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

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Abstract

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

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

Introduction

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

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

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

Methods

Study site

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

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

Tri-trophic system

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

The three dominant species of hymenopteran parasitoids reared from *R. fagi* in this study were all polyphagous species recorded as utilising leaf-mining insects on a variety of deciduous trees, including *Salix* spp. (Salicaceae), *Quercus* spp (Fagaceae), *Fagus* spp. (Fagaceae) and *Betula* spps (Betulaceae) (Askew & Shaw, 1974; Rott & Godfray, 2000). *Pnigalio longulus* (Zett.) (Eulophidae) and *Chrysocharis nephereus* (Walker) (Eulophidae) are common parasitoids of many species of leaf-mining insects including moths (Lepidoptera: Eriocraniidae, Gracillariidae and Nepticulidae), sawflies (Hymenoptera: Tenthredinidae) and weevils (Coleoptera: Curculionidae) (Askew & Shaw, 1974). Both species are likely to be multivoltine (Raske, 1978; Pschorn-Walcher & Heitland, 2000). *Colastes braconius* Haliday (Braconidae) is a multivoltine species (Wharton, 1993) known to parasitize a wide range of leaf-mining hosts, including both moths and weevils (Day & Watt, 1989; Rott & Godfray, 2000). Both *P. longulus* and *C. braconius* have ectoparasitic larval stages, while *C. nephereus* is an endoparasite (Rott & Godfray, 2000). All three species are idiobionts with clutch sizes of one (Rott & Godfray, 2000). Records for all three of these species suggest that they are normally associated with woodland habitats, although may be found on trees in more open situations where their hosts are present (Askew & Shaw, 1974; Day & Watt, 1989; Casas, 1990; Rott & Godfray, 2000; Jordano, 2003). In addition to the *R. fagi* hosts considered in this paper, leaf-miners of the *Eriocrania* spp. (Lepidoptera: Eriocraniidae) and *Phyllonorycter* spp. (Lepidoptera: Gracillariidae) were also found on birch trees within the woodland. This leaf-mining insects would also have provided potential hosts for these parasitoids (Askew & Shaw, 1974). The densities of both of these moth species were, however, much lower than those of the *R. fagi* on beech trees. Other than the birch and beech trees no other species of broad leafed trees were found within the woodland. The understory vegetation was dominated by grasses which do not support hosts of these parasitoids (Askew & Shaw, 1974; Rott & Godfray, 2000). Previous studies in Scottish beech woodlands have also found these same three species of parasitoids on *R. fagi* (Day & Watt, 1989).

Host-plant variables

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

Insect sampling

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

A sub-sample of ten randomly chosen leaves, each containing a single occupied *R. Fagi* leaf-mine, were removed from both the North and South aspect of each tree (20 leaves per tree, 1760 leaves in total). In all cases mines were checked to confirm that they contained larvae of *R. fag* by holding the mines up to direct sunlight. The sub-samples from each tree (n = 10 x 2) were placed into plastic pots covered with fine netting and subsequently kept in an open-air insectary adjacent to the woodland. This maintained a similar temperature and humidity regime to that of the adjoining woodland. Every two days the leaves were checked and emerging adult *R. fagi* and parasitoids were removed and transferred to 70 % alcohol. Inspection of the mines continued for a 4-week period after the last emergence of either the host or parasitoids. All parasitoids were subsequently identified to species and compared to reference material at the Hope Entomological Collection, Oxford.

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

Statistical analyses

The data from the North and South branches of each tree were combined for analyses. Percentage herbivory of beech by *R. fagi* (leaf-mine abundance per 100 leaves) and percentage parasitism of *R. fagi* (parasitoid count per 20 leaves) were modelled with generalised linear mixed models (GLMM) with Binomial error distribution and Logit link (SAS, 1999). The influence of four fixed effects on percentage herbivory by *R. fagi* were considered: 1) the position of beech trees within the woodland interior or at the woodland edge (EDGE); 2) the diameter at breast height of individual beech tree trunks (DBH); 3) the canopy area of *R. fagi* habitat patches (isolated beech individuals or clumps of beech trees with overlapping canopies) (PATCH); 4) distance to nearest neighbouring beech tree (DIST). Also considered was the two–way interaction between EDGE*DBH, EDGE*DIST, and EDGE*PATCH.

