

1 Can mixed stands of native and non-native tree species enhance diversity
2 of epigeic arthropods in plantation forests?

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14 **Highlights**

- 15 • Spider, staphylinid richness was similar in non-native spruce and native ash stands
- 16 • In contrast, carabid diversity was greater in ash than spruce or mixed stands
- 17 • Assemblages differed among forest types but beta diversity was greater in ash
- 18 • Equitably mixed stands support some species associated with native ash and
19 spruce
- 20 • Native ash enhances plantation diversity and heterogeneity

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23 **Key words:** spiders, carabids, staphylinids, forest plantations, mixed stands,
24 biodiversity

25

26 **Abstract**

27 In regions with low cover of natural forests and high cover of plantations
28 predominately comprised of non-native species, inclusion of a native tree species with
29 a more productive non-native species has the potential to enhance biodiversity and
30 meet production goals. In this context, we tested the alternative hypotheses that: i)
31 equitable mixes of a non-native and a native tree species support greater diversity of
32 ground-dwelling arthropods than single species stands; or, ii) native ash stands support
33 greater diversity of ground-dwelling arthropods than mixed or single species stands
34 that include a non-native conifer species. Active epigaeic spiders (Araneae) and beetles
35 (Coleoptera: Carabidae, Staphylinidae) were sampled using pitfall traps in three forest
36 types in Ireland: single species stands of non-native Norway spruce (*Picea abies*) or
37 native ash (*Fraxinus excelsior*), and mixed stands of these species.

38 Stands of Norway spruce did not negatively influence spider and staphylinid
39 diversity, suggesting that they maintain a similar range of biodiversity to mixed
40 plantations or stands of native ash. However, carabid beetle richness (but not
41 abundance) was negatively affected by the presence of spruce suggesting caution
42 when drawing conclusions about biodiversity impacts from single taxon studies. We
43 found that equitable mixes of spruce and ash supported many species associated with
44 native ash stands. Thus, we recommend that mixes with an equitable species ratio (e.g.
45 50:50) and containing a native species will enhance epigaeic arthropod diversity and
46 heterogeneity in plantations. Furthermore, our finding that ash stands supported
47 greater beta diversity than spruce stands supports current guidelines that recommend
48 a range of stand types, including native species, to enhance diversity within and
49 between stands.

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52 **Introduction**

53 Encouraging development of mixed species forests has been proposed as a way
54 of mitigating the negative impacts on biodiversity of environmental changes associated
55 with intensification of wood production or climate change (Pawson et al., 2013, Bravo-
56 Oviedo et al., 2014). In contrast to single species stands, mixes more effectively
57 support 1) ecosystem functions, including nutrient cycling and soil processes, than do
58 single species stands (Guckland et al., 2010, Brassard et al., 2013), 2) a greater capacity
59 for pest control by natural enemies (Jactel et al., 2005, Knoke et al., 2008), and 3) a
60 greater range of associated species (Butterfield and Malvido, 1992, Felton et al., 2010).
61 These benefits may enhance ecosystem health and resilience (Knoke et al., 2008) as
62 well as commercial yield (Mason and Connolly, 2013), and this has led to forest policies
63 promoting diversification of tree species at stand, landscape and regional scales
64 (Forest Service, 2000, European Commission, 2006, Forestry Commission, 2011).

65 Mixed species forests support biodiversity through provision of a wider range
66 of resources and available niches, and typically have greater habitat heterogeneity
67 than do single species stands (Saetre et al., 1997, Aubert et al., 2005, Cavard et al.,
68 2011). This is important for organisms directly associated with particular tree species
69 (Király and Ódor, 2010) but also may benefit those depending on characteristics of
70 particular single species stands, such as light availability or soil quality (Cavard et al.,
71 2011). Consequently, the influence of mixed stands on forest biodiversity likely results
72 from the combination of the particular tree species present and the variety in
73 resources they provide, rather than simply from increasing the number of tree species
74 (Vehviläinen et al., 2007, Schuldt et al., 2011).

75 In the context of plantation silviculture, tree mixes are typically employed to
76 enhance productivity of the commercial crop through amelioration of temperature or
77 wind extremes or improved soil conditions (Kerr et al., 1992, Mason and Connolly,
78 2013). Recent research, however, has also focused more broadly on the capacity of
79 mixed stands to provide benefits in terms of ecosystem function, resilience and species
80 conservation (Knoke et al., 2008). This may be particularly important in regions with
81 low cover of natural forest, in which plantations including non-native tree species may
82 also support native biodiversity associated with natural stands (Brockhoff et al.,
83 2008, Coote et al., 2012, Irwin et al., 2013, Irwin et al., 2014, Graham et al., 2014).

84 Furthermore, in countries such as Ireland or the UK where cover of natural forests is
85 much lower than that of non-native plantations ($\leq 5\%$ of forested area) (Watts, 2006,
86 Forest Service, 2007), inclusion of native tree species in mixed plantations may
87 enhance populations of flora and fauna associated with native tree species.

88 Mixed plantation forests are established at several spatial scales: at the stand
89 level, by planting 'intimate' mixes of alternate tree species in rows, or at larger scales,
90 by establishing a mosaic of single species in 'non-intimate' mixes within a forested
91 landscape (Forest Service, 2000). However, whilst there is evidence that the latter
92 policy leads to overall enhancement of biodiversity in such plantations (Oxbrough et
93 al., 2005, French et al., 2008, Coote et al., 2012), there is little evidence that the
94 intimate mixes established under current planting guidelines (Forest Service, 2000),
95 offer biodiversity benefits (Oxbrough et al., 2012, Coote et al., 2012, Barsoum et al.,
96 2013). In such intimate mixes the secondary species appears to have minimal impact
97 on canopy or understory conditions (Oxbrough et al., 2012). Nonetheless, there is
98 some evidence that more equitable mixes (40-60% of each species) can support
99 greater biodiversity within plantations (Li et al., 2012, Barsoum et al., 2013), although
100 this has yet to be explored at a large scale.

101 In this context, we use arthropods as a model to indicate whether equitable
102 mixes of two tree species, non-native Norway spruce *Picea abies* (L.) Karst and native
103 Ash *Fraxinus excelsior* L., can enhance forest biodiversity relative to that in single
104 species stands of either species. Arthropods are a key component of biodiversity in
105 forest ecosystems and have been used in many studies to indicate responses to
106 environmental change and inform forest management in plantations (Oxbrough et al.,
107 2005, Mullen et al., 2008, 2010, 2012, Barsoum et al., 2013). We selected three
108 taxonomic groups of epigeic arthropods, spiders (Order: Araneae), and carabid and
109 staphylinid beetles (Order: Coleoptera, Families: Carabidae, Staphylinidae), for study.
110 Together these taxa represent major functional groups (predators, omnivores,
111 fungivores and saprophages), have the advantage of being relatively well studied (in
112 comparison with other invertebrate taxa) and are effectively sampled by the same
113 method (Thiele, 1977, Bohac, 1999, Pearce and Venier, 2006). Here we test the
114 following alternative hypotheses:

- 115 1. *Equitably mixed forest stands will support greater species richness and beta*
116 *diversity than monocultures, will be characterized by the lower dominance, and*
117 *will support species associated with each tree species.* Mixes will support species
118 common to both single species stands, including specialist species associated with
119 native ash forests, resulting in greater diversity. An intimately mixed plantation
120 forest, in which both species are planted alternately in the same row, rather than
121 in discrete patches of the same species, will result in greater beta diversity within
122 stands than in either single species stand.
- 123 2. *Native Ash stands will support greater species richness and beta diversity than*
124 *Norway spruce stands, will have the most distinct arthropod assemblages and the*
125 *lowest dominance compared to both plantation forests.* In Ireland there are no
126 native spruce species and only three native conifers (yew *Taxus baccata*, juniper
127 *Juniperus communis*, Scots pine *Pinus sylvestris*, (but see Roche et al., 2009)), as
128 such there will be more species associated with single species stands of native ash
129 than those containing up to 40-60% non-native spruce. Further, evenness will be
130 greatest in ash single species stands, intermediate in mixes and lowest in spruce
131 stands.

