected at the centre of each fogging plot that corresponded to the forest type  
185 being sampled. The fogging plot consists of 16 plastic sheets (1.5m<sup>2</sup>), with a

186 combined area of 24m<sup>2</sup>, arranged around the central tree on the eight cardinal  
187 and ordinal compass bearings. Plastic sheets were suspended 1m above the  
188 ground to reduce the risk of contamination by ground-active species not  
189 sampled by fogging (Stork and Hammond 1997). Sampling sheets were  
190 separated by 0.5m from each other and all trees within the fogging plot. The  
191 fogging plot was at least 50m from the forest perimeter to reduce possible edge  
192 effects.

193

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

205

## 206 **2.2 Pitfall sampling**

207 Pitfall trapping was conducted for 63 days at each of the 18 study sites. At each  
208 site, pitfall traps were used to collect ground-dwelling spiders from three  
209 sampling plots. Each sampling plot was 50m apart and 50m away from the forest  
210 edge and comprised a transect of five pitfall traps spaced 2m apart. Pitfall traps

211 consisted of a plastic cup 7cm in diameter and 9cm in depth. Traps were filled  
212 with ethylene glycol (1cm deep) to act as a killing and preserving agent. All traps  
213 were set in mid-May 2007 and left *in situ* for nine weeks with traps serviced  
214 every three weeks. There was considerable animal disturbance (> 80% trap loss)  
215 at two of the spruce study sites sampled during 2007 and so these sites were re-  
216 sampled during the same period in 2008 with previous material being discarded.  
217 No other trap disturbance was recorded during the study. Catches from each site  
218 were pooled across the nine weeks for analyses giving a total of 945 trap days  
219 (63 days x 5 traps x 3 plots) per site.

220

### 221 **2.3 Analysis**

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

229

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

235

236 To visualise the community composition among forest types for each sampling  
237 method, we used non-Metric Multidimensional Scaling (NMDS), performed on a  
238 matrix of Bray-Curtis dissimilarities of abundance data (square root transformed  
239 and Wisconsin double standardization) using the vegan package. Differences in  
240 community composition between forest types were tested using the package  
241 mvabund (Wang et al. 2012), which allows hypothesis testing by multivariate  
242 implementation of generalised linear models. This method does not confound  
243 location with dispersion effects (a change in the mean-variance relationship),  
244 which can lead to misleading results and inflation of type-1 and 2 errors (Warton  
245 et al. 2012). Using likelihood-ratio-tests (LR) in the summary.manyglm function  
246 we tested for significant differences in assemblage composition of spruce and  
247 semi-natural ash and oak forests.

248

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

256

257 Species richness and abundance of woodland associated and generalist species  
258 were compared among forest types separately for ground and canopy sampling  
259 using generalised linear models (GLMs). The appropriate error term for each  
260 analysis was selected by patterns in residuals and by examining model

261 dispersion. Differences among forest type means were examined by Tukey  
262 pairwise comparisons using the glht function in the multcomp package (Hothorn  
263 et al. 2008). Spatial autocorrelation of GLM residuals was examined by Moran's I  
264 in the ape package v.3.0-6 (Paradis et al. 2004). In all instances, Moran's I was  
265 not significant ( $P > 0.05$ ).

266

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

275

276 **3. Results**

277 We identified 3933 spiders of 109 species from the 18 forest patches sampled.  
278 Pitfall trapping, where each of the 15 traps per site was active for 63 days as  
279 opposed to a single discrete trapping event per site for fogging, captured a  
280 greater overall abundance and richness of spiders (Fig. 1). Pitfall trapping  
281 captured 3205 spiders from 87 species whereas fogging captured 728 spiders  
282 from 36 species. Analysis of variance showed that species richness of the three  
283 forest types was significantly different for pitfall-trapped assemblages  
284 ( $F_{2,15}=5.141$ ,  $P=0.020$ ; ash mean ( $\pm$ SD)  $23.8\pm 4.6$ , oak mean  $25.7\pm 5.7$ , spruce  
285 mean  $17.7\pm 2.6$ ), with post hoc tests indicating that only oak and spruce were  
286 significantly different (Turkey  $P=0.020$ ). No differences in species richness were  
287 found between forest types for canopy-fogged assemblages (Kruskal-Wallis  
288  $\chi^2=0.467$ ,  $P>0.05$ ; ash mean ( $\pm$ SD)  $6.8\pm 2.2$ , oak mean  $6.7\pm 0.5$ , spruce mean  
289  $7.0\pm 2.6$ ). For details of species identification and classification of hunting and  
290 habitat guilds see Appendix B.