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

To consider overall changes in the diversity of the parasitoid assemblage Shannon-Wiener diversity (Krebs, 1999) of the parasitoids was correlated to the same fixed effects used in the models above for the assessment of parasitism rates by the individual parasitoid species. Note that the counts of individual parasitoid species were not included in this model as explanatory variables as they were used to derive the Shannon-Wiener diversity measure. This final model used a normal distribution with an identity link function.

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

Results

A total of 88 beech trees were sampled within the overall *Betula* dominated woodland, of which 15 trees were found to be present on the woodland edge in one of three patches. Sixteen patches, containing two or more beech trees, were present within the *Betula* dominated woodland, with the largest patch comprised of nine trees covering an area of 1265.6 m^2. From the 1,760 leaf-mines returned to the insectary 10.0 % yielded *R. fagi* adults (n = 176). Assuming the parasitoid larvae were solitary (Askew & Shaw, 1974), 31.0 % of mines were parasitized (551 parasitoids) by one of four species of hymenopteran parasitoid. This left 59.0 % of the mortality of the insectary reared *R. fagi* unexplained. Of the four parasitoids, three species represented 95 % of the total parasitoid abundance: *P. longulus* (n = 225 individuals); *C. nephereus* (n = 182); and *C. braconius* (n = 129). The remaining parasitoid (*Pnigalio soemius* (Walker) (Eulophidae)) was represented by only 15 individuals, and was excluded from subsequent analyses, with the exception of the calculations of Shannon-Wiener diversity.

Host-plant location, quality and patch size

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

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

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

Host-parasitoid interactions

Proportional parasitism by *C. braconius* was positively correlated with host-insect mine density (MINE) (Table 1, Fig. 6a), while *C. nephereus* parasitism rate was density-independent (Table 1). Furthermore, *P. longulus* parasitism showed an 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 response to host- insect mine density did not differ from zero ($b = -0.01$ $t = -0.15$ $p = 0.87$). However, for trees located at the woodland edge there was a negative correlation between *P. longulus* parasitism and host mine density ($b = -1.06$, $t = -3.09$ $p < 0.05$). Proportional parasitism by each of the three parasitoid species was not correlated with the density of the other parasitoid species in the assemblage (Table 1). Therefore, there was no evidence of direct interactions between parasitoid species using the same host resource influencing parasitism rates in the three parasitoid species considered here.

Parasitoid diversity

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

Discussion

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

High levels of mortality of the *R. fagi* larvae were not explained by parasitism, and indeed 59.0 % of the mortality remained unexplained. Previous work has, however, shown that *R. fagi* is highly susceptible to mortality resulting from phenological asynchrony with its host plant beech (Nielsen, 1968). Specifically, if egg laying does not occur soon after bud burst this limits subsequent development of the leaf-mines and so increases mortality rates. In addition to this factor, low temperatures in May have also been shown to result in high levels of mortality for *R. fagi*, although this effect has been more clearly demonstrated in Ireland than in Scotland (Day & Watt, 1989).

Isolation and patch size

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

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

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

Environmental gradients and patch quality

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

The importance of underlying environmental gradients in structuring the parasitoid assemblages were apparent in the form of interactions between parasitism rates and the location of beech trees at the woodland edge or interior. For example parasitism by *P. longulus* was density independent on host trees in the woodland interior, whereas at the woodland edge *R. fagi* experienced inverse density-dependent parasitism. Overall rates of parasitism also differed for *P. longulus* and *C. braconius* between woodland edge and interior. In addition, *C. braconius* parasitism rates were correlated with tree trunk diameter, a factor that provided an indirect index of tree age, health and size (Thomas, 2000). This response, however, was influenced by the location of beech trees at the woodland edge or interior. These responses concurred with the second prediction that underlying environmental gradients present within the woodland would alter the interaction between secondary and tertiary trophic levels. In this case the environmental gradients were the result of edge effects at the interface between the woodland and the clear cut areas of plantation forestry. Such an interface would result in local variation in environmental conditions, such as ambient temperature, timing of bud burst (and so host availability) and leaf nutritional quality (Murica, 1995).

