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THE POTENTIAL OF PARASITOID HYMENOPTERA AS BIOINDICATORS OF ARTHROPOD DIVERSITY IN AGRICULTURAL GRASSLAND

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Summary

1. As measuring biodiversity in its entirety is impossible, there is a need for bioindicators. This study tested the hypothesis that parasitoid Hymenoptera are potential bioindicators that provide a useful means to assess the wider biodiversity of arthropod populations in agro-ecosystems. There are a range of theoretical arguments to support such a claim, including the high trophic position of these taxa within the arthropod communities in which they occur, and the unique nature of their biological relationships with the majority of terrestrial arthropod groups.
2. An initial survey of 10 sites and subsequently a larger survey of 48 commercial farms were conducted and linear model analyses used to investigate the relationship between parasitoid Hymenoptera and the wider biodiversity of arthropod populations in agro-ecosystems. In addition, analysis of an historical data set, collected in 1976 and 1977, was undertaken to further investigate this relationship.
3. Of the five arthropod groups investigated in the initial 10-site survey, parasitoid Hymenoptera were found to have the greatest potential as bioindicators of overall arthropod taxon richness.
4. In the extended survey of 48 commercial farms, both abundance and taxon richness of parasitoid Hymenoptera had stronger relationships with overall arthropod taxon richness than any other arthropod group investigated.
5. The significant relationship between parasitoid abundance and other arthropod taxon richness was further supported with the historical data set. The relationship was found to change with season.

6. *Synthesis and applications* We show that within agricultural grasslands, both the abundance and taxon richness of parasitoid Hymenoptera are more closely related with overall arthropod diversity than any other arthropod group investigated. This provides a practicable and usable monitoring tool for tracking change in wider arthropod diversity in agro-ecosystems.

Keywords: agro-ecosystem, arthropod, biodiversity, bioindicator, diversity, parasitoid abundance, parasitoid Hymenoptera, taxon richness

Introduction

Following the signing of the Convention on Biological Diversity (CBD), which agreed to integrate biodiversity policy into all economic sectors (UNEP, 1992), the European Commission (2000, 2001) published a Biodiversity Action Plan (BAP) for Agriculture (COM(2001)162 vol. III) as part of a strategy to halt the global decline in biodiversity by 2010. Whilst this ambitious aim has not been met, the need to halt biodiversity loss remains (Nording, 2009). Amongst the recommendations of a meeting of the European Platform for Biodiversity Research Strategy (EPBRS) in Ireland in 2004, there was agreement on the urgent need to develop monitoring systems to evaluate the performance of the Common Agricultural Policy (CAP) in terms of halting biodiversity loss (EPBRS, 2004).

Measuring biodiversity in its entirety is impossible because of the numbers of species involved and the effort that would be required for their collective identification. There is therefore a need for the identification of appropriate bioindicators that can be monitored on the basis of their being representative of wider biodiversity (Duelli & Obrist, 2003a; New, 2005). McGeoch (1998), defined a biological indicator as: “a species, or group of species that readily reflects: the abiotic

or biotic state of an environment; represents the impact of environmental change on a habitat, community or ecosystem; or is indicative of the diversity of a subset of taxa, or of wholesale diversity within an area".

There can be no single indicator for all aspects of biodiversity in all contexts. The selection of appropriate bioindicators is likely to depend on the dimension of the wider environment being evaluated, e.g. the type of habitat, or economic sector. The issue is often guided by the availability of particular taxonomic expertise and resources (Duelli & Obrist, 2003b). However, an essential first step in selecting useful biodiversity indicators, is to identify taxa whose incidence best correlates with overall taxon richness in a particular context (Sauberer *et al*. 2004). In order for bioindicators to be used to their fullest advantage, it is also necessary to understand the ecological relationships between the chosen indicator group(s) and wider community structure, and the particular ecological influences they reflect (Paoletti, 1999).

Agriculture accounts for about 62% of total land use in Ireland (DAFF, 2008). Due to the intensification of farming methods, there has been a drastic change in the Irish landscape since the middle of the last century, and a widely perceived decline in biodiversity similar to that experienced across much of Western Europe. It has been suggested that between 1970 and 2000, species populations in European farmland declined by 23% (de Heer *et al*. 2005). Considering the relatively large proportion of farmed land in the Irish landscape, amelioration of the negative impacts of agricultural practices, leading to increased biodiversity within farmland, could have a positive influence on biodiversity throughout the wider countryside.