291

292 Fourteen species were common to both trapping methods, 73 species were  
293 unique to pitfall trapping (including 22 woodland species) and 22 to fogging  
294 (including five woodland species). Of the 87 species in pitfall traps, 16 (18%)  
295 species were unique to ash forest, 14 (16%) unique to oak and five (6%) unique  
296 to spruce. A larger proportion of species were unique to forest types in the  
297 fogged samples, from the 36 species captured, nine (25%) were unique to ash  
298 forests, seven (19%) were unique to oak forest and nine (25%) were unique to  
299 spruce plantations. Twenty five (29%) species were common to all forest types

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

302

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

309

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

315

316 Significant differences in community composition were found between forest  
317 types using both pitfall trapping and fogging methods (Deviance = 360.6,  
318 P=0.007; Deviance=137.4, P=0.004 respectively); however, assemblages sampled  
319 with pitfall trapping showed greater separation between forest types (Fig. 2).

320 Compared with spruce, semi-natural forests had significantly different species  
321 compositions for both pitfall trapped and fogged assemblages (P<0.001).

322 Although fogged ash and oak forests showed some overlap in NMDS space,  
323 assemblages in the two semi-natural forest types were significantly different (LR  
324 value=45.61, P=0.002).

325

326 Procrustes tests performed on the NMDS ordinations indicated significant  
327 concordance between pitfall trapped and fogged assemblages ( $m^2=0.77$ ,  
328 correlation coefficient = 0.48,  $P=0.026$ ); however, this was not sufficiently strong  
329 ( $m^2<0.50$ , correlation coefficient  $>0.7$ ) to regard robust surrogacy between  
330 sampling methods (Heino 2010).

331

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

344

345 Very few species of active hunting spider were recorded in either pitfall  
346 assemblages ( $n=10$ , mean per sample =  $0.8\pm 1.1$  SD) or fogged assemblages ( $n=2$ ,  
347 mean per sample =  $0.1\pm 0.3$  SD). In addition, no active hunting spiders were  
348 captured in spruce plantations (Fig. 4). Pitfall assemblages in spruce plantations



349 were confined to two web-hunting families, Linyphidae and Theridiidae; fogging  
350 assemblages also included web hunters from the family Tetragnathidae (Fig. 4).  
351  
352 CWM body size differed significantly between spiders sampled by pitfall traps  
353 and fogging ( $U=90$ ,  $P=0.022$ , pitfall trapping: mean ( $\pm$ SD)  $5.1\pm 2.7$ , range 1.7–  
354 13mm; fogging: mean  $3.2\pm 2.3$ , range 8.2–0.5mm). In pitfall-trapped assemblages,  
355 spider body-size was smaller in spruce than semi-natural forests, although the  
356 only significant difference in CWM spider body size was between oak and  
357 spruce ( $\chi^2=1.62$ ,  $P=0.011$ , ash mean ( $\pm$ SD)  $5.6\pm 1.4$ , oak mean  $6.5\pm 3.7$ , spruce  
358 mean  $3.1\pm 1.2$ ). No significant differences in body size were found between forest  
359 types sampled by fogging (ash mean ( $\pm$ SD)  $3.8\pm 3.3$ , oak mean  $2.9\pm 1.5$ , spruce  
360 mean  $2.8\pm 2.0$ ).  
361