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134 **2. Material and Methods**

135 *2.1. Study sites*

136 Mixed stands of non-native Norway spruce (*Picea abies* L. (H. Karst)) (hereafter
137 referred to as spruce) and native ash (*Fraxinus excelsior* L.) and single species stands of
138 each of these species were selected for study in Ireland. These species are commonly
139 found as mixtures in mature stands in Ireland. Candidate stands were selected from
140 national forest databases of planting records, and chosen for study after ground-
141 truthing site visits. The precise ratio of ash to spruce in mixed stands was estimated by
142 walking five equally-spaced 100m transects, separated by at least 30m, and counting
143 the stems of all tree species encountered. Mixed stands with between 40-60% ash, and
144 which met the criteria outlined below, were selected for study; all were 'intimately
145 mixed' with individuals of each tree species were planted together on a small scale.

146 A randomized complete block sampling design was used (Quinn and Keough,
147 2002). One plantation of each forest type (ash, mixed and spruce) was located in each
148 of five sampling clusters (Table 1). These clusters were located within 40km of each
149 other to ensure similar climatic conditions and stands included within them were
150 matched, in so far as possible, for site-specific characteristics such as tree
151 development, site history, soil type, elevation and slope (Table 1). Single species
152 stands of spruce and the mixes were at normal 'commercial maturity' and were
153 matched for tree age as well as development and thinning within clusters. In all but
154 one case, the origin of ash stands (planted or naturally regenerated) could not be
155 determined from records. However, stands were chosen to best match development
156 of trees in pure ash to those in mixed stands within each cluster of sites, and thus we
157 presumed they were likely naturally regenerated following forest clearance at similar
158 times. All stands were located on old woodland, as defined by continuous forest
159 presence on 1840s and 1920s historical maps. This minimised possible impacts of prior
160 land use.

161

162 *2.2 Arthropod sampling*

163 In each stand three sampling plots were established in representative areas
164 that were >50m from the stand edge and >50m apart. Active epigaeic arthropods were
165 collected using pitfall traps. A transect of five pitfall traps of 7cm diameter by 9cm
166 depth were set 1-2 m apart in each plot. Traps contained c. 2 cm depth of ethylene
167 glycol to kill and preserve the arthropods sampled. Pitfall traps were operated
168 continuously for 12 weeks from early May 2012 to late July over the main spring-
169 summer growing period, and emptied once every three weeks. Arthropods collected in
170 the traps were stored in 70% ethanol and identified using Roberts (1993) for spiders,
171 Luff (2007) for carabids and the sources listed in Supplementary Table S1 for
172 staphylinids. Nomenclature follows the World Spider Catalog (Natural History Museum
173 Bern, 2015), Luff (2007) and Duff (2012). Specimens from the staphylinid sub-family
174 Aleocharinae were not identified since adequate taxonomic literature was not
175 available. Voucher specimens are stored in the Edge Hill University Biology Department
176 museum collection.

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180 *2.3 Stand characteristics*

181 Various environmental variables were measured within stands to characterise
182 habitat structure and resource provisioning for ground-dwelling arthropods. At each
183 pitfall plot a 10x10m area was established where the following measurements were
184 taken: stem counts of each tree species, tree height using a digital clinometer, and
185 diameter at breast height (DBH, measured at 1.3m above the ground using a standard
186 diameter tape). Cover of dead wood (standing dead wood, downed logs and stumps
187 >7.5cm diameter) was also estimated. At each pitfall trap percentage cover was
188 estimated in a 1m² quadrat for the following layers: bryophytes, vascular ground
189 vegetation (<10cm), herb layer (10-50cm), and understory layer (sub-canopy). Canopy
190 openness was estimated three times in each plot using a spherical densiometer. Depth
191 of the litter layer was measured at each pitfall trap and two soil samples were taken
192 from each plot to measure pH with a glass electrode and deionised water following
193 standardised methods.

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196 *2.4. Data analysis*

197 For the environmental data, means were calculated for each variable at the plot
198 level. Arthropod counts from each trap were standardised by the number of trap days
199 to account for trap disturbance and loss. Analyses were carried out separately for each
200 taxonomic group, using data pooled for each stand, with the exception of rarefaction
201 curves and analyses of within-stand beta diversity that were analysed at the plot scale.

202 To compare species richness among forest types, while taking in to account
203 differences in abundance, we used sample-based rarefaction curves (Gotelli and
204 Colwell, 2001). Significant differences are inferred from a lack of overlap in 95%
205 confidence intervals between groups. To examine dominance we used a modified
206 version of the Berger-Parker dominance index (Berger and Parker, 1970) by calculating
207 the proportion of individuals between the three most abundant species and the total.
208 This is an intuitive and simple measure that better reflects dominance patterns in
209 arthropod communities, where several species may be equally dominant (Oxbrough et

210 al., 2005). Greater values indicate more dominance of these three most abundant
211 species in the community and a concurrent reduction in evenness.

212 Differences among forest types in abundance of the focal invertebrate groups
213 were tested using a generalised linear mixed model (GLMM) with a Poisson error
214 distribution. Geographic cluster was used as a random variable reflecting the
215 randomised complete block sampling design. When the data were over-dispersed, a
216 random variable with as many levels as sites (n=15) was also included in the model
217 (Bates et al., 2014). The number of stems within a plot were also analysed in this way.
218 Other data were analysed as GLMMs with a Binomial distribution of error for the
219 modified Berger-Parker index as appropriate for proportional data, and a Gaussian
220 distribution of error for the remaining stand environmental characteristics. Percent
221 cover data was arcsine transformed prior to analysis. Model checking followed the
222 procedures outlined in Crawley (2012). When global tests of GLMMs were significant,
223 pairwise comparisons were carried out and P-values were corrected for multiple
224 testing with the Holm procedure.

225 We used permutational multivariate analysis of variance (PERMANOVA) to
226 determine differences in species composition of arthropod assemblages among forest
227 types. We asked if Hellinger distances between samples were consistently longer
228 between groups than within groups, testing the results for significance using 9999
229 permutations. Permutations were conducted within clusters as consistent with the
230 randomised block sampling design. Post-hoc pairwise comparisons were not carried
231 out in the case of PERMANOVA because the number of possible permutations was too
232 low to reliably assess significance. Between-stands multivariate dispersion, to which
233 PERMANOVA is sensitive, was explored using GLMM. When these were significant,
234 PERMANOVA results were interpreted with caution.

235 Variability in assemblage composition within and between stands, calculated as
236 multivariate dispersion, was used as a measure of beta diversity following Anderson et
237 al. (2006). In comparison with Whitaker's original index this method allows testing for
238 differences in beta diversity between groups by comparison of multivariate dispersion
239 (Anderson et al., 2006). Hellinger distances from each sampling plot to the stand
240 median (within-stand) or from each stand to the forest type median (between-stands)
241 were calculated as the measure of multivariate dispersion. These were compared

242 between forest types in a GLMM with Gaussian distribution including cluster and stand
243 (within-stand) or only cluster (between-stand) as random variables.

244 Variation in assemblage composition between stands was further explored
245 through principal components analysis (PCA) to summarise our multivariate data in a
246 reduced number of dimensions calculated as linear combinations of the original
247 variables. The combined approach of PERMANOVA and PCA was used to determine the
248 relative importance of multivariate dispersion and forest type in shaping composition.
249 Data were Hellinger-transformed (Legendre and Gallagher, 2001) to allow the use of
250 methods that preserve Euclidean distances (such as PCA), and that are appropriate
251 when analysing species abundance data (Legendre and Legendre, 2012).

252 Analyses were carried out using the *vegan* (Oksanen et al., 2015), *lme4* (Bates et
253 al., 2014), *car* (Fox and Weisberg, 2011) and *multcomp* (Hothorn et al., 2008) packages
254 in R software (R Core Team, 2015). Rarefaction curves were constructed using Estimate
255 S Version 9 (Colwell, 2013).

256

257

258 **3. Results**

259 In total 2603 spider, 12 005 staphylinid and 6744 carabid adults were captured.
260 Among these, 1367 staphylinids could not be identified to species, either because they
261 were Aleocharinae (1337) or were damaged (30); these were included only in analyses
262 of overall abundance. In total, 84 spider, 102 staphylinid and 47 carabid species were
263 identified (see Supplementary Tables S2-4). As is commonly found for arthropod
264 assemblages, catches were dominated by a few very abundant species, such as the
265 spiders *Monocephalus fuscipes* and *Lepthyphantes zimmermanni*, the staphylinids
266 *Tachinus rufipes* and *Philonthus decorus*, and the carabids *Abax parallelepipedus* and
267 *Pterostichus madidus*. In fact, more than 50% of the total captures in each group were
268 accounted for by just 7 species: 4 spiders, 2 staphylinids and 1 carabid (Supplementary
269 Tables S2-4). In contrast, 51, 87 and 36 species from these groups respectively
270 accounted for less than 5% of the total catch in each group.