Parasitoid Hymenoptera are one of the most diverse groups of arthropods (Gauld & Bolton, 1988; Quicke, 1997), are an important part of agricultural

ecosystems (Altieri *et al*. 1993; Marino & Landis, 2000), and are known to be sensitive to habitat fragmentation and environmental changes (Kruess & Tscharntke, 1994; Siemann *et al*. 1998; Lewis & Whitfield, 1999; Komonen *et al*. 2000; Fraser *et al*. 2008a; Maeto *et al*. 2009). The aim of the current study was to test the hypothesis that, because of their close ecological relationships with practically all other insect groups (Gauld & Bolton, 1988; Quicke, 1997), the parasitoid Hymenoptera have good theoretical potential as functionally significant bioindicators within agro-ecosystems (LaSalle & Gauld, 1993). This hypothesis is tested within the context of agriculturally managed grasslands by:

1. Investigating relationships between the abundance and taxon richness of parasitoid Hymenoptera and the total taxon richness of other arthropod groups collected in sward samples from an initial study of 10 agricultural grassland sites.
2. Collecting a larger data set from an additional 48 commercial farm sites to better quantify observed relationships between parasitoid Hymenoptera and the taxon richness of other grassland arthropod taxa.
3. Further exploring the relationship between the abundance of parasitoid Hymenoptera and taxon richness of other arthropods using an historical data set collected in 1976 and 1977.

Materials and Methods

i) INITIAL SAMPLING AT TEN MONITORING SITES

Site selection

Ten individual grassland fields situated on farms representative of a range of farm management intensities were sampled across southeast Ireland in 2002. The fields

were selected at five paired locations: four field pairs were situated within Teagasc Research Centre lands (Solohead, Co. Tipperary; Grange, Co. Meath; Oak Park, Co. Carlow and Johnstown Castle, Co. Wexford) and on nearby commercial farms under similar farming management regimes. The fifth pair of fields, each of different management intensity, was situated on the University College Dublin (UCD) research farm at Lyons Estate in Co. Kildare. Further details of site locations and farm management systems can be found in Anderson *et al*. (2008a).

Arthropod sampling

Arthropods were sampled from one, randomly chosen, grassland field at each farm site using a Vortis Insect Suction Sampler (Burkard Manufacturing Co Ltd, Rickmansworth, Hertfordshire, UK) (Arnold, 1994). Where sites were being intensively rotationally grazed, samples were taken at the mid-point in sward re-growth (mean sward heights ranged between 7 and 14cm) within the grazing cycle. Ten samples were collected from each field, with one sample comprising the pooled catch from three randomly selected sampling spots, individually sampled for ten seconds. The total area sampled in each field was 0.6 m^2. All samples were collected during August 2002, in dry weather conditions between the hours of 11 am and 3 pm. Catches were preserved in 70% ethanol prior to sorting and identification. Five major arthropod groups dominated the collected samples. Hemiptera, Araneae and Coleoptera were identified to species level (see Helden *et al*. 2008a; Anderson *et al*. 2008a; Helden *et al*. 2008b respectively, for details of the taxonomic literature used). Diptera were identified to family level. The parasitoid Hymenoptera (hereafter referred to as parasitoids) were initially identified to family level, and subsequently to genus level using the literature listed by Anderson *et al.* 2008b.

Data analysis

After pooling all samples from individual fields, and so using sites as replicates (n=10), the relationships between the taxon richness of each major arthropod group in turn, and the total taxon richness of all other arthropod groups (excluding the group being evaluated) were determined using linear model analyses in the R statistical package; version 2.6.0 (R Development Core Team, 2006). Prior to running these analyses, the use of linear models was validated by testing the normality of response variables using the Shapiro-Wilk test.

ii) COMMERCIAL FARM SURVEY

Site selection

Fifty commercial farms were chosen for an extended survey of grassland arthropod populations in the relatively intensively managed East and South-eastern counties of Ireland (Carlow, Cork, Kilkenny, Laois, Meath, Waterford, Wexford and Wicklow). The Irish National Farm Survey (NFS) maintains a nationally representative database of Irish farm statistics by regular collation of farm management data from a sample of over 1,000 farms (Connolly *et al*. 2004). A random sub-sample of 50 predominantly grassland farms, proportionately stratified by selected counties and main livestock farm enterprise (dairying, beef cattle, and sheep) were selected from this database; see Anderson *et al*. (2008a) for further details of the selected farms. As two of the farms could only be sampled under less than optimal wet conditions, they were excluded from the analyses, leaving a total of 48 farms in the study.