362 **4. Discussion**

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

379

380 Pitfall trapping recorded greater species richness in ash and oak assemblages  
381 than spruce plantations. This is consistent with previous research showing low  
382 species richness of ground-dwelling invertebrates within managed coniferous  
383 forest sampled by pitfall trapping (Finch 2005, Fuller et al. 2008). In contrast, no  
384 differences in species richness were detected between forest types surveyed by  
385 fogging. The divergent patterns in ground and canopy richness may provide  
386 evidence for stratified biodiversity patterns between forest layers and may

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

404

#### 405 **4.1 Hunting guilds, habitat specialism and body size representation**

406 Web-hunting Linyphiids dominated the assemblages of both survey methods.  
407 Active hunters were represented by very few individuals in semi-natural forest  
408 types and there was a total absence of active-hunting species in spruce  
409 plantations for both trapping methods (proportion of active hunters: ash 1.8%,  
410 oak 0.5%). This is consistent with previous surveys of plantation forest  
411 conducted using pitfall trapping in the same region (Oxbrough et al. 2010, Fuller

412 et al. 2014). Barsoum et al. (2014) compared both Irish and English spider  
413 assemblages and found forest plantations in Ireland to be dominated by web-  
414 hunting Linyphiidae, whereas assemblages in England comprised a mixture of  
415 hunting guilds. In North American broad-leaf forests, Larrivée & Buddle (2009)  
416 found 21 species of hunting spiders from understory and canopies sampled by  
417 beating; while sweep netting by Stratton et al. (1978) found hunting spiders in  
418 the understories of three types of North American coniferous forest. The paucity  
419 of active hunters in the Irish forest fauna may be a result of meteorological  
420 conditions favouring smaller species such as the web-hunting Linyphiidae  
421 (Entling et al. 2010). This combined with the high dispersal potential of  
422 Linyphiidae that are able to balloon as adults over vast distances (Thomas et al.  
423 2003, Bell et al. 2005), may help to explain their dominance in the severely  
424 fragmented Irish forest system where less than 1% of the land cover was  
425 forested at the end of the 19<sup>th</sup> century (Forest Service 2007, Forest Europe et al.  
426 2011).

427

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

437 were able to support native forest beetles and compared to other non-native  
438 habitats, such as pasture and clearfell forestry sites, beetle composition in these  
439 mature plantations was most similar to native forest. This gradient of landscape  
440 suitability was also proposed by Brockerhoff et al. (2008) who suggest that  
441 plantation forest could provide useful habitat where pre-plantation areas are  
442 non-natural habitat. In the Irish context, plantation forest is not replacing semi-  
443 natural forested and it is unlikely the woodland specialists identified in the  
444 current study would be found in open habitat in the region (Oxbrough et al.  
445 2006, 2007). Therefore, given that semi-natural forest in the Irish landscape is  
446 scarce (1% of total land cover), these areas of plantation maybe important for  
447 the canopy fauna, providing essential habitat in an prodominatly open landscape.  
448 The disparity between ground and canopy results for woodland associated  
449 species highlights the need for greater sampling coverge in forest assessments.

450

451 While we show that pitfall catches provided a larger CWM body-size than  
452 fogging, this is not unexpected given the bias of pitfall trapping to select for  
453 larger species (Lang 2000), which are typically more active. Interestingly, we  
454 were able to detect a significant difference in body size between forest types  
455 from ground samples, differences that were not detected from canopy samples.  
456 From ground samples, spider body-size tended to be smaller in spruce  
457 plantations than oak and ash forests. This is an interesting finding and may  
458 result from different moisture and light regimes and would require targeted  
459 investigation to confirm the underlying drivers. Previous studies have indicated  
460 moisture and climate as potential drivers of body size variation (Wagner et al.  
461 2003, Entling et al. 2010). Wagner et al. (2003) demonstrated a reduction in

462 average body size and a change in dominant foraging mode (active to web), and  
463 suggested a moisture gradient could be driving stratification in their study of  
464 forest spider at various litter depths. At a European scale Entling et al. (2010)  
465 looked at size-climate relationships across European spider assemblages and  
466 concluded body size decreases from warm/dry to cool/moist climates.