271

272 **3.1 Environmental characteristics among forests types**

273 Stands in all forest types were characterised by trees of approximately the
274 same diameter and height; however, in ash and mixed stands stem density was
275 significantly greater than in spruce (Table 2). Conversely, canopy openness was
276 greatest in spruce, followed by mixed, and lowest in ash stands. Cover of dead wood
277 was similarly low across all plantation forest types. Soil pH was greatest in ash and
278 decreased from mixed to spruce stands, where it was significantly lower. Conversely,
279 litter depth was significantly greatest in the spruce stands, followed by mixed and then
280 ash. Overall, cover of litter and lower vegetation layers differed little between stand
281 types, with only needle litter cover being significantly greater in spruce than in ash.

282

283 **3.2 Species richness, abundance and dominance among forest types**

284 Species richness of spiders did not differ significantly among forest types (Figure
285 1), however staphylinid richness was higher in spruce than in mixed stands and carabid
286 species richness was significantly greater in ash than spruce stands and marginally
287 greater than in mixed stands. Overall abundance differed between forest types for
288 spiders ($\chi^2_{[3, N = 15]} = 47.70, P < 0.0001$) and staphylinids ($\chi^2_{[3, N = 15]} = 22.89, P < 0.0001$)
289 but not for carabids ($\chi^2_{[3, N = 15]} = 4.15, P = 0.13$). Spider abundance was significantly
290 higher in mixed and spruce than in ash stands ($P_{\text{adj}} < 0.0001$ in both cases), but did not
291 differ significantly between mixed and spruce forest types ($P_{\text{adj}} = 0.077$). Similarly,
292 staphylinid abundance was higher in mixed than in spruce stands ($P_{\text{adj}} < 0.0001$), but
293 was also greater in ash stands ($P_{\text{adj}} = 0.002$) (Figure 2). Dominance structure, as
294 reflected by the modified Berger-Parker index, did not vary significantly with forest
295 type in any of the arthropod groups ($P = 0.12-0.84$).

296

297 **3.3 Beta diversity within-stand and between-stands**

298 Beta diversity within stands differed between forest types for spiders ($\chi^2_{[3, N = 45]}$
299 $= 13.56, P = 0.001$, staphylinids ($\chi^2_{[3, N = 45]} = 10.27, P = 0.006$) and carabids ($\chi^2_{[3, N = 45]} =$
300 $6.72, P = 0.035$). For spiders, within-stand beta diversity was higher in ash than in
301 either mixed ($P_{\text{adj}} = 0.002$) or spruce stands ($P_{\text{adj}} = 0.006$) (Figure 2). For staphylinids
302 within-stand beta diversity was higher in both ash ($P_{\text{adj}} = 0.021$) and spruce ($P_{\text{adj}} =$
303 0.009) compared to mixed stands. Carabids showed a similar, albeit marginally
304 significant, trend (ash > mixed, $P_{\text{adj}} = 0.050$; spruce > mixed, $P_{\text{adj}} = 0.078$) (Figure 2).

305 Beta diversity between stands differed among forest types for spiders ($\chi^2_{[3, N =$
306 $_{15}] = 7.68, P = 0.022$) and carabids ($\chi^2_{[3, N = 15]} = 6.97, P = 0.031$) but not for staphylinids
307 ($\chi^2_{[3, N = 15]} = 0.37, P = 0.830$). Pairwise comparisons revealed that between-stands beta
308 diversity was higher in ash than in spruce stands for spiders ($P_{\text{adj}} = 0.022$) and in ash
309 than in mixed stands for carabids ($P_{\text{adj}} = 0.027$) (Figure 2).

310

311 ***3.4 Arthropod assemblages among forest types***

312 Species composition did not differ significantly among forest types for spiders
313 ($F_{[2,14]} = 1.25, P = 0.066$), but composition varied with forest type for both beetle
314 families (staphylinids ($F_{[2,14]} = 1.28, P = 0.027$); carabids ($F_{[2,14]} = 1.40, P = 0.008$)).
315 Although results from PERMANOVA could be influenced by differences in multivariate
316 dispersion between forest types (i.e. between stands beta diversity), the PCA
317 confirmed that these trends were due to differences in species composition (Figure 3).
318 For spiders, assemblages were not clearly distinct from each other, with those from
319 ash stands overlapping those from mixed and spruce stands, as well as generally
320 displaying greater spread across the plots than other taxa. Assemblages from mixed
321 and spruce stands were more tightly clustered, although the distinct groups were close
322 to each other. For staphylinids, assemblages of ash and mixed stands clustered
323 together, whereas those of spruce stands were distinct, although data from all three
324 forest types had a similar spread across the ordination. For carabids, assemblages of all
325 three forest types were broadly separated from each other, although dispersion of the
326 assemblages within mixed stands was less than for the other forest types.

327

328 **4. Discussion**

329 Plantation forests generally have lower diversity and fewer specialist species
330 than forests of natural origin (Brockerhoff et al., 2008). This has been attributed to a
331 range of factors, including shorter rotation length and reduced heterogeneity across
332 spatial scales (Brockerhoff et al., 2008, Coote et al., 2012, Irwin et al., 2014). However,
333 some authors have argued that such comparisons are not relevant in regions where
334 natural forest cover is low (Stephens and Wagner, 2007, O'Callaghan et al., 2016).
335 Instead, investigation of the conservation significance of plantations relative to that of
336 alternative land use regimes (Oxbrough et al., 2006, 2007) or the relative importance
337 of differing management approaches (e.g. selection of tree species, use of mixtures)
338 (Oxbrough et al., 2005, 2012, Barsoum et al., 2013), are of greater relevance for
339 supporting biodiversity. In this context, we tested the alternative hypotheses that
340 either: i), equitable mixes of a non-native and a native tree species support greater
341 diversity of ground-dwelling arthropods than single species stands; or ii), native ash
342 stands support greater diversity of ground-dwelling arthropods than do mixed or single
343 species stands that include a non-native conifer species.

344

345 **4.1 Arthropod diversity**

346 Responses of species richness to stand type differed among the arthropod
347 groups that we studied. For spiders and staphylinids neither hypothesis was
348 supported, i.e., there was no difference among stand types in the number for spider
349 species, whereas non-native spruce stands supported significantly more staphylinid
350 species than mixed stands. This suggests that spruce plantation forests, despite being
351 of non-native origin, support similar diversity of these groups, as stands containing a
352 native tree species component, whether in a mixed or single species stand. This
353 conclusion is consistent with results of previous research in plantation mixes
354 containing a spruce non-native species component (Oxbrough et al., 2012, Barsoum et
355 al., 2013), and suggests that forest structural features are more important than stand
356 type for explaining variation in biodiversity among plantation types. For instance,
357 cover of the lower vegetation layers is a key determinant of ground-dwelling spider
358 and staphylinid beetle diversity in plantation forests (Buse and Good, 1993, Oxbrough
359 et al., 2005) most likely through influences on food availability, refuges from

360 predation, web attachment points for spiders and micro-climate conditions (Uetz,
361 1991, Bohac, 1999). In this study, cover of bryophyte and herb layer vegetation was
362 similar among forest types, potentially providing a comparable range of microhabitats.
363 In contrast, Schuldt and Scherer-Lorenzen (2014) found a significant negative effect on
364 spider diversity where a non-native species was present, in this case Douglas fir
365 (*Pseudotsuga menziesii* (Mirb.) Franco) and concluded that tree species identity was a
366 more important determinant of arthropod diversity than tree diversity *per se*. Along
367 with our results, this suggests that non-native status may also be less important than
368 the tree species identity.

