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1 **Parasitism of the beech leaf-miner weevil in a woodland:**  
2 **Patch size, edge effects and parasitoid species identity.**

3

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21

22 **Abstract**

23

- 24 1. Deciduous woodlands are a key habitat for the diversity of invertebrates within  
25 the primarily agricultural landscape of lowland Scotland. Little is known,  
26 however, of the contribution that within site heterogeneity plays in  
27 maintaining invertebrate diversity within these habitats. We consider how  
28 habitat heterogeneity affects the beech leaf-mining weevil *Rhynchaenus fagi*  
29 L. (Curculionidae, Coleoptera) and its associated polyphagous parasitoids.
- 30 2. This was done by investigating host density and parasitism rates of the weevil  
31 as it fed on 88 beech trees (*Fagus sylvatica* L. (Fagaceae)) occurring in  
32 patches within a birch woodland. We aimed to assess how patch site, isolation  
33 and patch quality influenced parasitism rates and parasitoid diversity.
- 34 3. Herbivore leaf-mine abundance was greatest where beech trees were located  
35 on the edge. Parasitism rates were also affected by the location of the host  
36 insect at the woodland edge and interior. Depending on parasitoid species  
37 identity, parasitism rates showed independent, direct, and inverse responses to  
38 the density of leaf-mines. Parasitism rates showed direct and inverse  
39 responses to the patch sizes of beech trees, while overall parasitoid diversity  
40 was negatively correlated with patch size.
- 41 4. Heterogeneity in the location of the beech trees within this birch woodland  
42 plays a key role in determining local patterns of parasitism rates and parasitoid  
43 diversity. It is suggested that within site variation in the area of high quality  
44 resource patches, represented by the beech trees, was key to structuring these  
45 parasitoid communities. Niche separation was promoted by individual species  
46 capacity to locate host insects in this spatially complex habitat.

47

48 **Keywords:** parasitism, density-dependence, edge effects, patch size.

49

## 50 **Introduction**

51

52         Semi-natural deciduous woodland are an integral component of Scottish  
53 lowland landscape and represent key habitats for a verity of invertebrate taxa  
54 (Woodcock *et al.*, 2003a; Woodcock *et al.*, 2003b; Vanbergen *et al.*, 2006). These  
55 woodlands are often situated predominantly within areas arable or improved  
56 grassland, and represent long-lived habitat features that can provide important refuges  
57 many invertebrates in an otherwise intensively managed landscape (Petit & Usher,  
58 1998; Vanbergen *et al.*, 2005). While agro-forestry also represents a major  
59 component of forest cover in Scotland, such forests are predominantly composed of  
60 non-native conifers and represent low quality habitats for the majority of native  
61 woodland invertebrates (Watt *et al.*, 1998).

62         While the availability of deciduous woodlands has been shown to be a key  
63 components to the maintenance of invertebrate diversity within agricultural  
64 landscapes (Woodcock *et al.*, 2003a; Vanbergen *et al.*, 2005), little is known about the  
65 role that within site heterogeneity plays in the maintenance of insect populations.  
66 This study aims to assess the effect of heterogeneity in habitat structure on the  
67 diversity and numerical response of a suite of polyphagous hymenopteran parasitoids  
68 utilizing a monophagous leaf-mining beetle host. Habitat complexity is known to  
69 affect the capacity of parasitoids to disperse between host populations and so is of  
70 great importance in determining their population structure (Kareiva, 1987; Cronin &  
71 Strong, 1999). For example, reduced rates of parasitism for some parasitoids have  
72 been recorded in spatially complex habitats (Gols *et al.*, 2005). How these factors  
73 contribute to determining species abundance and overall diversity is an important

74 factor in understanding the role of deciduous woodlands within agricultural  
75 landscapes for maintaining invertebrate diversity.

76 In this study, populations of the beech leaf-miner - *Rhynchaenus fagi* - and its  
77 associated parasitoids were sampled from small patches of beech trees distributed in  
78 discrete clumps throughout a predominantly birch woodland (*Betula spp.*  
79 (*Betulaceae*)). As tertiary trophic levels are often more susceptible to habitat  
80 fragmentation than secondary consumers (Kareiva, 1987; Tschamtkke & Brandl,  
81 2004), we assessed the impacts of beech tree isolation and patch size on the  
82 parasitoids of *R. fagi*. This reflects the assumption that patch size will affect both the  
83 probability of local extinction, with smaller populations generally being at greater risk  
84 (Pimm *et al.*, 1988; Cronin, 2003). In addition to the impact of patch size and isolation  
85 we also investigated the role that *R. fagi* host density and environmental conditions  
86 associated with these patches has on both rates of parasitism and overall parasitoid  
87 diversity. We predict that: 1) small and isolated patches of beech trees would provide  
88 refuges for the host insect *R. fagi* from its parasitoids, resulting in low levels of  
89 parasitism and parasitoid diversity; 2) This response would be modulated by the  
90 location in relation to major environmental gradients (e.g. the woodland edge) and  
91 patch quality in terms of *R. fagi* host density.

92

## 93 **Methods**

94

### 95 *Study site*

96

97 The study site was undertaken within a single deciduous woodland (0.28 km<sup>2</sup>)  
98 stand in Banchory, Aberdeenshire, Scotland (57°04'N, 2°32'W). The woodland was  
99 dominated (>80% of the total area) by two species of birch (*Betula pendula* Roth and

100 *Betula pubescens* Ehrh.) with occasional patches of Scots pine (*Pinus sylvestris* L.).  
101 Grasses, particularly *Holcus* spp., *Festuca* spp. and *Deschampsia* spp. occurred  
102 throughout the understorey. Interspersed into this birch woodland were 88 beech trees  
103 (Fig. 1), the host-plant of the monophagous leaf-mining weevil *R. fagi*. The woodland  
104 was surrounded by either Scots pine dominated plantation, or adjoining the North-  
105 East edge of the woodland plantation that had been clear felled in 1998. Within a 2  
106 km radius of the study site there were no other patches of deciduous woodland.