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

Conclusions

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

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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.

	R. fagi (% herbivory)		***C. braconius*** (% parasitism)		***P. longulus*** (% parasitism)		***C. nephereus*** (% parasitism)	
	F $_{(ndf, ddf)}$	**P**	**F** $_{(ndf, ddf)}$	**P**	**F** $_{(ndf, ddf)}$	**P**	**F** $_{(ndf, ddf)}$	**P**
EDGE	**14.04** $_{(1, 77)}$	**<0.001**	**5.32** $_{(1, 82)}$	**0.02**	**10.69** $_{(1, 13)}$	**0.002**	NS	>0.05
MINE	**-**	**-**	**7.29** $_{(1, 82)}$	**<0.001**	**10.79** $_{(1, 81)}$	**0.001**	NS	>0.05
***C. braconius* (n)**	-	-	-	-	NS	>0.05	NS	>0.05
***P. longulus* (n)**	-	-	NS	>0.05	**-**	**-**	NS	>0.05
***C. nephereus* (n)**	-	-	NS	>0.05	NS	0.77	**-**	**-**
DBH	NS	>0.05	NS	>0.05	NS	0.07	**5.47** $_{(1, 48)}$	**0.02**
PATCH	NS	>0.05	NS	>0.05	**27.72** $_{(1, 11)}$	**<0.001**	**25.56** $_{(1, 36)}$	**<.001**
DIST	NS	>0.05	NS	>0.05	NS	>0.05	NS	>0.05
DBH*EDGE	NS	>0.05	**4.10** $_{(1, 82)}$	**0.05**	NS	>0.05	NS	>0.05
PATCH*EDGE	NS	>0.05	NS	>0.05	NS	>0.05	NS	>0.05
DIST*EDGE	NS	>0.05	NS	>0.05	NS	>0.05	NS	>0.05
MINE*EDGE	-		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 (± 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 (± 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 sub-sample 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^2).

Fig. 6 Partial residual percentage parasitism of *R. fagi* on a linear predictor scale in response to host mine density (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