369 In contrast to our results for spiders and staphylinids, richness of carabids
370 corroborated our second hypothesis, i.e., there was a negative influence of spruce on
371 carabid diversity in either mixed or as single species stands. This may be attributed to
372 differences in resource availability or alterations to more complex ecological
373 interactions between forest types. For instance, molluscs which are common carabid
374 prey items (Digweed, 1993, Lovei and Sunderland, 1996), are more species rich in
375 deciduous forests compared to conifer (Abele et al., 2014). Mollusc diversity is strongly
376 negatively associated with pH in forest environments (Gärdenfors et al., 1995), which
377 is typically lower when conifers are present in stands, as we found here. Whereas
378 Koivula et al (1999) have found that interspecific competition between carabids and
379 wood ants is somewhat ameliorated when deciduous litter is present. Taken together,
380 our data suggest that these contributing factors vary inconsistently among stand types
381 for all arthropod groups, and that for carabids, aggregations of native ash within
382 plantations is important to maintain a greater range of species.

383 Similarly to the results for species richness, the pattern of arthropod abundance
384 among stands was not consistent with either of our hypotheses: it was not negatively
385 impacted by the presence of non-native spruce in stands or particularly enhanced in
386 mixed stands. Instead, abundance of spiders and staphylinids was greatest in both
387 spruce and mixed stands compared to those of pure ash, and there was no difference
388 in abundance of carabids across stand types. The modified Berger-Parker dominance
389 index gave similar results across all three forest types indicating that this trend was not
390 due to a dramatically more uneven community structure in stands containing spruce
391 (i.e. indicating disproportionate abundance of two or three well-adapted species).

392 Indeed, these results suggest that stands with an element of spruce have equal or
393 greater resource availability for epigeaic arthropods than do stands with an ash
394 component. This finding is consistent with findings by Schuldt and Scherer-Lorenzen
395 (2014) in mixes of Norway spruce with other broadleaved tree species.

396 A key resource available in the ground layer micro-habitat of forests is the
397 litter, which is an important determinant of diversity and abundance for ground-
398 dwelling arthropods (Uetz, 1979, Uetz, 1991, Chen and Wise, 1999, Magura et al.,
399 2002). Enhanced litter layers positively influence the availability of food resources for
400 predators, fungivores and saprophagous species (Chen and Wise, 1999) and also
401 stabilise microclimate conditions, favouring spiders, carabids and other arthropods
402 (Thiele, 1977, Koivula et al., 1999). We found that litter depth was successively greater
403 in stands containing spruce, where it probably decomposes more slowly than does the
404 highly palatable ash litter (Jacob et al., 2010), thus providing a greater structural
405 resource than stands containing ash. However, it should be noted that ash stands
406 potentially provide a greater food resource for arthropod trophic webs at the time of
407 leaf fall.

408

409 **4.2 Arthropod Assemblages**

410 In contrast to species diversity, we found that for all arthropod groups, beta
411 diversity supported our second hypothesis, i.e., variation in species composition was
412 greater within ash stands than in mixed stands. There was a greater range in number
413 of stems, understory cover, bryophyte cover and both depth and cover of leaf litter,
414 indicating that ash stands had greater habitat heterogeneity. These data also suggest
415 that open or closed canopy micro-habitats were patchy at a small-scale, a stand
416 characteristic known to positively influence ground-dwelling arthropod diversity in
417 managed forests (Niemelä and Spence, 1994, Oxbrough et al., 2005, Ziesche and Roth,
418 2008). This habitat heterogeneity may contribute to the greater beta diversity in ash
419 stands. Further, arthropod beta diversity between-stands was also higher for ash
420 stands than for spruce and mixed stands for spiders, or mixed stands for carabids.
421 Thus, we suggest that presence of spruce homogenises conditions among stands, thus
422 decreasing total diversity at region-wide scale.

423 Responses of assemblages to forest stand type varied among the arthropod
424 groups, and they were blurred by differences in between-stand diversity, particularly
425 for spiders. However, data for carabids and spiders are more or less consistent with
426 our first hypothesis, i.e., mixed stands supported a suite of species somewhat
427 intermediate between those of ash and spruce. This was not as clear for staphylinids,
428 in which spruce and mixed stands supported different assemblages, but mixed stands
429 supported assemblages that tended toward those of ash stands, suggesting the
430 influence of ash on species composition in mixed stands was greater than that of
431 spruce. Together, these responses suggest that stand mixes can play a role in
432 supporting species typical of native stands.

433 Several of our environmental variables were at an intermediate state in mixed
434 stands as is consistent with hypothesis one. This included litter depth and soil pH,
435 reflecting the common observation that spruce plantations have more acidic soils
436 (Adam, 1999). Both parameters are known to influence arthropod assemblage
437 structure in forest ecosystems (Thiele, 1977, Bultman and Uetz, 1982, Magura et al.,
438 2002, Savin et al., 2007, Schuldt et al., 2008). Additionally mixed stands supported an
439 intermediate coverage of needle and leaf litter. Such differences in litter type are
440 particularly important for spider assemblages (Ziesche and Roth, 2008), where fine-
441 scale structural differences in microhabitat influence web building (Bultman and Uetz,
442 1982, 1984). This may explain why the family Linyphiidae, in which species are
443 generally small- bodied (<3mm) and spin sheet webs in detritus microhabitats,
444 dominated our catch (83% of species; 95% of individuals).

445 Differences in arthropod assemblages among our three forest types are also
446 likely driven by effects related to canopy openness. For instance, stands which
447 contained a deciduous component (e.g. ash, mixed) will have reduced canopy cover for
448 at least five months each year, creating temporal heterogeneity in factors related to
449 penetration of sunlight. However, ash stands also had lower overall canopy openness
450 reflecting greater stem density and a well-developed understory largely comprised of
451 naturally regenerated hazel (*Corylus avellana* L.). Hazel may have persisted in the seed
452 bank (all sites were located on old woodland) and proliferated in the more amenable
453 conditions under ash canopies in comparison with spruce, where hazel was less
454 common and there was insufficient light. Such factors directly influence arthropods

455 through mediation of temperature and moisture levels on the forest floor (Penne et
456 al., 2010), but also through indirect effects on vegetation as previously discussed
457 (Thiele, 1977, Uetz, 1991, Bohac, 1999). In addition, although structural differences in
458 vegetation cover may have been minor among forest types, plant species composition
459 differs markedly between spruce and ash plantations (Coote et al., 2012). This may
460 have a corresponding influence on arthropods through effects on resource availability
461 (Lange et al., 2014), including litter input, micro-structure and prey.

462

463 **4.3 Conclusions and recommendations for management**

464 We found that three common epigeic arthropod groups responded differently
465 to stand type. Such variability in detailed arthropod responses to environmental
466 change is not uncommon in forest ecosystems (Irwin et al., 2014, Pedley et al., 2014)
467 and likely reflects large overall diversity of this group. However, this does not preclude
468 more general recommendations for forest management for supporting epigeic
469 arthropods being made (Pearce and Venier, 2006). Our findings highlight the potential
470 importance of including a native species in mixed stands. This is clearly desirable in
471 Irish plantation settings where the addition of common ash supported species
472 associated with natural ash stands as well as the spruce component. The current *Irish*
473 *Forest Biodiversity Guidelines* for mixed plantations recommend that the dominant
474 species should comprise not more than 80% of the stand (Forest Service, 2000),
475 however, previous work has showed little impact on arthropod assemblages when
476 mixing at these lower levels (Oxbrough et al., 2012, Barsoum et al., 2013). Instead,
477 based on the present work, we recommend including more equitable mixes (i.e., c.
478 50:50 ratio of native to non-native tree species) to enhance diversity of these groups
479 within stands.

480 We also found that single species stands of ash supported greater within and
481 between stand beta diversity than stands containing spruce. This, coupled with the
482 similar richness greater richness found in ash stands, suggests that presence of ash
483 aggregations will enhance arthropod diversity at both within- and between-stand
484 (plantation) levels. This supports current recommendations for establishment of a
485 range of tree species at a larger scale (Forest Service, 2000).

486 Finally and somewhat surprisingly, non-native Norway spruce did not have a
487 detectable negative influence on diversity of either spiders or staphylinids. Thus, with
488 respect to these groups, spruce sustain biodiversity for these two groups similar to
489 that maintained in mixed or native ash stands. However, richness of carabids (though
490 not number of individuals) was negatively affected by the presence of spruce. This
491 suggests caution when drawing conclusions from single taxon studies, and that for
492 carabid conservation mixed plantations are more desirable than pure spruce plantings.