Arthropod Sampling

Arthropods were sampled from one randomly chosen, grassland pasture on each farm in July 2005, using the Vortis Insect Suction Sampler. Based on the experience gained from sampling at the original ten sites, the numbers of samples collected from each field was increased from 10 to 20, and the size of each aggregate sample increased from three to six randomly selected sampling spots, individually sampled for ten seconds. The total area sampled per field was, therefore, increased four-fold from 0.6 m^2 to 2.4 m^2. All other sampling details were as previously described.

Vegetation sampling

Botanical species richness and the mean relative abundance of dominant plant species was estimated within swards on each of the 48 farm sites. Data were collected from 50 randomly located circular quadrats (3 dm^2) per sward, using the dry weight rank (DWR) method ('t Mannetje & Haydock, 1963) with yield correction (Jones & Hargreaves, 1979). The three most abundant species in each quadrat were ranked in order of their abundance while all remaining plant species were recorded on a presence-absence basis. Species were identified according to Stace (1997). Mean vegetation height was estimated within each sward by recording height measurements at 50 randomly selected locations using a Filips Folding Plate Pasture Meter (www.jenquip.co.nz).

Data analysis

Using pooled data from individual sites as replicates (n=48), the relationships between the taxon richness of each major arthropod group in turn, and that of all other arthropod groups were quantified as described previously. Sample date was included

as a covariate in these models. Additionally, the larger sample size collected in the commercial farm survey enabled the relationship between the abundance of each arthropod group, and the total taxon richness of other arthropod groups to be similarly quantified. Response variables were again tested for normality using the Shapiro-Wilk test to validate the use of linear models.

The relationships between arthropod taxon richness and plant species richness or mean sward height respectively were investigated using linear models as described previously.

iii) HISTORICAL DATA SET

Available data

Use was made of an extensive dataset collected in 1976-77 (Purvis & Curry, 1981), to further test the relationship between parasitoid incidence and the total diversity of other arthropod taxa in an agricultural grassland experiment contrasting different sward grazing and cutting treatments. Unfortunately the level of taxonomic resolution available at the time of these studies, precluded parasitoid identification beyond family level. However, data for the total abundance of parasitoid individuals and the total taxonomic richness of other major sward arthropod groups identified to levels similar to the current study, were available from D-Vac suction samples (Dietrick, 1961) taken on a monthly basis from replicated field plots (see Purvis & Curry (1981) for further details). For the purpose of the current study, catches were pooled across all experimental plots in each sampling month (May, June, July and August) and year (1976 and 1977). The total area of each pooled monthly sample was 9 m^2.

Data analysis

As a Shapiro-Wilk test showed that the response variables in this data set were non-normal, a linear model was not appropriate. Instead, generalised linear mixed modelling using the lmer function from the lme4 package in R version 2.6.0 (R Development Core Team, 2007) was used to investigate the relationship between the total abundance of parasitoids and the taxon richness of other arthropods. As we were only interested in a general prediction, a maximal model with a Poisson error structure, including parasitoid abundance and sampling month as fixed effects, and year of sampling as a random effect, was fitted. Likelihood ratio tests ($\chi 2$) were used to determine which model parameters were significant.

Results

i) Initial 10-site study

The total sample of arthropods collected from the entire sampled area of 6 m^2 in the initial 10-site survey contained 70 species of Coleoptera (720 individuals); 16 species of Hemiptera (2,110 individuals); 13 species of Araneae (2,119); 75 parasitoid genera, representing 16 families (2,054 individuals) and 25 families of Diptera (3,975 individuals). When relationships between the taxon richness of individual major arthropod groups and total other arthropod taxon richness (excluding the evaluated group) were investigated, only the parasitoid, identified initially to family and later to genus level, showed a potentially useful significant relationship, although the relationship at genus level was weaker than that for family (Table 1). When making multiple simultaneous assessments of the significance of individual correlation statistics, a Bonferroni adjustment of the critical probability value (dividing the conventionally accepted 5% error by the number of relationships being

simultaneously tested) is normally advocated to guard against the multiplied risk of error (Sauberer *et al*. 2004). However, this adjustment is conservative, and when routinely applied in the assessment of significance can increase the risk of a type II error, whereby a genuinely significant finding can be erroneously rejected. We therefore interpret the findings from the initial 10-site study as providing an indication of support for our original hypothesis that parasitoid Hymenoptera are the most useful arthropod bioindicator group within an agro-ecosystem context.