467

#### 468 **4.2 Vertical stratification**

469 While we show stratification of spider families between forest layers, it was not  
470 simply that active ground-hunting families such as Lycosidae and Clubionidae  
471 dominated the ground catches because all sampling was dominated by small web  
472 spinners. Very few studies have attempted to look at both canopy and ground  
473 dwelling spider assemblages (but see Docherty and Leather 1997, Pinzon et al.  
474 2011, 2013) as vertical stratification of spider guilds in forests is difficult to  
475 study given the very different survey strategies required, which can lead to  
476 sampling designs that are not comparable. Most studies concerning vertical  
477 stratification in temperate and boreal forests have looked at discrete elements,  
478 focusing on canopy-understory stratification (Larrivé and Buddle 2009, Aikens  
479 and Buddle 2012) or different litter layers (Wagner et al. 2003) where vertical  
480 stratification and shifts in family dominance have been reported.

481

482 Although all samples were dominated by Linyphiidae in the current study, pitfall  
483 traps did contain five active hunting families in comparison to just two recorded  
484 from fogging. Of these families, only Anyphaenidae was recorded from both  
485 ground and canopy sampling, indicating strong family stratification of  
486 assemblages. In sampled canopies, web-hunters from the families Theridiidae

487 and Tetragnathidae are also abundant. The only non-Linyphiidae species caught  
488 in moderate abundance in the pitfall traps was the Theridiidae, *Robertus lividus*,  
489 a ground-dwelling habitat generalist. The majority of spiders identified in the  
490 indicator analysis in both the canopy and the ground belonged to the same guild:  
491 web-hunting species of Linyphiidae, with *Tetragnatha montana*, a dominant  
492 spider in ash canopies, the only exception. Differential representation of spider  
493 families between methods in the current study and the large number of species  
494 unique to each method (pitfall n=73, fogging n=22) indicates strong  
495 stratification. This stratification illustrates the need to incorporate multiple  
496 sampling methods across various forest strata if a more complete understanding  
497 of the forest fauna is required. This corresponds to the findings from North  
498 American spruce where a strong difference in assemblage composition was  
499 recorded between forest layers (Pinzon et al. 2011, 2013).

500

## 501 **Conclusions**

502 Our study set out to examine the correspondence between pitfall trapping and  
503 canopy fogging sampling methods for defining differences in spider assemblage  
504 structure in several forest types. Our findings show that if fine detailed species  
505 and family based information (e.g. habitat association, hunting guild, body size)  
506 is required, then separate targeted surveys are needed, as results were not  
507 consistent between methods. Furthermore, many species were unique to a single  
508 survey methods, so if management priorities are to maintain or increase  
509 diversity, then monitoring of both ground and canopy fauna needs to be  
510 undertaken. Comparisons using solely species incidence obtained by either  
511 survey method should be avoided. This coarse metric reduces data complexity,

512 can be highly susceptible to sampling effort and can be misleading in habitats  
513 that contain numerous non-specialist species such as ecotones, disturbed and  
514 small-fragmented habitats (Downie et al. 1996, Niemela 1997).

515

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

532

### 533 **Acknowledgements**

534 We thank the Irish National Parks & Wildlife Service (NPWS), Coillte, the Forest  
535 Service Northern Ireland, and private landowners for site access. Many people  
536 assisted with fieldwork and invertebrate sorting in the laboratory, including



537 Mark Wilson, Veronica French, Oisín Sweeney, Rob Deady, Tadeusz Kirakowski,  
538 and Eoin O' Callaghan. Thanks to Dr. Tom Gittings, Dr. Stephen Mc Cormack, Dr.  
539 Roy Anderson, and Peter Smithers for verification of specimens. This research  
540 was funded by the Department of Agriculture, Food & Marine and the Irish  
541 Research Council for Science, Engineering and Technology.