493 In regions with low cover of natural forests and high cover of plantations
494 predominately comprised of non-native species, our work underscores the importance
495 of including native tree species in plantations for biodiversity conservation.
496 Nonetheless, from a forestry perspective, it may be unrealistic to propose that every
497 stand be managed to support species associated with native forest. Instead, we
498 recommend establishment of more equitably mixed stands, when mixes are desired to
499 enhance commercial value, to ensure habitat for a wider variety of species. Inclusion of
500 both sufficiently large patches of native species, among non-native single species crop
501 trees in plantations will enhance diversity of these arthropod groups and
502 heterogeneity at the plantation scale.

503

504

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513

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- 740

Table 1 Characteristics of stands

Sampling area	Stand type	Percent ash stems	Elevation (m.a.s.l)	Slope	Soil type†	Size ha	Age yrs	Mean ±SE DBH (cm)*	Mean ±SE height (m)‡	Latitude-Longitude
Cork	Ash	100%	180	Flat	Acidic: Lithosols/Regisols	5.9	50+	19 ±2.1	26 ±1.5	52° 12' 18" - 8° 35' 1"
Cork	Mixed	47%	230	Flat	Acidic: Lithosols/Regisols	5.9	41	22 ±2.0	22 ±1.8	52° 20' 5" - 8° 29' 36"
Cork	Spruce	0%	130	Flat	Acidic: Lithosols/Regisols	3.6	48	29 ±4.0	20 ±0.9	52° 19' 56" - 8° 28' 39"
Galway	Ash	100%	40	Flat	Basic: Grey Brown Podzolics / Brown Earths	15	50+	25 ±3.5	33 ±1.1	53° 4' 46" - 8° 52' 13"
Galway	Mixed	55%	30	Flat	Basic: Grey Brown Podzolics / Brown Earths	7.6	37	22 ±1.8	22 ±1.8	53° 25' 15" - 8° 48' 13"
Galway	Spruce	0%	30	Flat	Basic: Grey Brown Podzolics / Brown Earths	11	38	32 ±3.1	29 ±0.8	53° 15' 3" - 8° 42' 47"
Meath	Ash	100%	80	Flat	Acidic: Surface/Ground water Gleys	3.3	67	24 ±2.2	25 ±1.4	53° 5' 10" - 6° 47' 38"
Meath	Mixed	51%	80	Flat	Acidic: Surface/Ground water Gleys	3.1	43	22 ±2.2	23 ±2.2	53° 36' 55" - 6° 30' 1"
Meath	Spruce	0%	30	Flat	Acidic: Surface/Ground water Gleys	7.1	49	43 ±3.8	24 ±0.6	53° 54' 59" - 6° 47' 10"
Roscommon	Ash	100%	40	Flat	Acidic: Surface/Ground water Gleys	11	50+	19 ±0.1	23 ±0.1	53° 51' 46" - 7° 56' 45"
Roscommon	Mixed	46%	40	Flat	Acidic: Peaty gleys	6.6	48	25 ±0.1	28 ±2.8	53° 51' 49" - 7° 57' 54"
Roscommon	Spruce	0%	30	Flat	Acidic: Surface/Ground water Gleys	4.6	48	31 ±1.4	23 ±1.1	53° 29' 53" - 8° 12' 31"
Wicklow	Ash	100%	180	Moderate	Acidic: Surface/Ground water Gleys	4.4	50+	33 ±5.3	26 ±2.8	52° 45' 53" - 6° 38' 12"
Wicklow	Mixed	52%	60	Steep	Acidic: Lithosols/Regisols	4	59	42 ±3.5	20 ±3.7	52° 39' 45" - 6° 13' 4"
Wicklow	Spruce	0%	50	Steep	Acidic: Lithosols/Regisols	10.6	63	22 ±0.6	44 ±1.8	52° 48' 13" - 6° 11' 56"

†As defined by Environmental Protection Agency of Ireland; * Diameter at Breast Height (cm) (DBH); ‡Tree height (m)

Table 2 Environmental characteristics of the stand types. Medians (min. and max. values) are shown and differences tested with GLMM.

Variable	Ash	Mixed	Spruce	GLMM [2, N = 15]	Post hoc
10x10m plots †					
Canopy height (m)	25 (14-33)	22 (20-28)	24 (20-44)	$\chi^2 = 1.27$	
Diameter at Breast Height	24 (13-33)	22 (22-42)	31 (22-43)	$\chi^2 = 3.15$	
Number of stems	9 (6-18)	10 (5-13)	6 (3-8)	$\chi^2 = 8.36^*$	Ash & Mixed > Spruce
Understory cover (%)	15 (0-26)	5 (1-7)	0 (0-2)	$\chi^2 = 15.01^{***}$	Ash > Spruce & Mixed
Canopy openness (%)	6 (5-6)	11 (5-17)	17 (11-25)	$\chi^2 = 45.05^{***}$	Spruce > Mixed > Ash
Dead wood cover (%)	1 (0-8)	3 (0-4)	3 (0-7)	$\chi^2 = 0.79$	
Soil pH	4.7 (4.5-6.6)	4.8 (3.8-5.1)	3.5 (3.3-5.2)	$\chi^2 = 29.00^{***}$	Ash & Mixed > Spruce
1x1m plots ‡					
Litter depth (cm)	1.5 (0.9-2.4)	2 (1.7-2.5)	3.4 (2.8-3.9)	$\chi^2 = 54.01^{***}$	Spruce > Mixed > Ash
Leaf litter cover (%)	15 (10-67)	7 (3-11)	1 (1-20)	$\chi^2 = 4.53$	
Needle litter cover (%)	0	4 (3-11)	11 (1-50)	$\chi^2 = 7.65^*$	Spruce > Ash
Bryophyte cover (%)	79 (31-90)	83 (53-91)	76 (51-94)	$\chi^2 = 1.05$	
Herb layer cover (%)	43 (11-64)	31 (5-65)	35 (1-83)	$\chi^2 = 1.13$	

* P = 0.01- 0.05; ***P = <0.001

†Mean values per stand; ‡Mean value per plot within a stand

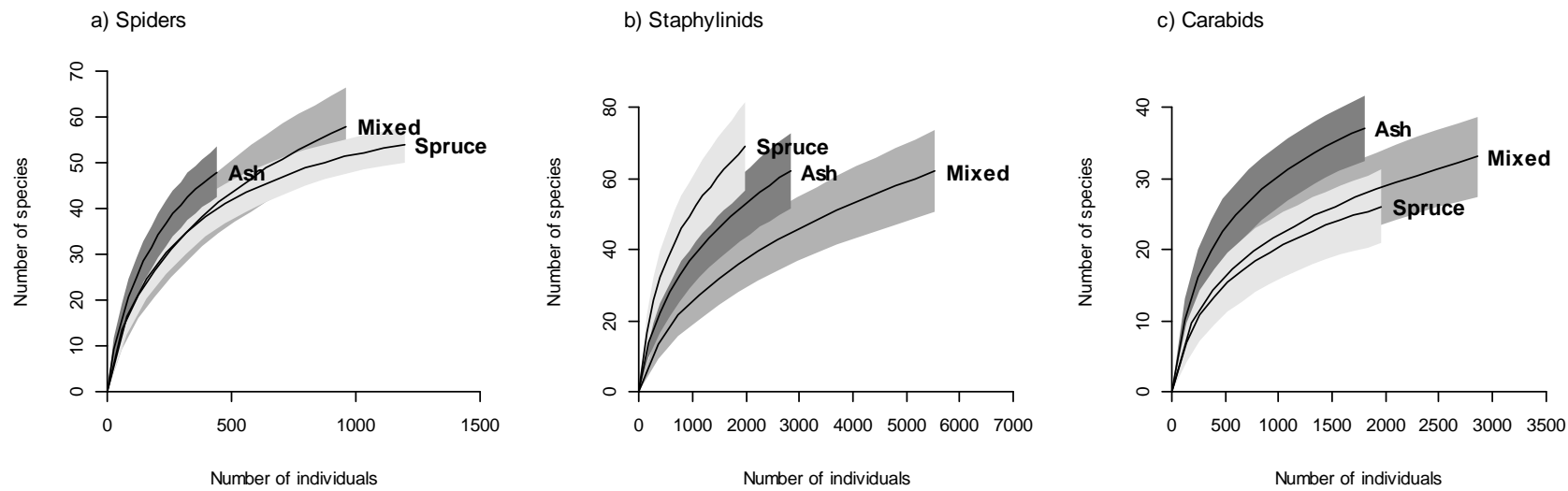


Figure 1 Sample-based rarefaction curves of species richness for (a) spiders, (b) staphylinids and (c) carabids among the forest types. Shaded areas represent 95% confidence intervals.