107

#### 108 *Tri-trophic system*

109

110 *Rhynchaenus fagi* is a univoltine leaf-mining weevil which feeds as larvae  
111 exclusively on beech trees, although adults will feed on a variety of plants (Bale &  
112 Luff, 1978). Adult weevils over winter primarily within leaf litter (Bale, 1984) until  
113 mid-March, when the majority of adults will migrate to beech trees just prior to bud-  
114 burst. Eggs are laid in the leaf mid-rib from where a linear blotch-mine develops,  
115 within which the larvae feed on both the palisade and spongy parenchyma (Nielsen,  
116 1966). From oviposition to emergence of the weevil takes approximately 30-35 days,  
117 with adults appearing towards the end of June (Bale & Luff, 1978). *Rhynchaenus fagi*  
118 is recorded as host to ten species of chalcid wasps (Askew & Shaw, 1974) as well as  
119 at least one braconid (Day & Watt, 1989).

120 The three dominant species of hymenopteran parasitoids reared from *R. fagi* in  
121 this study were all polyphagous species recorded as utilising leaf-mining insects on a  
122 variety of deciduous trees, including *Salix* spp. (Salicaceae), *Quercus* spp (Fagaceae),  
123 *Fagus* spp. (Fagaceae) and *Betula* spp (Betulaceae) (Askew & Shaw, 1974; Rott &  
124 Godfray, 2000). *Pnigalio longulus* (Zett.) (Eulophidae) and *Chrysocharis nephereus*  
125 (Walker) (Eulophidae) are common parasitoids of many species of leaf-mining insects

126 including moths (Lepidoptera: Eriocraniidae, Gracillariidae and Nepticulidae),  
127 sawflies (Hymenoptera: Tenthredinidae) and weevils (Coleoptera: Curculionidae)  
128 (Askew & Shaw, 1974). Both species are likely to be multivoltine (Raske, 1978;  
129 Pschorn-Walcher & Heitland, 2000). *Colastes braconius* Haliday (Braconidae) is a  
130 multivoltine species (Wharton, 1993) known to parasitize a wide range of leaf-mining  
131 hosts, including both moths and weevils (Day & Watt, 1989; Rott & Godfray, 2000).  
132 Both *P. longulus* and *C. braconius* have ectoparasitic larval stages, while *C.*  
133 *nephereus* is an endoparasite (Rott & Godfray, 2000). All three species are idiobionts  
134 with clutch sizes of one (Rott & Godfray, 2000). Records for all three of these  
135 species suggest that they are normally associated with woodland habitats, although  
136 may be found on trees in more open situations where their hosts are present (Askew &  
137 Shaw, 1974; Day & Watt, 1989; Casas, 1990; Rott & Godfray, 2000; Jordano, 2003).  
138 In addition to the *R. fagi* hosts considered in this paper, leaf-miners of the *Eriocrania*  
139 spp. (Lepidoptera: Eriocraniidae) and *Phyllonorycter* spp. (Lepidoptera:  
140 Gracillariidae) were also found on birch trees within the woodland. This leaf-mining  
141 insects would also have provided potential hosts for these parasitoids (Askew &  
142 Shaw, 1974). The densities of both of these moth species were, however, much lower  
143 than those of the *R. fagi* on beech trees. Other than the birch and beech trees no other  
144 species of broad leafed trees were found within the woodland. The understory  
145 vegetation was dominated by grasses which do not support hosts of these parasitoids  
146 (Askew & Shaw, 1974; Rott & Godfray, 2000). Previous studies in Scottish beech  
147 woodlands have also found these same three species of parasitoids on *R. fagi* (Day &  
148 Watt, 1989).

149

150 *Host-plant variables*

151

152 For each of the 88 beech trees present within the woodland the following  
153 measurements were taken. Tree trunk diameter at breast height (DBH) and canopy  
154 diameter (mean of 2 measures per tree) were measured for each of the 88 beech trees  
155 in the woodland. The individual canopy diameter of each tree was then used to  
156 calculate the canopy area of beech habitat patches (PATCH). Such patches were  
157 represented by both individual trees and clumps of trees whose canopies overlapped  
158 to provide a continuous patch of beech canopy to dispersing *R. fagi*. As some beech  
159 trees occurred on the edge of the woodland adjoining areas of clear-cut coniferous  
160 plantation forestry, trees were categorised as being either woodland edge or interior  
161 (EDGE). During winter 2005, so that tree foliage would not interfere with satellite  
162 reception, geographical co-ordinates of each tree were obtained with a GPS (Garmin  
163 12). Using the latitude and longitude of each tree the Euclidean distance between trees  
164 was calculated. The Euclidean distance to the nearest neighbouring beech tree (DIST)  
165 was then included in models as a measure of tree isolation (Hanski *et al.*, 1994).

166

#### 167 *Insect sampling*

168

169 Sampling was carried out between 15-18/6/2005, towards the end of *R. fagi*  
170 larval development at this site (pers. obs. BAW). A branch was excised from both the  
171 North and South aspect of each of the 88 beech trees at a height of between 1.5 and  
172 4.0 m off the ground. The proportion of leaves mined by *R. fagi* was calculated based  
173 on a random sample of 100 leaves from each tree, 50 leaves taken from one of two  
174 randomly chosen branches.

175 A sub-sample of ten randomly chosen leaves, each containing a single  
176 occupied *R. Fagi* leaf-mine, were removed from both the North and South aspect of  
177 each tree (20 leaves per tree, 1760 leaves in total). In all cases mines were checked to



178 confirm that they contained larvae of *R. fagi* by holding the mines up to direct sunlight.  
179 The sub-samples from each tree (n = 10 x 2) were placed into plastic pots covered  
180 with fine netting and subsequently kept in an open-air insectary adjacent to the  
181 woodland. This maintained a similar temperature and humidity regime to that of the  
182 adjoining woodland. Every two days the leaves were checked and emerging adult *R.*  
183 *fagi* and parasitoids were removed and transferred to 70 % alcohol. Inspection of the  
184 mines continued for a 4-week period after the last emergence of either the host or  
185 parasitoids. All parasitoids were subsequently identified to species and compared to  
186 reference material at the Hope Entomological Collection, Oxford.