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562 **References**

- 563 Aikens, K. R., and C. M. Buddle. 2012. Small-scale heterogeneity in temperate  
564 forest canopy arthropods: stratification of spider and beetle assemblages.  
565 Canadian Entomologist 144:526-537.  
566
- 567 Barsoum, N., L. Fuller, F. Ashwood, K. Reed, A. S. Bonnet-Lebrun, and F. Leung.  
568 2014. Ground-dwelling spider (Araneae) and carabid beetle (Coleoptera:  
569 Carabidae) community assemblages in mixed and monoculture stands of oak  
570 (*Quercus robur* L./*Quercus petraea* (Matt.) Liebl.) and Scots pine (*Pinus sylvestris*  
571 L.). Forest Ecology and Management 321:29-41.  
572
- 573 Bell, J. R., D. A. Bohan, E. M. Shaw, and G. S. Weyman. 2005. Ballooning dispersal  
574 using silk: world fauna, phylogenies, genetics and models. Bulletin of  
575 Entomological Research 95:69-114.  
576
- 577 Berndt, L. A., E. G. Brockerhoff, and H. Jactel. 2008. Relevance of exotic pine  
578 plantations as a surrogate habitat for ground beetles (Carabidae) where native  
579 forest is rare. Biodiversity and Conservation 17:1171-1185.  
580
- 581 Brockerhoff, E. G., H. Jactel, J. A. Parrotta, C. P. Quine, and J. Sayer. 2008.  
582 Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and  
583 Conservation 17:925-951.  
584
- 585 De Cáceres, M., P. Legendre, and M. Moretti. 2010. Improving indicator species  
586 analysis by combining groups of sites. Oikos 119:1674-1684.

587

588 Docherty, M., and S. R. Leather. 1997. Structure and abundance of arachnid  
589 communities in Scots and lodgepole pine plantations. *Forest Ecology and*  
590 *Management* 95:197-207.

591

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

595

596 Duffey, E. 1968. An ecological analysis of spider fauna of sand dunes. *Journal of*  
597 *Animal Ecology* 37:641-674.

598

599 Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species:  
600 The need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-  
601 366.

602

603 Entling, W., M. H. Schmidt-Entling, S. Bacher, R. Brandl, and W. Nentwig. 2010.  
604 Body size-climate relationships of European spiders. *Journal of Biogeography*  
605 37:477-485.

606

607 Erwin, T. L. 1982. Tropical forests their richness in Coleoptera and other  
608 Arthropod species. *Coleopterists Bulletin* 36:74-75.

609

610 Finch, O. D. 2005. Evaluation of mature conifer plantations as secondary habitat  
611 for epigeic forest arthropods (Coleoptera : Carabidae; Araneae). *Forest Ecology*  
612 *and Management* 204:21-34.

613

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

616

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

619

620 Fuller, L., M. Newman, S. Irwin, T. Kelly, and J. O'Halloran. 2014. Ground-dwelling  
621 spider diversity in rare European oak and yew woodlands and the impact of  
622 grazing. *Biodiversity and Conservation* 23:1911-1929.

623

624 Fuller, R. J., T. H. Oliver, and S. R. Leather. 2008. Forest management effects on  
625 carabid beetle communities in coniferous and broadleaved forests: implications  
626 for conservation. *Insect Conservation and Diversity* 1:242-252.

627

628 Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of  
629 Carabidae (Coleoptera). *Journal of Animal Ecology* 33:301-310.

630

631 Gunnarsson, B. 1992. Fractal dimension of plants and body size distribution in  
632 spiders. *Functional Ecology* 6:636-641.

633

634 Halaj, J., D. W. Ross, and A. R. Moldenke. 2000. Importance of habitat structure to  
635 the arthropod food-web in Douglas-fir canopies. *Oikos* 90:139-152.  
636

637 Heino, J. 2010. Are indicator groups and cross-taxon congruence useful for  
638 predicting biodiversity in aquatic ecosystems? *Ecological Indicators* 10:112-117.  
639

640 Higgins, G. T., J. R. Martin, and P. M. Perrin. 2004. National survey of native  
641 woodland in Ireland, Dept. of the Environment, Heritage and Local Government.  
642

643 Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general  
644 parametric models. *Biometrical Journal* 50:346-363.  
645

646 Hsieh, Y. L., and K. E. Linsenmair. 2012. Seasonal dynamics of arboreal spider  
647 diversity in a temperate forest. *Ecology and Evolution* 2:768-777.  
648