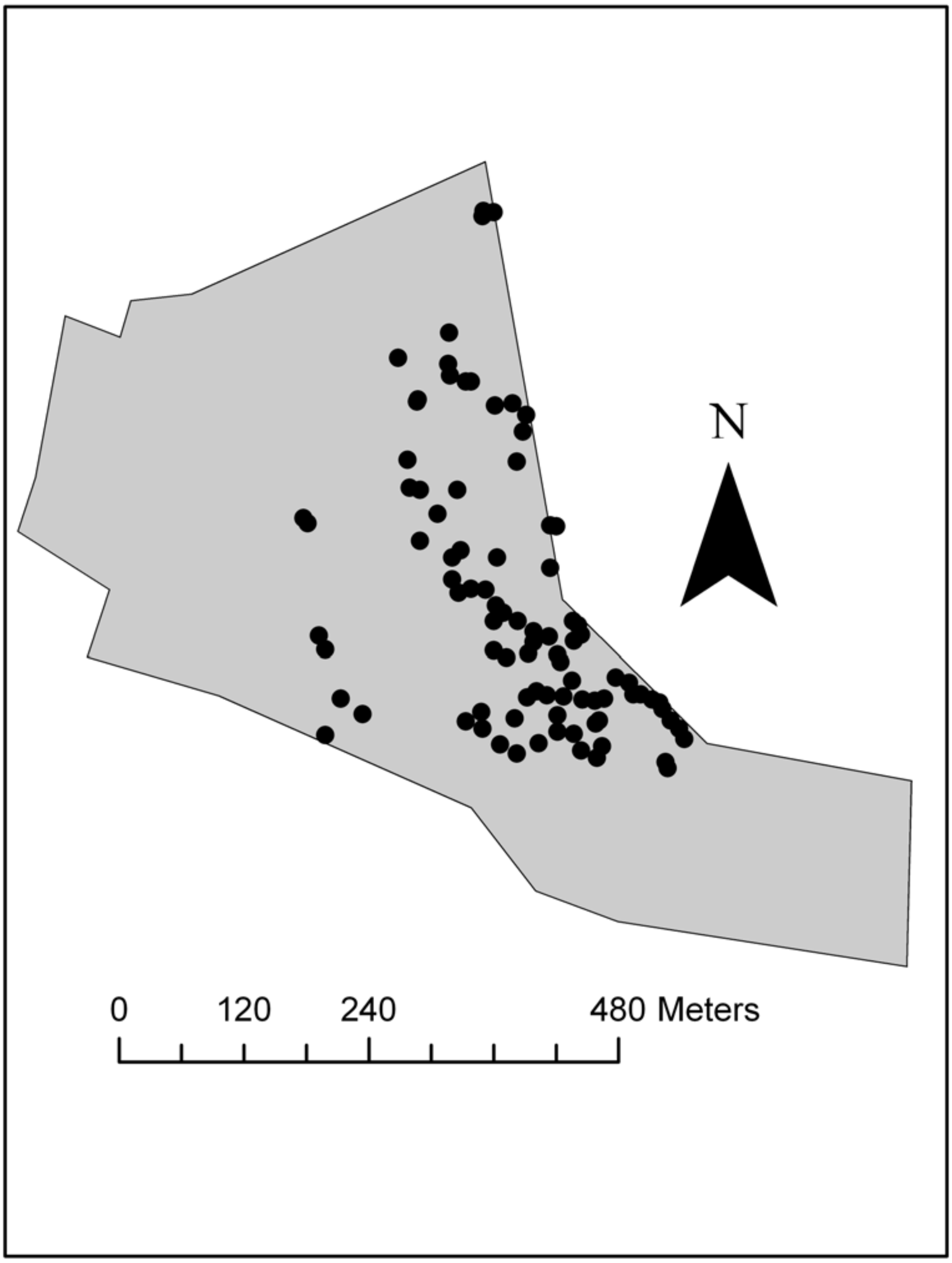


Fig.2

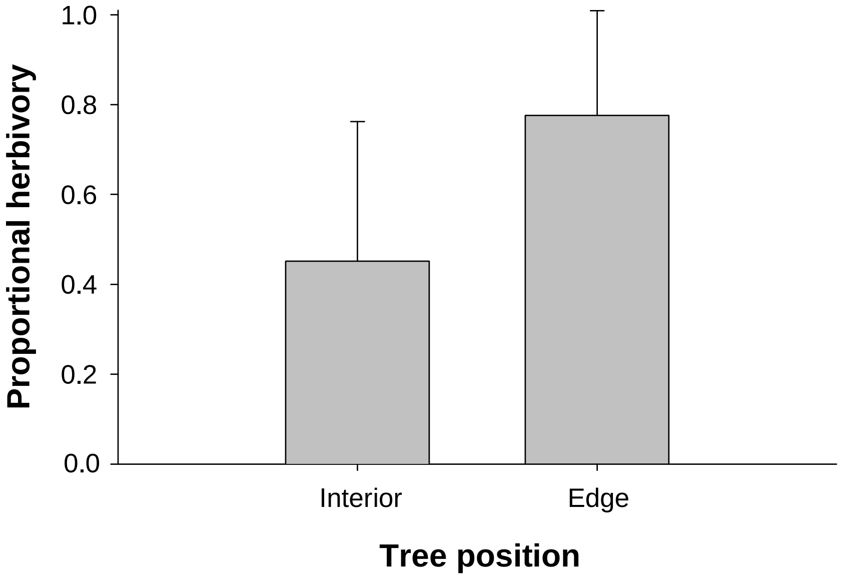

Proportional herbivory
1.0
0.8
0.6
0.4
0.2
0.0
Interior
Edge
Tree position

Fig 3

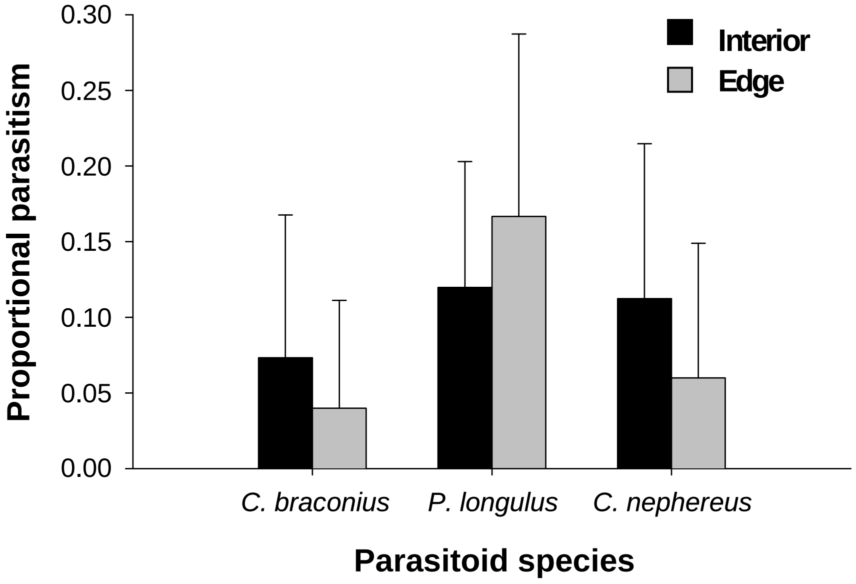

0.30
0.25
0.20
0.15
0.10
0.05
0.00