187         As *R. fagi* leaf-mines were collected over a relatively short period (four days)  
188 this may have led to an underestimation of parasitism rates, particularly where  
189 parasitoid species attacked late instars in their host's development. As all three  
190 parasitoids of this study were idiobionts and so associated with later instars of larval  
191 development this was a potential bias in the sampling method (Rott & Godfray, 2000;  
192 Grabenweger, 2003). However, underestimation of parasitism rates were likely to be  
193 minimal as the collection of *R. fagi* leaf-mines coincided with the latter stages of  
194 larval development towards the end of June (Bale & Luff, 1978).

195

#### 196 *Statistical analyses*

197

198         The data from the North and South branches of each tree were combined for  
199 analyses. Percentage herbivory of beech by *R. fagi* (leaf-mine abundance per 100  
200 leaves) and percentage parasitism of *R. fagi* (parasitoid count per 20 leaves) were  
201 modelled with generalised linear mixed models (GLMM) with Binomial error  
202 distribution and Logit link (SAS, 1999). The influence of four fixed effects on

203 percentage herbivory by *R. fagi* were considered: 1) the position of beech trees within  
204 the woodland interior or at the woodland edge (EDGE); 2) the diameter at breast  
205 height of individual beech tree trunks (DBH); 3) the canopy area of *R. fagi* habitat  
206 patches (isolated beech individuals or clumps of beech trees with overlapping  
207 canopies) (PATCH); 4) distance to nearest neighbouring beech tree (DIST). Also  
208 considered was the two-way interaction between EDGE\*DBH, EDGE\*DIST, and  
209 EDGE\*PATCH.

210         Similar models were constructed for the parasitism rates caused by each of the  
211 three parasitoid species. In addition to the main effects and interactions described  
212 above, percentage parasitism of *R. fagi* by each parasitoid species was also correlated  
213 to the main effect of host insect density (MINES), count of other potentially  
214 competing parasitoid species per tree (either *P. longulus*, *C. braconius* or *C.*  
215 *nephereus*) and the interaction of MINE density with tree position (EDGE\*MINE).  
216 Host insect density of the *R. fagi* mines provided a measure of the habitat quality of  
217 the beech trees for the parasitoids. Note that the abundance for each parasitoid  
218 species was not included as a covariate in the analysis of its own parasitism rates. The  
219 interactions of DBH, DIST, PATCH and MINE with EDGE were intended to account  
220 for variation in environmental conditions associated with the edges of woodlands, e.g.  
221 greater daily variation in temperature (Murica, 1995; Tschamtkke & Brandl, 2004). In  
222 all analyses percentage herbivory or parasitism rates were treated as proportions.

223         To consider overall changes in the diversity of the parasitoid assemblage  
224 Shannon-Wiener diversity (Krebs, 1999) of the parasitoids was correlated to the same  
225 fixed effects used in the models above for the assessment of parasitism rates by the  
226 individual parasitoid species. Note that the counts of individual parasitoid species  
227 were not included in this model as explanatory variables as they were used to derive

228 the Shannon-Wiener diversity measure. This final model used a normal distribution  
229 with an identity link function.

230 In all GLMMs the random categorical variables fitted were ‘patch’ (n = 43)  
231 and ‘tree’ (n = 88), which accounted for overdispersion at the observation level.  
232 Solution of fixed effects (EDGE, PATCH, DBH, MINES, DIST, *P. longulus*, *C.*  
233 *braconius*, *C. nephereus*) and interactions with EDGE were estimated by residual  
234 maximum likelihood (REML). Denominator degrees of freedom were estimated using  
235 Satterthwaite’s approximation (Littell *et al.*, 1996). Main effect and interaction terms  
236 were added step-wise to models with elimination of the least significant term until the  
237 most parsimonious model was found. Where an interaction term was found to be  
238 significant its component main effects were not deleted, even if individually non-  
239 significant. F-ratios adjusted for other significant model terms (SAS Type 3 tests) and  
240 are reported for all main effects and significant interactions. Partial residual plots were  
241 constructed to show the evidence for the effect of particular covariates, after  
242 controlling for random and other significant fixed effects in the model, and include a  
243 fitted line to show the slopes of the relationships.

244

## 245 **Results**

246

247 A total of 88 beech trees were sampled within the overall *Betula* dominated  
248 woodland, of which 15 trees were found to be present on the woodland edge in one of  
249 three patches. Sixteen patches, containing two or more beech trees, were present  
250 within the *Betula* dominated woodland, with the largest patch comprised of nine trees  
251 covering an area of 1265.6 m<sup>2</sup>. From the 1,760 leaf-mines returned to the insectary  
252 10.0 % yielded *R. fagi* adults (n = 176). Assuming the parasitoid larvae were solitary  
253 (Askew & Shaw, 1974), 31.0 % of mines were parasitized (551 parasitoids) by one of

254 four species of hymenopteran parasitoid. This left 59.0 % of the mortality of the  
255 insectary reared *R. fagi* unexplained. Of the four parasitoids, three species represented  
256 95 % of the total parasitoid abundance: *P. longulus* (n = 225 individuals); *C.*  
257 *nephereus* (n = 182); and *C. braconius* (n = 129). The remaining parasitoid (*Pnigalio*  
258 *soemius* (Walker) (Eulophidae)) was represented by only 15 individuals, and was  
259 excluded from subsequent analyses, with the exception of the calculations of  
260 Shannon-Wiener diversity.

261

#### 262 *Host-plant location, quality and patch size*

263

264 Percentage herbivory by *R. fagi* on beech trees was greater at the woodland  
265 edge compared to trees in the woodland interior (Fig. 2, Table 1). The proportion of  
266 leaves with *R. fagi* mines was not correlated with any other measured parameter  
267 (DBH, PATCH, and DIST, see Table 1). The location of the beech tree at either the  
268 woodland edge or interior influenced the parasitism rate of *R. fagi* differently  
269 according to parasitoid identity (Fig. 3, Table 1). *P. longulus* parasitism was greater at  
270 the woodland edge, while *C. braconius* parasitism rate was higher in the woodland  
271 interior (Fig.3, Table 1). *C. nephereus* parasitism rate was also higher in the interior,  
272 but this was not statistically significant after controlling for other effects (Fig.3, Table  
273 1).