649 Ji, Y., L. Ashton, S. M. Pedley., et al. 2013. Reliable, verifiable and efficient  
650 monitoring of biodiversity via metabarcoding. *Ecology Letters* 16:1245-1257.  
651

652 Lang, A. 2000. The pitfalls of pitfalls: a comparison of pitfall trap catches and  
653 absolute density estimates of epigeal invertebrate predators in arable land.  
654 *Anzeiger Fur Schadlingskunde-Journal of Pest Science* 73:99-106.  
655

656 Larrivé, M., and C. M. Buddle. 2009. Diversity of canopy and understory spiders  
657 in north-temperate hardwood forests. *Agricultural and Forest Entomology*  
658 11:225-237.

659

660 Lowman, M. D., and P. K. Wittman. 1996. Forest canopies: Methods, hypotheses,  
661 and future directions. *Annual Review of Ecology and Systematics* 27:55-81.

662

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

665

666 Marc, P., A. Canard, and F. Ysnel. 1999. Spiders (Araneae) useful for pest  
667 limitation and bioindication. *Agriculture Ecosystems & Environment* 74:229-  
668 273.

669

670 Melbourne, B. A. 1999. Bias in the effect of habitat structure on pitfall traps: An  
671 experimental evaluation. *Australian Journal of Ecology* 24:228-239.

672

673 Niemelä, J. 1997. Invertebrates and boreal forest management. *Conservation*  
674 *Biology* 11:601-610.

675

676 Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, and et al. 2010.

677 *Vegan: Community Ecology Package*. R package Version 1.17-2.

678 [http://CRAN.Rproject.org/package = vegan](http://CRAN.Rproject.org/package=vegan).

679

680 Oxbrough, A., S. Irwin, T. C. Kelly, and J. O'Halloran. 2010. Ground-dwelling  
681 invertebrates in reforested conifer plantations. *Forest Ecology and Management*  
682 259:2111-2121.

683

684 Oxbrough, A. G., T. Gittings, J. O'Halloran, P. S. Giller, and T. C. Kelly. 2006. The  
685 initial effects of afforestation on the ground-dwelling spider fauna of Irish  
686 peatlands and grasslands. *Forest Ecology and Management* 237:478-491.  
687

688 Oxbrough, A. G., T. Gittings, J. O'Halloran, P. S. Giller, and T. C. Kelly. 2007.  
689 Biodiversity of the ground-dwelling spider fauna of afforestation habitats.  
690 *Agriculture Ecosystems & Environment* 120:433-441.  
691

692 Oxbrough, A. G., T. Gittings, J. O'Halloran, P. S. Giller, and G. F. Smith. 2005.  
693 Structural indicators of spider communities across the forest plantation cycle.  
694 *Forest Ecology and Management* 212:171-183.  
695

696 Ozanne, C. M. P., D. Anhuf, S. L. Boulter, M. Keller, R. L. Kitching, C. Korner, F. C.  
697 Meinzer, A. W. Mitchell, T. Nakashizuka, P. L. S. Dias, N. E. Stork, S. J. Wright, and  
698 M. Yoshimura. 2003. Biodiversity meets the atmosphere: A global view of forest  
699 canopies. *Science* 301:183-186.  
700

701 Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of Phylogenetics and  
702 Evolution in R language. *Bioinformatics* 20:289-290.  
703

704 Pawson, S. M., E. G. Brockerhoff, E. D. Meenken, and R. K. Didham. 2008. Non-  
705 native plantation forests as alternative habitat for native forest beetles in a  
706 heavily modified landscape. *Biodiversity and Conservation* 17:1127-1148.  
707

708 Pedley, S. M., and P. M. Dolman. 2014. Multi-taxa trait and functional responses  
709 to physical disturbance. *Journal of Animal Ecology* 83:1542-1552.  
710

711 Pedley, S. M., R. D. Martin, A. Oxbrough, S. Irwin, T. C. Kelly, and J. O'Halloran.  
712 2014. Commercial spruce plantations support a limited canopy fauna: Evidence  
713 from a multi taxa comparison of native and plantation forests. *Forest Ecology  
714 and Management* 314:172-182.  
715