Proportional parasitism
Interior
Edge
C. braconius
P. longulus
C. nephereus
Parasitoid species

Fig 4

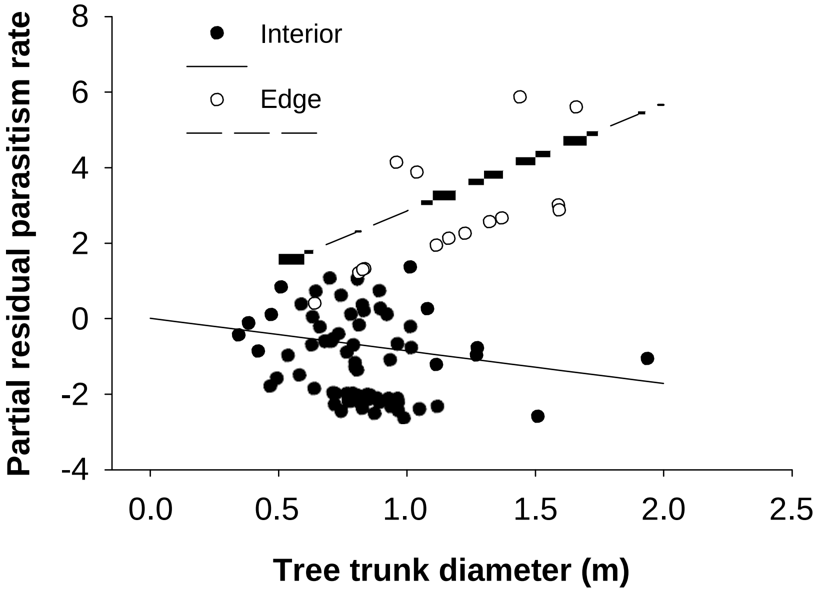

Interior
Edge
Partial residual parasitism rate
8
6
4
2
0
-2
-4
0.0
0.5
1.0
1.5
2.0
2.5
Tree trunk diameter (m)