274 Individual beech tree trunk diameter (DBH) was positively correlated (GLMM  
275 slope estimate: 0.8750) with proportional parasitism of *R. fagi* by *C. nephereus* (Table  
276 1). An interaction between DBH and tree location for *C. braconius* parasitism rate  
277 showed a positive correlation with DBH for trees at the woodland edge and negative  
278 for trees within the interior (Fig. 4). The parasitism rate by *P. longulus* was  
279 uninfluenced by tree trunk diameter (Table 1).

280           The canopy area (PATCH) of the beech tree patches – the host-insect resource  
281 – was a predictor of proportional parasitism for two of the three parasitoid species.  
282 *Pnigalio longulus* was positively (Table 1, Fig. 5a) and *C. nephereus* negatively  
283 correlated (Table 1, Fig. 5b) to patch canopy area, while *C. braconius* parasitism rate  
284 was not affected by canopy area (Table 1). While the area of patches was an  
285 important determinant of parasitism rates, tree isolation, as defined by the Euclidean  
286 distance (DIST) to the nearest neighbouring beech tree, had no influence on the  
287 parasitism rate of any of the parasitoid species (Table 1).

288

#### 289 *Host-parasitoid interactions*

290

291           Proportional parasitism by *C. braconius* was positively correlated with host-  
292 insect mine density (MINE) (Table 1, Fig. 6a), while *C. nephereus* parasitism rate was  
293 density-independent (Table 1). Furthermore, *P. longulus* parasitism showed an  
294 interaction between host insect mine density and beech tree location (MINE\*EDGE:  $F_{(1, 81)}=11.50$ ,  $p = 0.001$ , Fig. 6b). For trees in the woodland interior the slope of the  
295 response to host- insect mine density did not differ from zero ( $b = -0.01$   $t = -0.15$   $p =$   
296  $0.87$ ). However, for trees located at the woodland edge there was a negative  
297 correlation between *P. longulus* parasitism and host mine density ( $b = -1.06$ ,  $t = -3.09$   
298  $p < 0.05$ ). Proportional parasitism by each of the three parasitoid species was not  
299 correlated with the density of the other parasitoid species in the assemblage (Table 1).  
300 Therefore, there was no evidence of direct interactions between parasitoid species  
301 using the same host resource influencing parasitism rates in the three parasitoid  
302 species considered here.

304

305 *Parasitoid diversity*

306

307 Shannon-Wiener diversity of the parasitoid assemblage was negatively  
308 correlated with the canopy area of the beech tree patches ( $F_{1,16} = 7.22$ ,  $p = 0.02$ ; Fig.  
309 5c). Parasitoid diversity was not affected by EDGE, DBH, DIST, MINES or any of  
310 the interaction terms with EDGE.

311

## 312 **Discussion**

313

314 The density of leaf-mines on the host trees was unexpectedly high, particularly  
315 at the woodland edge, where *c.* 78 % of leaves was found to be mined. Previous  
316 studies have shown that 75-85% of leaves present in the lower stratum of the canopy  
317 (the area sampled in this study) have some form of phytophagous invertebrate  
318 damage, although this comprised damage from all species of leaf-chewing and leaf-  
319 mining insects (Phillipson & Thompson, 1980). It is possible that the high abundances  
320 of *R. fagi* in these Scottish woodlands may be due to the reduced impact of top down  
321 control resulting from a comparatively impoverished fauna of parasitoids in this  
322 Northern part of the UK (Askew & Shaw, 1974). It should be noted, however, that  
323 while this parasitoid fauna may be species poor it was comparable in size to that  
324 found in previous work in other Scottish woodlands (Day & Watt, 1989). While there  
325 is some potential that competitive release from parasitoids may explain the high  
326 densities of *R. fagi* in this woodland (Kareiva, 1982), rates of parasitism are known to  
327 be highly variable between years for this species (Day & Watt, 1989).

328

329 High levels of mortality of the *R. fagi* larvae were not explained by parasitism,  
330 and indeed 59.0 % of the mortality remained unexplained. Previous work has,

331 however, shown that *R. fagi* is highly susceptible to mortality resulting from  
332 phenological asynchrony with its host plant beech (Nielsen, 1968). Specifically, if  
333 egg laying does not occur soon after bud burst this limits subsequent development of  
334 the leaf-mines and so increases mortality rates. In addition to this factor, low  
335 temperatures in May have also been shown to result in high levels of mortality for *R.*  
336 *fagi*, although this effect has been more clearly demonstrated in Ireland than in  
337 Scotland (Day & Watt, 1989).

338

### 339 *Isolation and patch size*

340

341 The isolation of beech trees within the woodland was not found to have any  
342 effect on *R. fagi* density, its subsequent parasitism or the overall diversity of the  
343 parasitoids. This finding contradicts first prediction that small and isolated patches of  
344 beech trees would provide refuges from parasitism rates for *R. fagi*. Small patches of  
345 beech trees were, however, found to provide refuges from high parasitism rates from  
346 the parasitoid *P. longulus*. This finding concurs with other studies that have  
347 demonstrated that a reduction in habitat patch area will reduce rates of parasitism for a  
348 number of parasitoid species (Roland & Taylor, 1997; Doak, 2000; Cronin, 2004).  
349 Higher rates of parasitism, however, were also found within small patches for the  
350 parasitoid *C. nephreus*, while overall parasitoid diversity was found to decrease as  
351 patch size increased. This effect may have been caused by a number of different  
352 processes. For example, intrinsic differences in the ability of parasitoids to colonise,  
353 disperse and locate new hosts may have driven these responses to patch size (Kareiva,  
354 1987; Hanski, 1999). Alternatively, competition or interference from *P. longulus* may  
355 have resulted in searching behaviour by *C. nephreus* that gave the appearance of a  
356 species targeted smaller patches. There was, however, no direct evidence that *P.*

357 *longulus* had a negative effect on *C. nephereus*, although this was based on rates of  
358 parasitism only. It was possible that interspecific competition between *C. nephereus*  
359 and *P. longulus* occurred during the process of searching for the *R. fagi* host (Sato,  
360 1995; Wieber *et al.*, 1995).