716 Peres-Neto, P. R., and D. A. Jackson. 2001. How well do multivariate data sets  
717 match? The advantages of a Procrustean superimposition approach over the  
718 Mantel test. *Oecologia* 129:169-178.  
719

720 Pinzon, J., J. R. Spence, and D. W. Langor. 2011. Spider Assemblages in the  
721 Overstory, Understory, and Ground Layers of Managed Stands in the Western  
722 Boreal Mixedwood Forest of Canada. *Environmental Entomology* 40:797-808.  
723

724 Pinzon, J., J. R. Spence, and D. W. Langor. 2013. Diversity, species richness, and  
725 abundance of spiders (Araneae) in different strata of boreal white spruce stands.  
726 *Canadian Entomologist* 145:61-76.  
727

728 R Development Core Team. 2012. R: A language and environment for statistical  
729 computing. R Foundation for Statistical Computing, Vienna, Austria.  
730

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



733

734 Roberts, M. J. 1996. Spiders of Britain and Northern Europe. HarperCollins

735 Publishers Ltd, London.

736

737 Robinson, J. V. 1981. The effect of architectural variation in habitat on a spider

738 community - an experimental field-study. *Ecology* 62:73-80.

739

740 Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in

741 terrestrial systems: A review of the effects of carnivore removals on plants.

742 *American Naturalist* 155:141-153.

743

744 Southwood, T. R. E., G. R. W. Wint, C. E. J. Kennedy, and S. R. Greenwood. 2005.

745 The composition of the arthropod fauna of the canopies of some species of oak

746 (*Quercus*). *European Journal of Entomology* 102:65-72.

747

748 Spence, J. R., D. W. Langor, J. Niemelä, H. A. Cárcamo, and C. R. Currie. 1996.

749 Northern forestry and carabids: The case for concern about old-growth species.

750 *Annales Zoologici Fennici* 33:173-184.

751

752 Standen, V. 2000. The adequacy of collecting techniques for estimating species

753 richness of grassland invertebrates. *Journal of Applied Ecology* 37:884-893.

754

755 Stork, N. E., and P. M. Hammond. 1997. Sampling arthropods from tree crowns by

756 fogging with knockdown insecticides: lessons from studies of oak tree beetle

757 assemblages in Richmond Park (UK). Pages 3-26 in N. E. Stork, J. Adis, and R. K.  
758 Didham, editors. *Canopy Arthropods*. Chapman and Hall, London.  
759  
760 Stratton, G. E., G. W. Uetz, and D. G. Dillery. 1978. A comparison of the spiders of  
761 three coniferous tree species. *Journal of Arachnology* 6:219-226.  
762  
763 Straw, N. A., N. J. Fielding, and A. Waters. 1996. Phytotoxicity of insecticides used  
764 to control aphids on Sitka spruce, *Picea sitchensis* (Bong) Carr. *Crop Protection*  
765 15:451-459.  
766  
767 Thomas, C. F. G., P. Brain, and P. C. Jepson. 2003. Aerial activity of linyphiid  
768 spiders: modelling dispersal distances from meteorology and behaviour. *Journal*  
769 *of Applied Ecology* 40:912-927.  
770  
771 Topping, C. J., and K. D. Sunderland. 1992. Limitations to the use of pitfall traps in  
772 ecological-studies exemplified by a study of spiders in a field of winter-wheat.  
773 *Journal of Applied Ecology* 29:485-491.  
774  
775 Vasconcelos, H. L., J. M. S. Vilhena, W. E. Magnusson, and A. Albernaz. 2006. Long-  
776 term effects of forest fragmentation on Amazonian ant communities. *Journal of*  
777 *Biogeography* 33:1348-1356.  
778  
779 Wagner, J. D., S. Toft, and D. H. Wise. 2003. Spatial stratification in litter depth by  
780 forest-floor spiders. *Journal of Arachnology* 31:28-39.  
781

782 Wang, Y., U. Naumann, S. T. Wright, and D. I. Warton. 2012. mvabund- an R  
783 package for model-based analysis of multivariate abundance data. *Methods in*  
784 *Ecology and Evolution* 3:471-474.