ii) Commercial farm survey - Arthropods

A total of 95,910 adult arthropods, representing 431 recognised taxa were collected from a total pooled sample area of 120 m^2. This included 36 Araneae species, 179 Coleoptera species, 63 Hemiptera species, 121 parasitoid genera and 32 families of Diptera. With the exception of Coleoptera abundance and species richness, sampling date was found to be significant in all relationships investigated (Table 2). Analyses showed that with the exception of Coleoptera and Araneae, the taxon richness of all major arthropod groups was significantly related to the total taxon richness of all other groups (Table 2). The statistical significance of these relationships ($p<0.05$) was maintained even after Bonferroni adjustment of the acceptable probability of error. However, parasitoid taxon richness provided the greatest r^2 value for relationships with total other arthropod taxon richness (Table 2).

The total abundances of Coleoptera, Hemiptera and parasitoids were also significantly related to the total taxon richness of all other groups (Table 2). However after Bonferroni adjustment, only parasitoid abundance remained a statistically significant predictor of the total taxon richness of all other groups (Table 2). Overall, the abundance and genera richness of parasitoids (r^2 = 0.597 and 0.559, respectively)

provided the best relationship with total arthropod taxon richness, with the species richness of Hemiptera having the 'next best' relationship with overall arthropod taxon richness (r^2 of 0.486) (Table 2).

For most tested models, sampling date accounted for the majority of the variance in the model (Table 2). However, date accounted for 20.11% of the total 48.60% of the variance explained by the model using Hemiptera taxon richness, and only 10.4% of the total 55.87% of variance explained by the model using parasitoid taxon richness (Table 2). As with taxon richness, very little model variance (9.61%) was explained by date when using parasitoid abundance as a predictor of total arthropod taxon richness (Table 2).

iii) Commercial farm survey – Plants

A total of 32 species of plant were identified from the swards on the 50 surveyed farms and *Lolium perenne* was the dominant species (Appendix 1). Sward height had a significant relationship (p=0.051) with total arthropod taxon richness, but only explained 3.5% of the variance, while date explained 30.33% (Table 2). However, there was no significant relationship between plant species richness and arthropod taxon richness, although date was once again significant (Table 2).

iv) Historical data set

The data from the 1970's showed a similarly strong relationship between parasitoid abundance and other arthropod taxon richness (Table 3). There were significant interactions between parasitoid abundance and sampling month, suggesting that seasonality has a strong influence on the relationship (Table 3). As the two years differed in climate, model outputs were plotted separately (Fig. 1). Although the

overall numbers of parasitoids and other arthropod taxa varied between the two years, the overall seasonal trends in the relationship between other arthropod diversity and parasitoid abundance is the same in both years. Earlier in the season, the slope of the line is relatively steep, when the abundance of parasitoids is relatively low. Towards the end of the season, however, parasitoid abundance reaches a peak and the slope begins to flatten (Fig. 1). It is important to not extrapolate beyond the data, as the relationship will reach an asymptote as the seasonal diversity of arthropod taxa reaches a late summer peak (Purvis and Curry, 1980).

Discussion

Our studies demonstrate that parasitoid Hymenoptera have much potential as an indicator group of arthropod taxon richness in agricultural grasslands. The initial study of 10 grassland sites, provided some evidence to support our original hypothesis regarding the potential bioindicator value of parasitoids at least at family level. However, increasing the level of taxonomic resolution from families to genera in the analysis of this original data set, did not improve the observed relationship ($r^2 = 0.750$ and 0.454 for parasitoid families and genera, respectively). Both the numbers of sites and the size of samples taken in this initial study were small. As a large total number of (75) parasitoid genera were collected in the relatively small total pooled sample, totalling only 6 m^2 of grassland (0.6 m^2 x 10 sites), it seems likely that the actual collection of any individual genus in this initial study was subject to a high degree of uncertainty and random chance. In these circumstances, it might be expected that the inventory of parasitoid families collected would be more comprehensive and representative of the individual sites, and might therefore show a clearer relationship with total observed arthropod diversity.