361 Other studies have shown that several smaller habitat patches may support  
362 more species than larger patches of an equivalent combined size, a response that is  
363 attributed in part to the quality of the surrounding habitat matrix within which these  
364 patches are situated (Tscharntke *et al.*, 2002). All the parasitoids were polyphagous  
365 and so could have utilised leaf-mining insects on other tree species in the woodland  
366 (Askew & Shaw, 1974; Rott & Godfray, 2000). It may be the case that the more  
367 widely dispersed smaller patches occurred in areas of woodland that provided higher  
368 quality resources in terms of alternative host insects. Indeed, the fact that all the  
369 parasitoids reared from the *R. fagi* host were polyphagous and so could utilise  
370 alternative hosts on other tree species makes any response to patch size unexpected.  
371 In particular, moth larvae of the leaf-mining genus *Phyllonorycter* spp. (Lepidoptera,  
372 Gracillariidae) were present throughout the woodland on birch trees. *Phyllonorycter*  
373 spp. represented potential alternative hosts for both *C. nephereus* and the braconid *C.*  
374 *braconius* (Rott & Godfray, 2000). However, while the *Phyllonorycter* spp. did  
375 represent potential alternative hosts for the parasitoids, the density of *R. fagi* leaf-  
376 mines on the host trees (beech) remained several orders of magnitude greater than  
377 those of *Phyllonorycter* spp. on birch trees (AJV, BAW pers.obs). Therefore, it may  
378 be the case that *R. fagi* leaf-mines on their host (beech) represented a locally super-  
379 abundant resource for these parasitoids, rather than the only host resource that they  
380 could use within the woodland.

381

382 *Environmental gradients and patch quality*



383

384 High quality habitats for the parasitoids were considered to be trees with high  
385 densities of the host insect *R. fagi*. As the second prediction suggested this did  
386 influence rates of parasitism, although the directions of these responses were not  
387 consistent between parasitoid species. Density-dependent parasitism of *R. fagi* was  
388 found for *C. braconius*, while parasitism by *C. nephereus* was density independent,  
389 and that of *P. longulus* was dependent on the location of the beech trees at either the  
390 woodland edge or interior. The aggregation of parasitoids to patches of high host  
391 density has been shown to contribute to temporal stability in host–parasitoid  
392 interactions (e.g. Hassell & May, 1973). Such density dependent effects in parasitism  
393 rates have been suggested to be caused by species-specific searching behaviour  
394 resulting in increased attraction to, and residency time in, areas of high host density  
395 (Hassell, 1978; Stiling, 1987; Doak, 2000). Patterns of inverse density-dependence  
396 may reflect longer handling times during host location and oviposition (Waage, 1983;  
397 Visser *et al.*, 1999), or the occurrence of interference reducing parasitoid efficiency in  
398 exploiting high density patches (Stiling, 1987; Taylor, 1993). Overall in this study,  
399 the different parasitoid responses to host density broadly reflect the suggestion by  
400 Stirling (1987) that direct and inverse dependence occur in 25 % and 23 % of host-  
401 parasitoid interactions respectively.

402 The importance of underlying environmental gradients in structuring the  
403 parasitoid assemblages were apparent in the form of interactions between parasitism  
404 rates and the location of beech trees at the woodland edge or interior. For example  
405 parasitism by *P. longulus* was density independent on host trees in the woodland  
406 interior, whereas at the woodland edge *R. fagi* experienced inverse density-dependent  
407 parasitism. Overall rates of parasitism also differed for *P. longulus* and *C. braconius*  
408 between woodland edge and interior. In addition, *C. braconius* parasitism rates were

409 correlated with tree trunk diameter, a factor that provided an indirect index of tree  
410 age, health and size (Thomas, 2000). This response, however, was influenced by the  
411 location of beech trees at the woodland edge or interior. These responses concurred  
412 with the second prediction that underlying environmental gradients present within the  
413 woodland would alter the interaction between secondary and tertiary trophic levels.  
414 In this case the environmental gradients were the result of edge effects at the interface  
415 between the woodland and the clear cut areas of plantation forestry. Such an interface  
416 would result in local variation in environmental conditions, such as ambient  
417 temperature, timing of bud burst (and so host availability) and leaf nutritional quality  
418 (Murica, 1995).

419

420         The findings of this study must be considered within the context of some  
421 methodological issues. As emergence, rather than dissection, was used to define  
422 parasitism rates, the direct assessment of multi- and superparasitism, as well as  
423 whether species were primary or hyperparasitoids was not possible. However, as the  
424 biology of all three parasitoids used in this study was known (e.g. Askew & Shaw,  
425 1974; Rott & Godfray, 2000) the ambiguity introduced by this limitation of the  
426 methodology is thought to be of limited importance. It was also possible that as no  
427 dissections of the larvae in leaf-mines were used over wintering parasitoids may have  
428 been missed in this study. Species of *Pnigalio*, have been recorded as over wintering  
429 in the mines of their hosts (Raske, 1978). However, given that the mines of the *R. fagi*  
430 occur early in the season a long period is available for these multivoltine parasitoids  
431 to find alternative hosts (Pschorn-Walcher & Heitland, 2000). Given this length of  
432 time it was thought unlikely that many of the parasitoids would have over wintered  
433 within *R. fagi* leaf-mines.