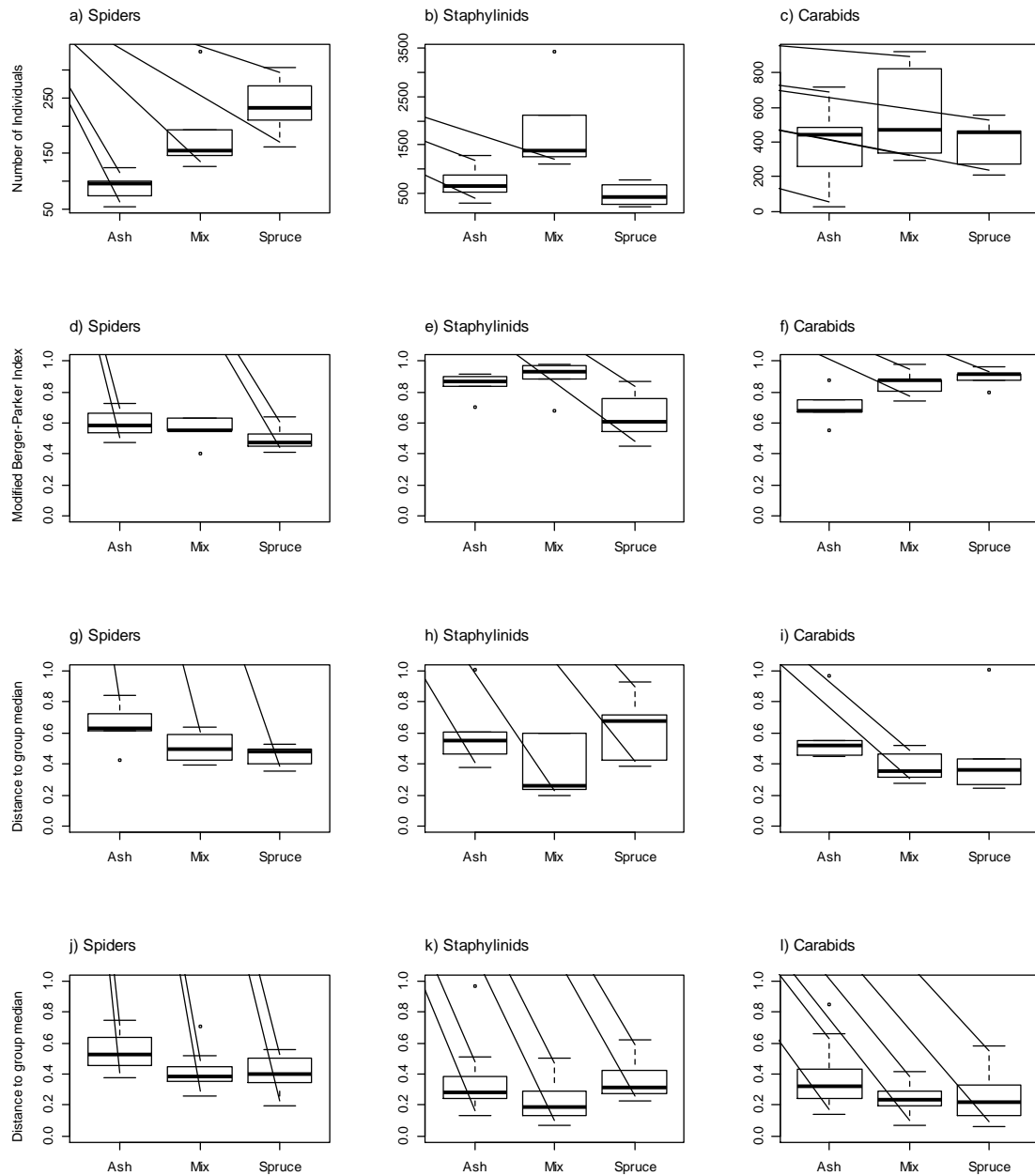


Figure 2. Abundance (a-c), dominance (d-f) and within-stand (g-i) and between-stand beta diversity (j-l) of spiders, staphylinids and carabids in ash, mixed and spruce plantation forests. Boxplots show the median (black bold line), the first and third quartiles (lower and upper limits of the box), the range of the data up to 1.5 times the interquartile limits (whiskers) and outliers out of this range (individual dots).

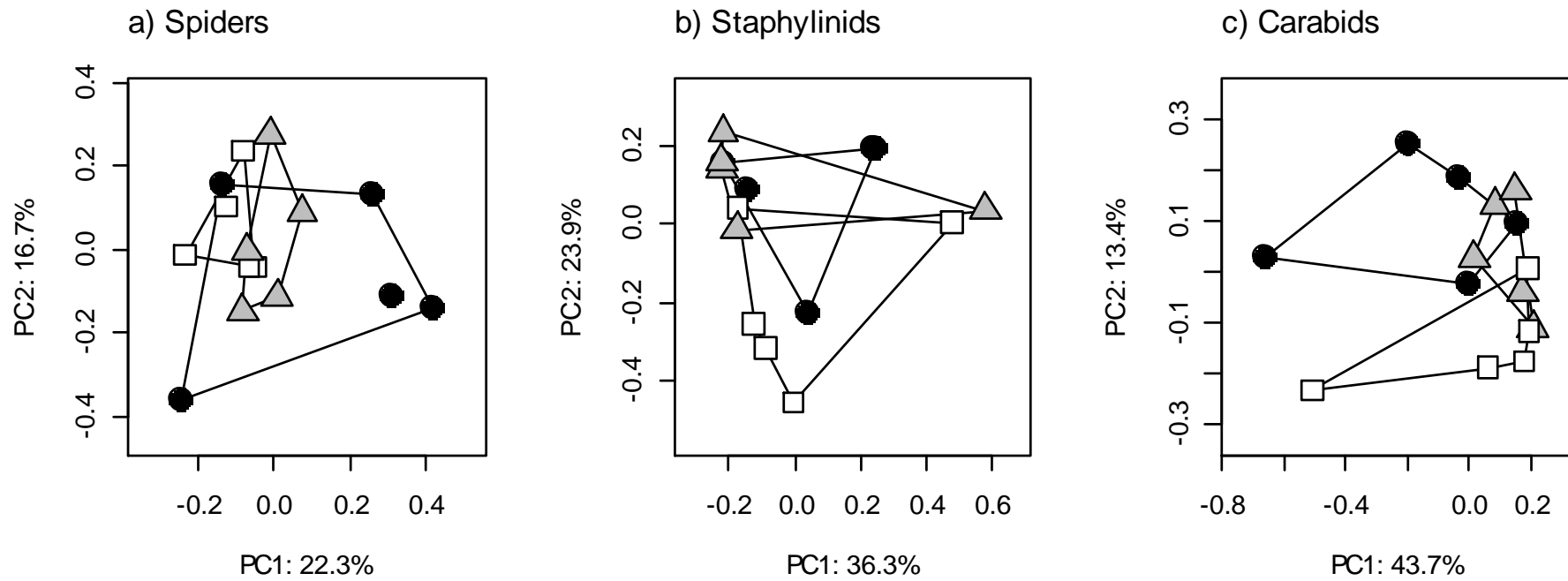


Figure 3. PCA plots for a) spiders, b) staphylinids and c) carabids. Percentage of represented variance is indicated for each axis. Forest types are indicated with symbols (black dots = ash; grey triangles = mixed; white squares = spruce). Convex hulls contain all stands of each forest type.

Supplementary Table S1. Reference list of the keys used for staphylinid identification.