785

786 Warton, D. I., S. T. Wright, and Y. Wang. 2012. Distance-based multivariate  
787 analyses confound location and dispersion effects. *Methods in Ecology and*  
788 *Evolution* 3:89-101.

789

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

792

793 Yanoviak, S. P., N. M. Nadkarni, and J. C. Gering. 2003. Arthropods in epiphytes: a  
794 diversity component that is not effectively sampled by canopy fogging.  
795 *Biodiversity and Conservation* 12:731-741.

796

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

801

802 Zheng, G., S. Q. Li, and X. D. Yang. 2015. Spider diversity in canopies of  
803 Xishuangbanna rainforest (China) indicates an alarming juggernaut effect of  
804 rubber plantations. *Forest Ecology and Management* 338:200-207.

805

806 Ziesche, T. M., and M. Roth. 2008. Influence of environmental parameters on  
807 small-scale distribution of soil-dwelling spiders in forests: What makes the  
808 difference, tree species or microhabitat? *Forest Ecology and Management*  
809 255:738-752.

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830 **Table 1.** Indicator species identified from the three sampled forest types  
 831 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	<i>Ceratinella scabrosa</i>	Generalist	web	0.831	0.013
	Pitfall trap	Linyphiidae	<i>Lepthyphantes tenebricola</i>	Woodland	web	0.808	0.039
	Canopy fog	Tetragnathidae	<i>Tetragnatha montana</i>	Generalist	web	0.773	0.044
Oak	Pitfall trap	Linyphiidae	<i>Walckenaeria acuminata</i>	Generalist	web	0.850	0.012
	Pitfall trap	Linyphiidae	<i>Microneta viaria</i>	Generalist	web	0.793	0.039
	Pitfall trap	Linyphiidae	<i>Walckenaeria dysderoides</i>	Generalist	web	0.772	0.033
Spruce	Pitfall trap	Linyphiidae	<i>Centromerus dilutus</i>	Generalist	web	0.840	0.015
	Pitfall trap	Linyphiidae	<i>Diplocephalus latifrons</i>	Woodland	web	0.809	0.042
	Pitfall trap	Linyphiidae	<i>Monocephalus fuscipes</i>	Woodland	web	0.727	0.050
	Canopy fog	Linyphiidae	<i>Pelecopsis nemoralis</i>	Woodland	web	0.921	0.006
	Canopy fog	Linyphiidae	<i>Lepthyphantes obscurus</i>	Woodland	web	0.816	0.030

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840 **Figure descriptions:**

841

842 Fig. 1. Individual-based rarefaction curves for a) pitfall trapped and b) canopy  
843 fogged spider assemblages from three forest types (ash, oak and spruce).

844

845 Fig. 2. Non-Metric Multidimensional Scaling (NMDS) ordination comparing the  
846 spider assemblage composition of three forest types for a) pitfall trapping  
847 assemblages and b) canopy fogged assemblages. Stress scores for each  
848 ordination are 0.14 and 0.15 respectively. Points are sampled sites with lines  
849 connecting to habitat centroids and polygons represent 95% confidence interval  
850 of forest type centroids.

851

852 Fig. 3. Mean ( $\pm$  s.e) spider abundance and species richness of woodland and  
853 generalist species per forest type for pitfall trapping and canopy fogging.  
854 Asterisks indicate significant differences from the forest type with the greatest  
855 species richness or abundance in each plot as derived from generalised linear  
856 models (Tukey pairwise comparisons  $P < 0.05$ ). See Appendix C for model  
857 statistics. Thick central line separates abundance and species richness plots.

858

859 Fig. 4. Total species richness per spider family recorded in three forest types  
860 (ash, oak and spruce). Spiders sampled by pitfall trapping are shown in the top  
861 three plots, those sampled by canopy fogging are shown in the bottom three  
862 plots. Families in each plot are split (dotted line) by those families that exhibit a  
863 web-hunting (Web) strategy and those with an active-hunting (Active) strategy.

864