434

435 *Conclusions*

436

437           Deciduous woodlands play an important role in supporting invertebrate  
438 biodiversity in the agricultural landscape of lowland Scotland (Woodcock *et al.*,  
439 2003a; Woodcock *et al.*, 2003b; Vanbergen *et al.*, 2006). The responses of the  
440 parasitoid species associated with *R. fagi* to effects of host insect density, habitat  
441 patch area and the spatial location of the host-plant has demonstrated that the structure  
442 of these woodlands will potentially play a role in determining their contribution to  
443 landscape scale biodiversity effects. Areas of high quality resources within these  
444 woodlands, here represented by patches of beech trees with their super-abundant leaf-  
445 miner *R. fagi*, will influence the spatial distribution of parasitism and parasitoid  
446 diversity, even for polyphagous species. In addition we have shown that  
447 environmental gradients through these woodlands will also modify the pattern of  
448 assemblage structure for these parasitoids. Habitat heterogeneity within woodlands is  
449 therefore likely to promote niche separation between the parasitoid species that show  
450 different functional responses to local patterns of patch quality and size. This  
451 variation in parasitism rates and parasitoid diversity indicates the complex and  
452 variable nature of responses by parasitoids to spatial habitat structure and host density  
453 in natural environments.

454

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456

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461

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570

571



**Table 1.** The effect of beech tree position (EDGE), host insect (*R. fagi*) density (MINES), beech trunk diameter (DBH), beech patch area (PATCH), Euclidean distance to nearest neighbouring beech tree (DIST) on percentage *R. fagi* herbivory and proportional parasitism of *R. fagi* by three parasitoid species. Also tested is the influence on parasitism rates of the count of other parasitoid competitors in the assemblage (*C. braconius* (n) *P. longulus* (n) *C. nephereus* (n)). Summary results of F-tests from GLMM with binomial error distribution and Logit link where: ndf = numerator degrees of freedom; ddf = denominator degrees of freedom; F = value of F-statistic; P = probability value. Model simplification was by step-wise removal of the least significant term, with interactions dropped before main effects; NS = Non-significant at P<0.05; - = where a model term was not included in a model, see methods section.

	<i>R. fagi</i> (% herbivory)		<i>C. braconius</i> (% parasitism)		<i>P. longulus</i> (% parasitism)		<i>C. nephereus</i> (% parasitism)	
	<b>F</b> (ndf, ddf)	<b>P</b>	<b>F</b> (ndf, ddf)	<b>P</b>	<b>F</b> (ndf, ddf)	<b>P</b>	<b>F</b> (ndf, ddf)	<b>P</b>
<b>EDGE</b>	<b>14.04</b> (1, 77)	<b>&lt;0.001</b>	<b>5.32</b> (1, 82)	<b>0.02</b>	<b>10.69</b> (1, 13)	<b>0.002</b>	NS	>0.05
<b>MINE</b>	-	-	<b>7.29</b> (1, 82)	<b>&lt;0.001</b>	<b>10.79</b> (1, 81)	<b>0.001</b>	NS	>0.05
<b><i>C. braconius</i> (n)</b>	-	-	-	-	NS	>0.05	NS	>0.05
<b><i>P. longulus</i> (n)</b>	-	-	NS	>0.05	-	-	NS	>0.05
<b><i>C. nephereus</i> (n)</b>	-	-	NS	>0.05	NS	0.77	-	-
<b>DBH</b>	NS	>0.05	NS	>0.05	NS	0.07	<b>5.47</b> (1, 48)	<b>0.02</b>
<b>PATCH</b>	NS	>0.05	NS	>0.05	<b>27.72</b> (1, 11)	<b>&lt;0.001</b>	<b>25.56</b> (1, 36)	<b>&lt;.001</b>
<b>DIST</b>	NS	>0.05	NS	>0.05	NS	>0.05	NS	>0.05
<b>DBH*EDGE</b>	NS	>0.05	<b>4.10</b> (1, 82)	<b>0.05</b>	NS	>0.05	NS	>0.05
<b>PATCH*EDGE</b>	NS	>0.05	NS	>0.05	NS	>0.05	NS	>0.05
<b>DIST*EDGE</b>	NS	>0.05	NS	>0.05	NS	>0.05	NS	>0.05
<b>MINE*EDGE</b>	-	-	NS	>0.05	NS	>0.05	NS	>0.05



## Figure captions

**Fig. 1.** ArcGIS map of the study site, showing the dispersion and location of the individual beech trees (closed symbols) in the birch-dominated woodland (shaded grey polygon).

**Fig. 2** Mean ( $\pm$  SD) proportional herbivory by *R. fagi* on beech trees according to the location of the trees in the woodland edge or interior.