In the larger study of 48 grassland sites, the area sampled within individual fields was increased to 2.4 m^2. In this case, both abundance and genera richness of parasitoids, and taxon richness of Diptera and Hemiptera were found to have positive relationships with other arthropod taxon richness. The relationship between parasitoid abundance and overall arthropod taxon richness was the strongest observed. Sampling date explained much of the model variance for Diptera especially and to a lesser extent Hemiptera. However, it accounted for much less variance in the parasitoid models. This relationship between the number of parasitoid individuals and overall arthropod richness is again supported by the results from the historical data set.

Many invertebrate groups have been shown to be good potential indicators of environmental change (Holloway & Stork, 1991; Andersen, 1995; Tscharntke *et al.,* 1998; McGeoch, *et al*., 2002; Akutsu *et al*., 2007). Spiders (Scott, 2006) and Coleoptera such as the Carabidae (Asteraki *et al*. 1995; Butterfield *et al*. 1995) have been used as indicators in biodiversity assessment. However, Lawton *et al*. (1998) investigated correlations between birds, butterflies, flying beetles, canopy beetles, canopy ants, leaf litter ants, termites and soil nematodes and found that no one group was a good indicator of taxon richness. It might be expected that hymenopteran parasitoids would be good indicators of arthropod diversity as they are amongst the most speciose taxa on the planet and parasitise virtually all other arthropod groups (Askew & Shaw, 1986; Hassell, 1986; Altieri *et al*., 1993; Hawkins, 1993; LaSalle, 1993; Quicke, 1997). They play an important ecological role as parasitoids and are important in biological control (Altieri *et al*. 1993). Parasitoid Hymenoptera from the family Braconidae were found to be useful for monitoring the recovery of forest biodiversity in plantation stands in the Indonesian forests of East Kalimantan (Maeto *et al*. 2009).

As managed grasslands have a clearly simplified botanical diversity, it was not surprising that in the current study, botanical species richness was a poor predictor of arthropod diversity. Studies of less intensively managed semi-natural and natural habitats, have shown a bottom-up influence in which botanical and vegetation structural diversity reflect diversity at higher trophic levels (Lawton & Schroder, 1977; Crisp *et al*. 1998; Siemann *et al*. 1998). Similarly, the diversity of hedgerow invertebrates has been found to be strongly related to plant diversity (Bowden & Dean, 1977) and plants have also been shown to be good indicators of arthropod taxon richness (Asteraki *et al*. 2004; Sauberer *et al*. 2004) and higher trophic taxa such as birds (Sauberer *et al*. 2004). Fraser *et al*. (2008b) found that vegetation of woodlands in agricultural landscapes can be used as a surrogate indicator of the species richness of one group of parasitoids, the pimpline Hymenoptera, for conservation purposes.

However, our data suggest that, the trend towards vegetation simplification in agro-ecosystems may make taxa at higher levels in the trophic pyramid more sensitive to changes in the ecosystem. A similar observation was noted by Purvis *et al*. (2009) regarding the apparently greater sensitivity of parasitic 'Cuckoo' bumblebees (*Psithyrus* spp.) to agricultural changes in comparison to non-parasitic *Bombus* spp. In the current study, mean sward height did have a significant relationship with overall arthropod taxon richness, but this was not as strong as the relationship with parasitoid abundance or taxon richness.

Our studies have shown that parasitoids, and in particular the abundance of parasitoids, had the strongest relationship with total observed arthropod taxon richness, supporting their use as bioindicators in agricultural grasslands. This observation has particular significance as identification of parasitoids requires a