- Booth, R. 1984. A provisional key to the British species of *Tachyporus* (Coleoptera, Staphylinidae) based on elytral chaetotaxy. *Circaea* 2, 15-19.
- Freude, H., Harde, K.W., Lohse, G.A. (Eds.) 1964. Die Käfer Mitteleuropas. Bd. 4, Staphylinidae I (Micropeplinae bis Tachyporinae). Krefeld: Goecke & Evers.
- Freude, H., Harde, K.W., Lohse, G.A. (Eds.) 1974. Die Käfer Mitteleuropas. Bd. 5, Staphylinidae II (Hypocyphtinae und Aleocharinae). Pselaphidae. Krefeld: Goecke & Evers.
- Hammond, P.M. 1973. Notes on British Staphylinidae 3. The British species of *Sepedophilus* Gistel (*Conosomus* auctt.). *Entomologist's monthly magazine* 108, 130-165.
- Lott, D.A. 2009. The Staphylinidae (Rove Beetles) of Britain and Ireland: Scaphidiinae, Piestinae, Oxytelinae. Vol. 12, Pt. 5. (Handbooks for the identification of British Insects). Royal Entomological Society. 106 pp.
- Lott, D.A., Anderson, R. 2009. The Staphylinidae (rove beetles) of Britain and Ireland: Oxyporinae, Steninae, Euaesthetinae, Pseudopsinae, Paederinae, Staphylininae. Vol. 12, Pts. 7 and 8. (Handbooks for the identification of British Insects). Royal Entomological Society. 340 pp.
- Pearce, E.J. 1957. Coleoptera, Pselaphidae. Vol. IV, Pt. 9. (Handbooks for the identification of British Insects). Royal Entomological Society. 32 pp.
- Telfer, M.G. 2012. Joy's keys to Tachyporinae. Adapted from pages 82-92 and plates 25-27 of Joy, N.H. 1932. A practical handbook of British beetles. Two volumes. H.F. & G. Witherby.
- Tottenham, C.E. 1954. Coleoptera, Staphylinidae section (a) Piestinae to Euaesthetinae. Vol. IV, Pt. 8(a). (Handbooks for the identification of British Insects). Royal Entomological Society. 79 pp.

Supplementary Table S2. Spiders collected in each forest type. Nomenclature follows Roberts (1993).

	Ash	Mixed	Spruce	Total
<i>Agyneta conigera</i>	0	1	8	9
<i>Agyneta ramosa</i>	25	36	70	131
<i>Agyneta subtilis</i>	7	29	12	48
<i>Amaurobius fenestralis</i>	0	1	0	1
<i>Asthenargus paganus</i>	1	2	17	20
<i>Bathypantes gracilis</i>	5	0	1	6
<i>Bathypantes nigrinus</i>	3	2	7	12
<i>Centromerita concinna</i>	0	2	0	2
<i>Centromerus arcanus</i>	0	1	1	2
<i>Centromerus dilutus</i>	0	5	3	8
<i>Ceratinella brevipes</i>	2	10	5	17
<i>Ceratinella brevis</i>	7	0	8	15
<i>Ceratinella scabrosa</i>	18	32	36	86
<i>Clubiona compta</i>	2	1	1	4
<i>Clubiona trivialis</i>	0	1	0	1
<i>Cryphoeca silvicola</i>	0	2	3	5
<i>Cyclosa conica</i>	0	1	0	1
<i>Dicymbium tibiale</i>	89	46	12	147
<i>Diplocephalus latifrons</i>	31	56	23	110
<i>Diplocephalus picinus</i>	18	55	35	108
<i>Diplocephalus tibiale</i>	1	0	0	1
<i>Diplostylor concolor</i>	9	0	1	10
<i>Dismodicus bifrons</i>	2	0	3	5
<i>Drapetisca socialis</i>	0	1	0	1
<i>Enoplognatha ovata</i>	1	0	0	1
<i>Episinus angulatus</i>	0	1	0	1
<i>Erigone atra</i>	2	0	0	2
<i>Erigonella hiemalis</i>	0	10	0	10
<i>Gonatium rubellum</i>	0	2	2	4
<i>Gongylidiellum vivum</i>	1	1	6	8
<i>Gongylidium rufipes</i>	2	2	2	6
<i>Hahnia helveola</i>	0	0	1	1
<i>Hypselistes jacksoni</i>	0	0	1	1
<i>Kaestneria dorsalis</i>	0	1	0	1
<i>Lepthyphantes alacris</i>	19	95	140	254
<i>Lepthyphantes cristatus</i>	0	1	1	2
<i>Lepthyphantes flavipes</i>	4	12	61	77
<i>Lepthyphantes mengei</i>	0	0	4	4
<i>Lepthyphantes minutus</i>	1	0	0	1
<i>Lepthyphantes obscurus</i>	0	0	8	8
<i>Lepthyphantes pallidus</i>	7	1	8	16
<i>Lepthyphantes ramosa</i>	1	0	0	1
<i>Lepthyphantes tenebricola</i>	34	123	81	238
<i>Lepthyphantes tenuis</i>	0	1	0	1
<i>Lepthyphantes zimmermanni</i>	40	102	233	375
<i>Leptorhoptrum robustum</i>	1	1	0	2

<i>Linyphia hortensis</i>	2	3	1	6
<i>Maro minutus</i>	0	0	11	11
<i>Maso sundevalli</i>	0	1	0	1
<i>Meta mengei</i>	2	5	3	10
<i>Micrargus herbigradus</i>	0	1	0	1
<i>Microneta viaria</i>	6	2	2	10
<i>Monocephalus alacris</i>	0	5	0	5
<i>Monocephalus castaneipes</i>	0	1	0	1
<i>Monocephalus fuscipes</i>	51	214	199	464
<i>Neon reticulatus</i>	0	0	1	1
<i>Neriere clathrata</i>	1	3	3	7
<i>Neriere montana</i>	1	3	1	5
<i>Neriere peltata</i>	4	7	11	22
<i>Oedothorax fuscus</i>	2	0	0	2
<i>Ozyptila trux</i>	0	0	2	2
<i>Pachygnatha clercki</i>	0	0	3	3
<i>Pachygnatha listeri</i>	2	1	0	3
<i>Pardosa amentata</i>	0	0	1	1
<i>Pardosa lugubris</i>	1	1	4	6
<i>Pelecopsis elongata</i>	1	0	0	1
<i>Pelecopsis nemoralis</i>	0	2	0	2
<i>Pholcomma gibbum</i>	0	1	0	1
<i>Pirata hygrophilus</i>	1	0	0	1
<i>Pocadicnemis juncea</i>	0	4	2	6
<i>Porrhomma pallidum</i>	0	2	2	4
<i>Robertus lividus</i>	0	6	19	25
<i>Saaristoa abnormis</i>	2	9	41	52
<i>Saloca diceros</i>	0	7	0	7
<i>Segestria senoculata</i>	1	0	0	1
<i>Tapinocyba insecta</i>	21	18	21	60
<i>Tapinocyba pallens</i>	1	6	31	38
<i>Tetragnatha montana</i>	0	1	0	1
<i>Theridion pallens</i>	1	0	0	1
<i>Walckenaeria acuminata</i>	10	20	27	57
<i>Walckenaeria cuspidata</i>	3	0	0	3
<i>Walckenaeria dysderoides</i>	0	2	9	11
<i>Walckenaeria nudipalpis</i>	1	0	3	4
<i>Zora spinimana</i>	1	0	2	3
Number of individuals	448	962	1193	2603
Number of species	48	58	54	84

Supplementary Table S3. Staphylinids collected in each forest type. Nomenclature follows (Duff, 2012).