Fig. 5

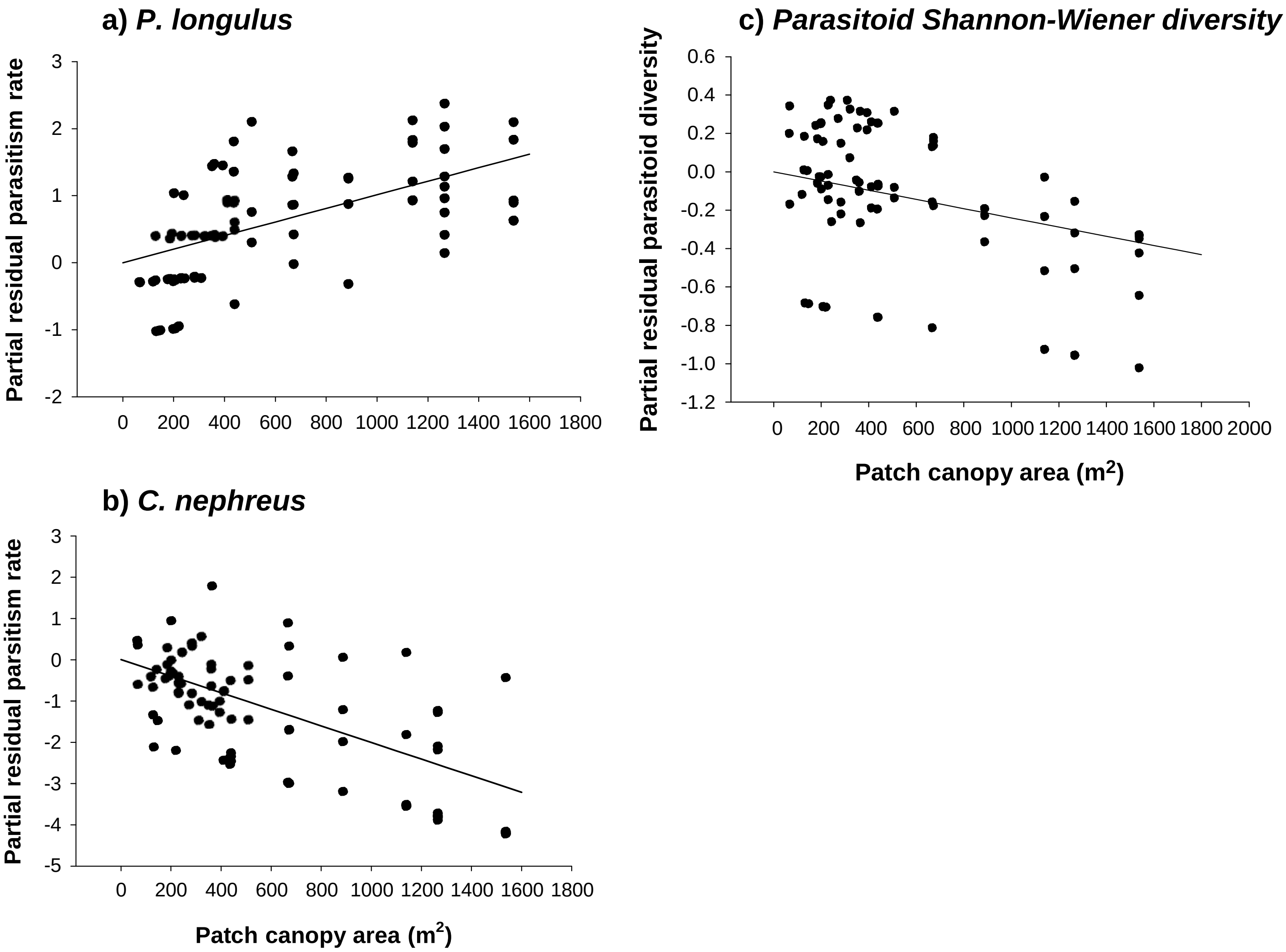
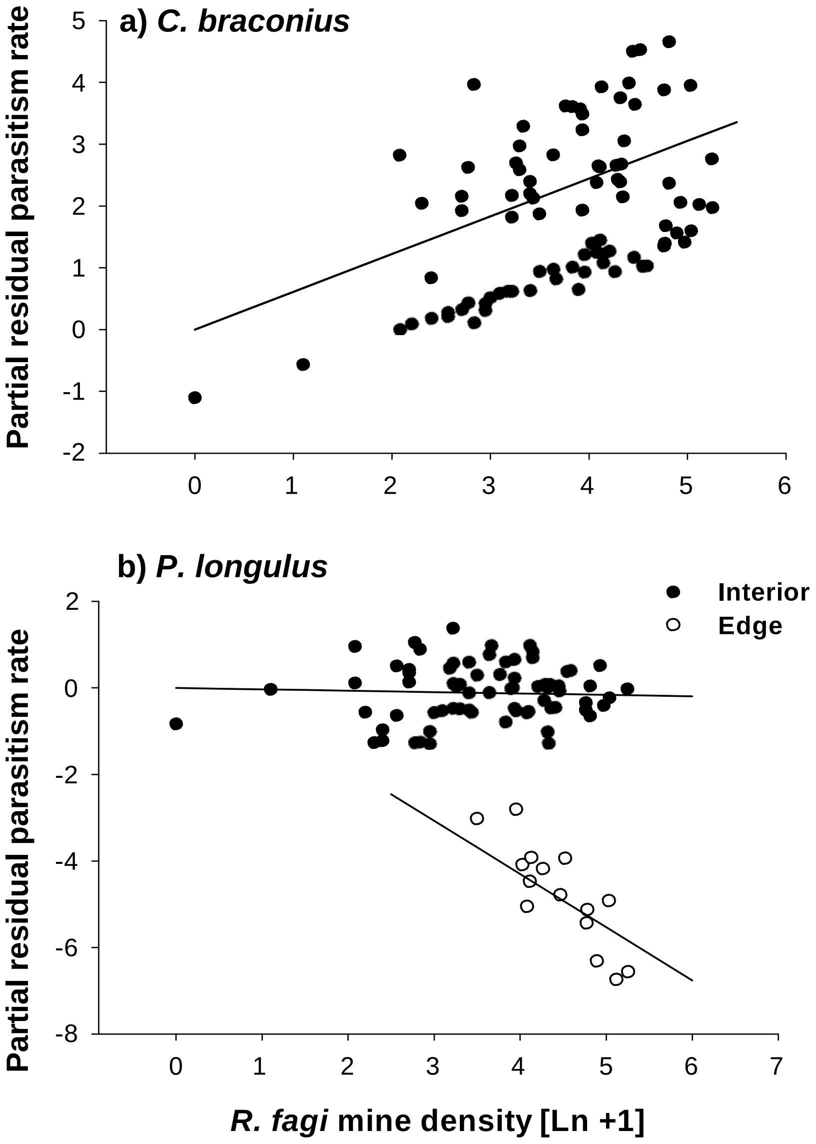

a) *P. longulus*
Partial residual parasitism rate
3
2
1
0
-1
-2
0
200
400
600
800
1000
1200
1400
1600
1800
c) *Parasitoid Shannon-Wiener diversity*
Partial residual parasitoid diversity
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Patch canopy area (m^2)
b) *C. nephreus*
Partial residual parsitism rate
3
2
1
0
-1
-2
-3
-4
-5
0
200
400
600
800
1000
1200
1400
1600
1800
Patch canopy area (m^2)

Fig. 6


a) *C. braconius*
Partial residual parasitism rate
5
4
3
2
1
0
-1
-2
0
1
2
3
4
5
6
b) *P. longulus*
● Interior
○ Edge
Partial residual parasitism rate
2
0
-2
-4
-6
-8
0
1
2
3
4
5
6
7
R. fagi mine density [Ln +1]