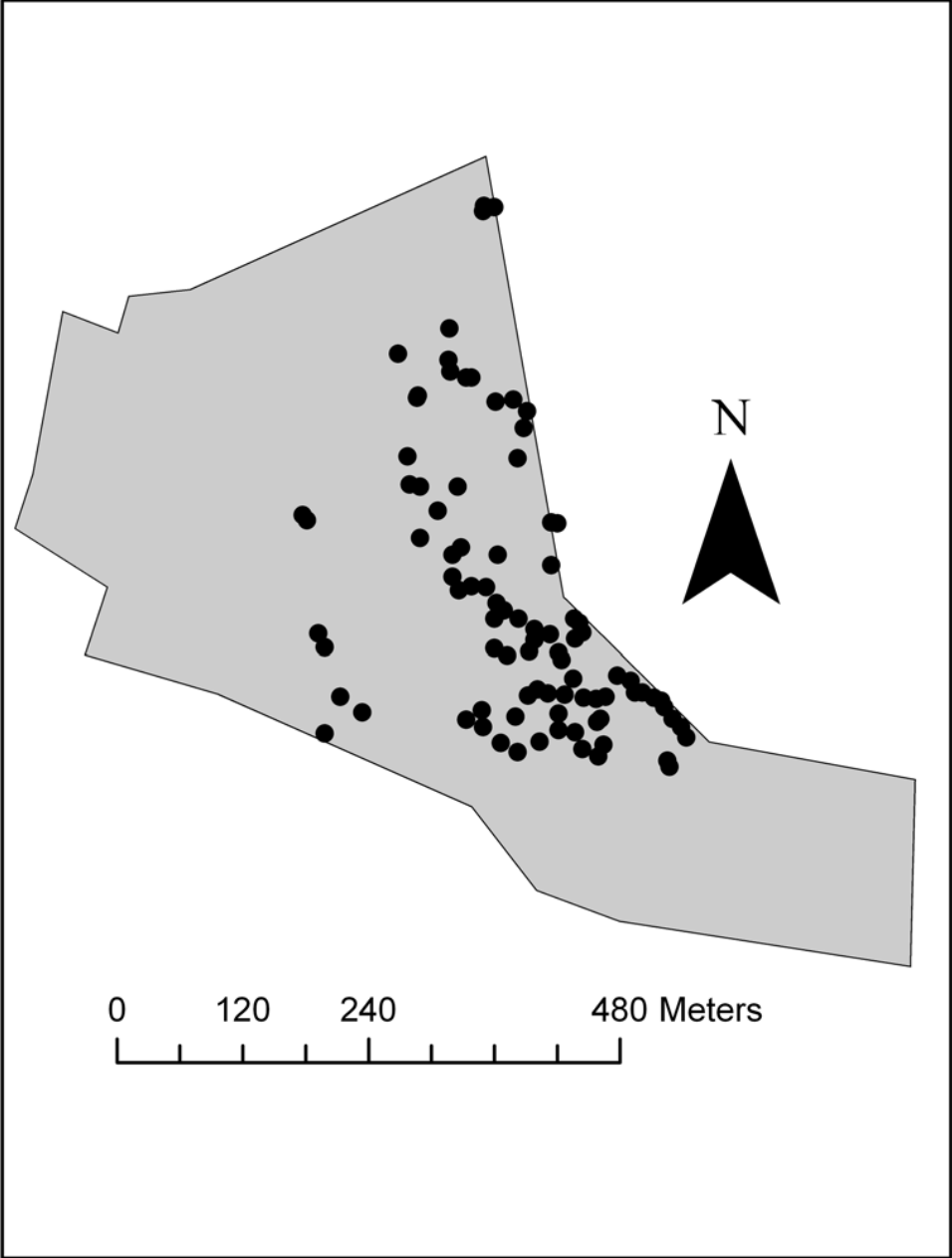
**Fig. 3** Mean ( $\pm$  SD) proportional parasitism of the three dominant parasitoids of the beech leaf-miner *R. fagi* according to beech tree position in the woodland interior and edge.

**Fig. 4** Partial residual percentage parasitism of *R. fagi* on a linear predictor scale by *C. braconius* in response to beech tree trunk diameter at either the woodland edge or interior. Fitted line from GLMM with parasitism modelled as the proportion of parasitoids per subsample of twenty leaves using a binomial error distribution and Logit link function.

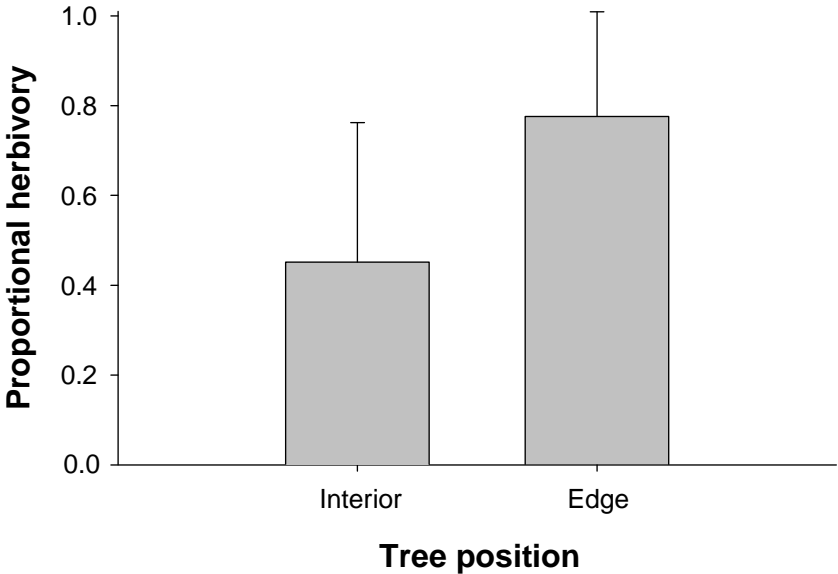
**Fig. 5** Partial residual percentage parasitism of *R. fagi* on a linear predictor scale by (a) *P. longulus*, (b) *C. nephereus* and (c) overall parasitoid Shannon-Wiener diversity in response to beech patch canopy area (m<sup>2</sup>).

**Fig. 6** Partial residual percentage parasitism of *R. fagi* on a linear predictor scale in response to host mine density ( $\text{Ln } R. fagi + 1$ ) for (a) *C. braconius* and (b) *P. longulus*. The graph for *P. longulus* also indicates the interaction between host mine density and the position of beech trees on the woodland edge or interior.