	Ash	Mixed	Spruce	Total
<i>Acidota crenata</i>	0	1	0	1
<i>Anotylus rugosus</i>	61	35	4	100
<i>Anotylus sculpturatus</i>	4	4	15	23
<i>Anotylus tetracarlinatus</i>	0	2	0	2
<i>Anthobium unicolor</i>	16	5	0	21
<i>Atrecus affinis</i>	1	0	1	2
<i>Bisnius fimetarius</i>	9	10	9	28
<i>Bisnius puella</i>	0	1	2	3
<i>Bolitobius cingulatus</i>	0	0	2	2
<i>Brachygluta fossulata</i>	0	0	1	1
<i>Bryaxis puncticollis</i>	1	0	0	1
<i>Bryophacis crassicornis</i>	0	0	1	1
<i>Carpelimus elongatulus</i>	1	1	1	3
<i>Euplectus duponti</i>	14	0	0	14
<i>Euplectus</i> sp. 1	0	1	0	1
<i>Gabrius appendiculatus</i>	0	0	1	1
<i>Gyrophypnus angustatus</i>	2	2	0	4
<i>Habrocerus</i>				
<i>capillaricornis</i>	5	4	9	18
<i>Ischnosoma splendidum</i>	0	0	8	8
<i>Lathrobium brunnipes</i>	3	4	9	16
<i>Lathrobium fulvipenne</i>	0	1	8	9
<i>Lathrobium geminum</i>	0	1	2	3
<i>Lesteva sicula heeri</i>	19	8	0	27
<i>Lesteva</i> sp. 1	0	0	1	1
<i>Lordithon exoletus</i>	1	0	2	3
<i>Lordithon lunulatus</i>	1	2	1	4
<i>Megarthrus denticollis</i>	0	1	0	1
<i>Megarthrus depressus</i>	7	3	7	17
<i>Megarthrus sinuaticollis</i>	0	1	0	1
<i>Micropeplus</i> sp. 1	1	0	0	1
<i>Micropeplus</i>				
<i>staphylinoides</i>	1	2	0	3
<i>Mycetoporus clavicornis</i>	0	0	1	1
<i>Mycetoporus despectus</i>	6	1	1	8
<i>Mycetoporus lepidus</i>	1	0	11	12
<i>Mycetoporus longulus</i>	0	0	1	1
<i>Mycetoporus rufescens</i>	1	1	6	8
<i>Ocypus brunnipes</i>	0	0	1	1
<i>Ocypus olens</i>	8	42	19	69
<i>Olophrum piceum</i>	0	0	1	1
<i>Omalium excavatum</i>	0	0	2	2
<i>Omalium italicum</i>	25	2	0	27
<i>Omalium rivulare</i>	1	8	1	10
<i>Omalium rugatum</i>	1	1	16	18
<i>Omalium</i> sp. 1	0	0	1	1

<i>Othius punctulatus</i>	44	52	133	229
<i>Othius subuliformis</i>	11	4	44	59
<i>Parabolitobius inclinans</i>	0	0	1	1
<i>Philonthus albipes</i>	0	0	1	1
<i>Philonthus carbonarius</i>	1	2	1	4
<i>Philonthus cognatus</i>	1	3	1	5
<i>Philonthus decorus</i>	777	2044	471	3292
<i>Philonthus laminatus</i>	1	4	1	6
<i>Philonthus mannerheimi</i>	1	0	1	2
<i>Philonthus marginatus</i>	1	1	2	4
<i>Philonthus politus</i>	3	0	1	4
<i>Philonthus splendens</i>	1	1	0	2
<i>Philonthus succicola</i>	0	0	1	1
<i>Philonthus tenuicornis</i>	1	0	1	2
<i>Philonthus varians</i>	0	1	0	1
<i>Phloeocharis subtilissima</i>	0	0	1	1
<i>Phloeostiba plana</i>	0	1	0	1
<i>Proteinus ovalis</i>	0	0	1	1
<i>Quedius cinctus</i>	1	0	0	1
<i>Quedius curtipennis</i>	28	109	104	241
<i>Quedius fuliginosus</i>	39	36	52	127
<i>Quedius fumatus</i>	23	18	5	46
<i>Quedius invreae</i>	0	1	0	1
<i>Quedius maurorufus</i>	0	1	0	1
<i>Quedius picipes</i>	0	1	8	9
<i>Quedius umbrinus</i>	2	0	0	2
<i>Rugilus rufipes</i>	1	1	33	35
<i>Sepedophilus</i>				
<i>immaculatus</i>	1	1	5	7
<i>Sepedophilus littoreus</i>	1	0	0	1
<i>Sepedophilus marshami</i>	4	2	38	44
<i>Sepedophilus nigripennis</i>	4	10	39	53
<i>Staphylinus</i>				
<i>erythropterus</i>	137	38	93	268
<i>Stenus bimaculatus</i>	20	1	2	23
<i>Stenus brunnipes</i>	1	1	0	2
<i>Stenus carbonarius</i>	1	0	1	2
<i>Stenus clavicornis</i>	1	0	0	1
<i>Stenus crassus</i>	1	0	0	1
<i>Stenus flavipes</i>	0	0	1	1
<i>Stenus impressus</i>	16	9	8	33
<i>Stenus juno</i>	0	1	0	1
<i>Stenus nanus</i>	0	1	0	1
<i>Stenus ochropus</i>	5	0	0	5
<i>Stenus sp. 1</i>	1	0	0	1
<i>Tachinus elongatus</i>	0	1	2	3
<i>Tachinus laticollis</i>	312	49	30	391
<i>Tachinus marginellus</i>	3	0	0	3
<i>Tachinus pallipes</i>	9	18	5	32
<i>Tachinus proximus</i>	1	1	0	2
<i>Tachinus rufipes</i>	1371	2979	511	4861
<i>Tachyporus atriceps</i>	6	29	49	84

<i>Tachyporus</i>				
<i>chrysomelinus</i>	1	0	0	1
<i>Tachyporus nitidulus</i>	0	5	32	37
<i>Tachyporus obtusus</i>	1	1	0	2
<i>Tachyporus solutus</i>	0	1	1	2
<i>Tachyporus</i> sp. 1	5	0	1	6
<i>Tasgius melanarius</i>	3	4	11	18
<i>Xantholinus linearis</i>	12	24	185	221
<i>Xantholinus longiventris</i>	2	0	1	3
Aleocharinae	506	496	335	1337
Number of individuals	3551	6096	2358	12005
Number of species	36	39	32	102

Supplementary Table S4. Carabids collected in each forest type. Nomenclature follows Luff (2007).

	Ash	Mixed	Spruce	Total
<i>Abax parallelepipedus</i>	555	1569	1340	3464
<i>Agonum fuliginosum</i>	7	0	3	10
<i>Agonum micans</i>	1	0	0	1
<i>Agonum muelleri</i>	1	1	0	2
<i>Amara plebeja</i>	3	1	1	5
<i>Amara similata</i>	2	1	0	3
<i>Anchomenus dorsalis</i>	3	0	0	3
<i>Asaphidion curtum</i>	2	0	0	2
<i>Asaphidion flavipes</i>	3	0	0	3
<i>Badister bullatus</i>	0	1	0	1
<i>Badister soldalis</i>	3	3	0	6
<i>Batenus livens</i>	1	0	0	1
<i>Bembidion lampros</i>	15	8	1	24
<i>Bembidion mannerheimii</i>	57	3	0	60
<i>Bembidion tetracolum</i>	2	0	2	4
<i>Calathus fuscipes</i>	0	2	0	2
<i>Calathus rotundicollis</i>	5	3	2	10
<i>Carabus granulatus</i>	119	32	73	224
<i>Carabus nemoralis</i>	75	192	2	269
<i>Carabus problematicus</i>	0	16	23	39
<i>Clivina fossor</i>	5	1	4	10
<i>Cychrus caraboides</i>	10	2	2	14
<i>Dyschirius globosus</i>	12	1	0	13
<i>Elaphrus cupreus</i>	0	3	0	3
<i>Harpalus rufipes</i>	1	0	0	1
<i>Laemostenus terricola</i>	0	1	0	1
<i>Leistus fulvibarbis</i>	21	22	4	47
<i>Loricera pilicornis</i>	11	33	14	58
<i>Nebria brevicollis</i>	255	228	13	496
<i>Nothiophilus biguttatus</i>	0	2	0	2
<i>Notiophilus biguttatus</i>	20	71	49	140
<i>Ocys harpaloides</i>	4	4	1	9
<i>Ophonus puncticeps</i>	1	0	0	1
<i>Oxysephalus fuscipes</i>	3	1	2	6
<i>Oxysephalus obscurus</i>	2	0	11	13
<i>Pterostichus cristatus</i>	0	3	0	3
<i>Pterostichus madidus</i>	148	490	138	776
<i>Pterostichus melanarius</i>	163	124	84	371
<i>Pterostichus niger</i>	32	10	152	194
<i>Pterostichus nigrata</i>	2	1	11	14
<i>Pterostichus rhaeticus</i>	2	0	2	4
<i>Pterostichus strenuus</i>	79	14	5	98
<i>Pterostichus vernalis</i>	0	1	0	1
<i>Stomis pumicatus</i>	0	0	1	1
<i>Synuchus vivalis</i>	2	0	0	2
<i>Trechus obtusus</i>	246	33	53	332

<i>Trichocellus placidus</i>	0	1	0	1
Number of individuals	1873	2878	1993	6744
Number of species	37	34	26	47