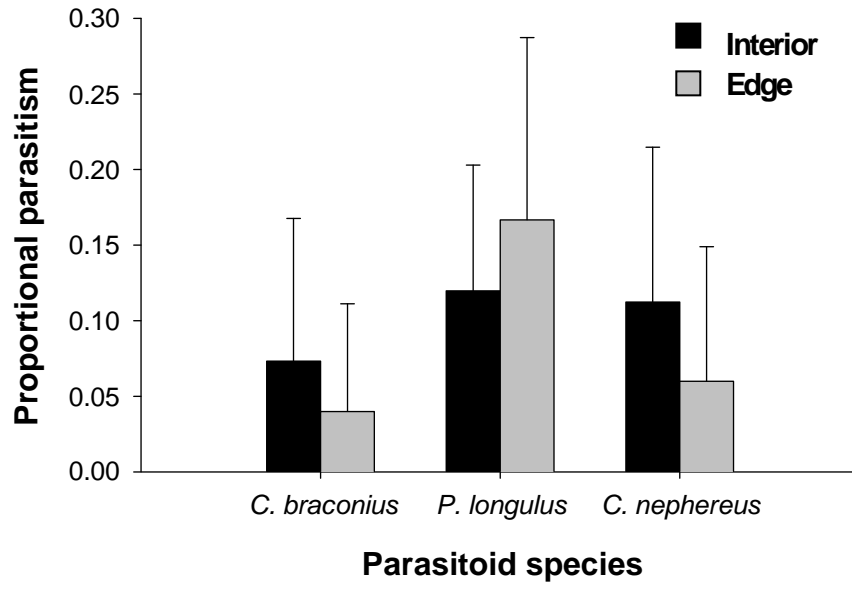
**Fig. 1**



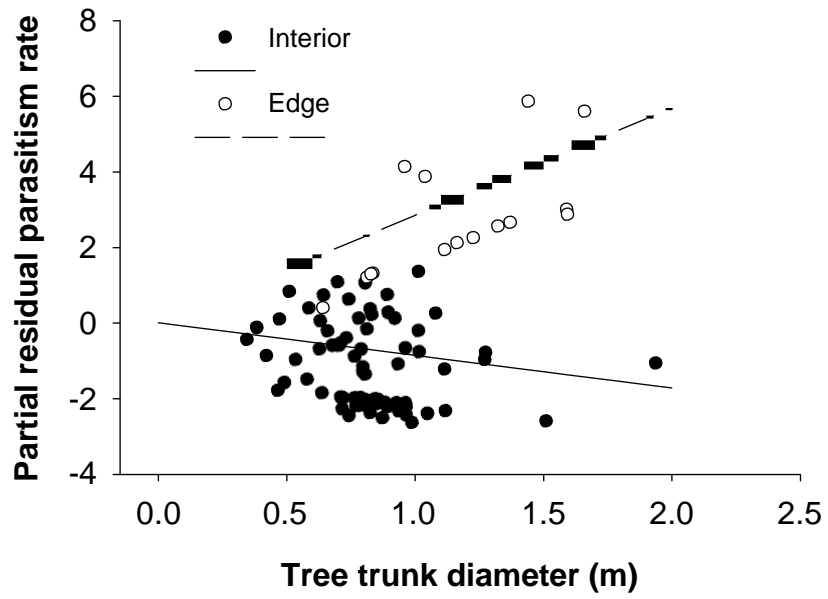
**Fig.2**



**Fig 3**



**Fig 4**



**Fig. 5**

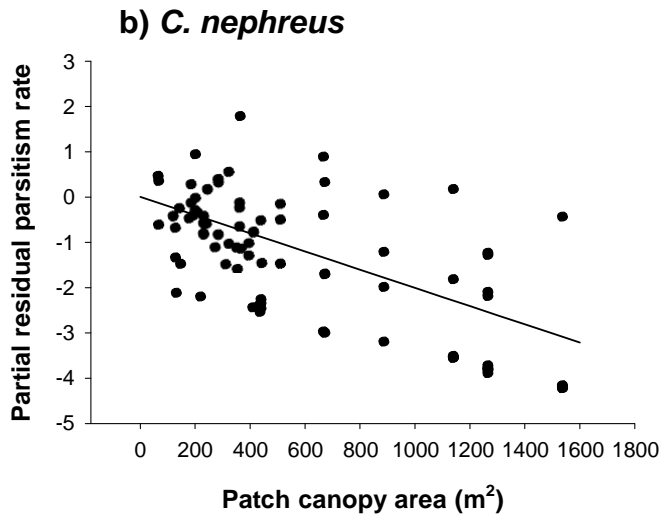
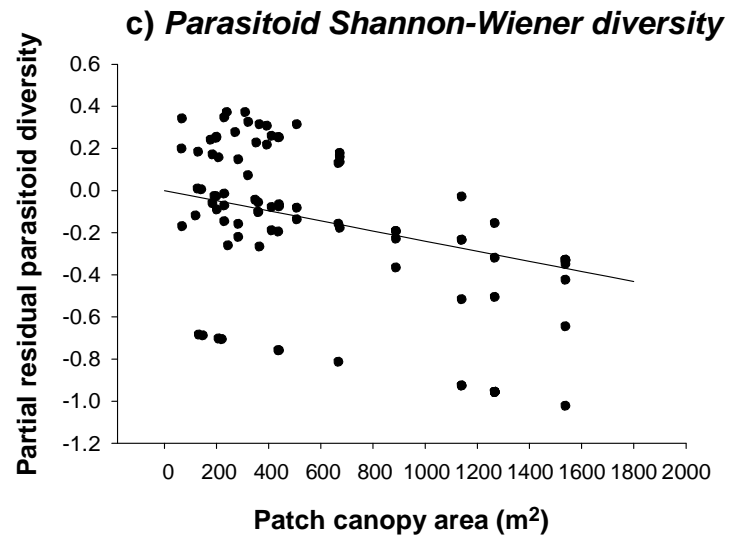
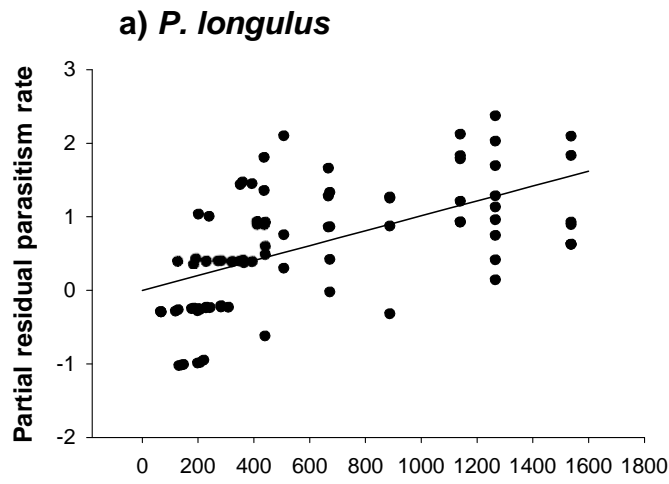




Fig. 6