relatively high level of expertise and time, and so would be logistically difficult to integrate into any realistic framework of widespread monitoring. The sampling and quantification of parasitoid abundance, however, is relatively straightforward and a practicable option for routine monitoring that eliminates the need for identification skills. However, this relationship needs to be used with a degree of caution. The abundance relationship has the form of a species accumulation curve, suggesting that at any given site, as more sampling is undertaken, greater numbers of individual parasitoids and other arthropod taxa are recovered. As more sampling is undertaken, the numbers of other arthropod taxa start to level off as a more complete inventory for the site is made, but the numbers of parasitoid individuals will continue to increase (Fig. 1). For use in routine monitoring, it is therefore important that an effort be made to understand the seasonal influence on the relationship in the context being studied, and that subsequently, equal sampling effort is made for all sites being compared and sites should be sampled as close together in season as possible. Our current study of 48 commercial farm sites was sampled over approximately five weeks and the resulting model using parasitoid abundance as a predictor of other arthropod taxon richness showed that sampling date explained only 9.6% of the variance. However, as Fig. 1 shows, both the number of taxa and individuals, and the relationship between them, is likely to vary much more over a whole growing season. It seems plausible that the parasitoid abundance relationship may hold in other agro-ecosystems with constrained botanical diversity, such as arable crops, making parasitoid Hymenoptera a more widely useful bioindicator group for agro-ecosystems. However, the relationship needs to be tested in other crop habitats. The use of parasitoids as bioindicators of arthropod taxon richness offers another important potential advantage, in that improving knowledge of taxonomy of the groups makes it possible

to identify most taxa to at least genus level, and our knowledge of parasitoid-host group relationships is increasing incrementally. Additional information may therefore be gained by identifying parasitoid taxa and making use of knowledge of host ranges to gain an insight into underlying ecological effects resulting from environmental and/or management changes. Further studies to demonstrate this additional potential within the context of agro-ecosystems are ongoing.

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Table 1: Summary of the relationships between taxon richness of individual arthropod groups and the total taxon richness of all other arthropod groups using data from the initial 10-site study.

Major Group (level of taxonomic resolution)	**r^2**	**p-value***
Coleoptera (species)	0.187	0.213
Diptera (families)	0.005	0.853
Hemiptera (species)	0.016	0.729
Hymenoptera (genera)	0.455	0.032
Hymenoptera (families)	0.750	0.002
Hymenoptera (abundance of individuals)	0.099	0.376
Araneae (species)	0.007	0.817

* Bonferroni-adjusted critical p-value = 0.05/6 = **0.0083**

Table 2: Summary of regression models describing relationships between taxon richness or abundance of individual arthropod groups, plant species richness and mean sward height, and the total taxon richness of all other arthropod groups using data from the commercial farm survey.

Model parameter		r^2	p-value*	% Variance explained
Richness of:	Coleoptera species (Sample date)	0.170	0.084 (0.396)	15.40 (1.51)
	Diptera families (Sample date)	0.435	0.003 (<0.001)	9.65 (33.87)
	Hemiptera species (Sample date)	0.486	<0.001 (<0.001)	28.49 (20.11)
	Hymenoptera genera (Sample date)	0.559	<0.001 (<0.001)	42.47 (13.40)
	Hymenoptera families (Sample date)	0.467	0.001 (<0.001)	(27.14) (19.52)
	Araneae species (Sample date)	0.304	0.104 (0.004)	15.74 (14.62)
	Plant species (Sample date)	0.321	0.101 (<0.001)	0.05 (32.09)
Abundance of:	Coleoptera (Sample date)	0.234	0.010 (0.770)	23.23 (0.15)
	Diptera (Sample date)	0.316	0.676 (<0.001)	0.79 (30.80)
	Hemiptera (Sample date)	0.384	0.021 (<0.001)	20.31 (18.10)
	Hymenoptera (Sample date)	0.597	<0.001 (0.002)	50.06 (9.61)
	Araneae (Sample date)	0.293	0.158 (0.009)	17.79 (11.56)
	Mean Sward Height (Sample date)	0.338	0.051 (<0.001)	3.5 (30.35)

*Bonferroni-adjusted critical p-value = 0.05/12 = 0.004

Table 3: Results from the likelihood ratio tests, following a generalised linear mixed model (lmer) investigating the relationship between parasitoid abundance and total taxon richness of other arthropods collected in 1976 and 1977. Parasitoid abundance and sampling month were fixed effects and year of sampling was a random effect. For the likelihood ratio tests, year was the null model and other parameters (sampling month and parasitoid abundance) and interactions (shown by *) were systematically added to subsequent models.

Parameter tested	χ^2	p-value
Sampling month	73.40	<0.001
Parasitoid abundance	89.05	<0.001
Year*month	13.85	0.003
Year*Parasitoid abundance	16.21	<0.001
Parasitoid abundance*month	77.97	<0.001

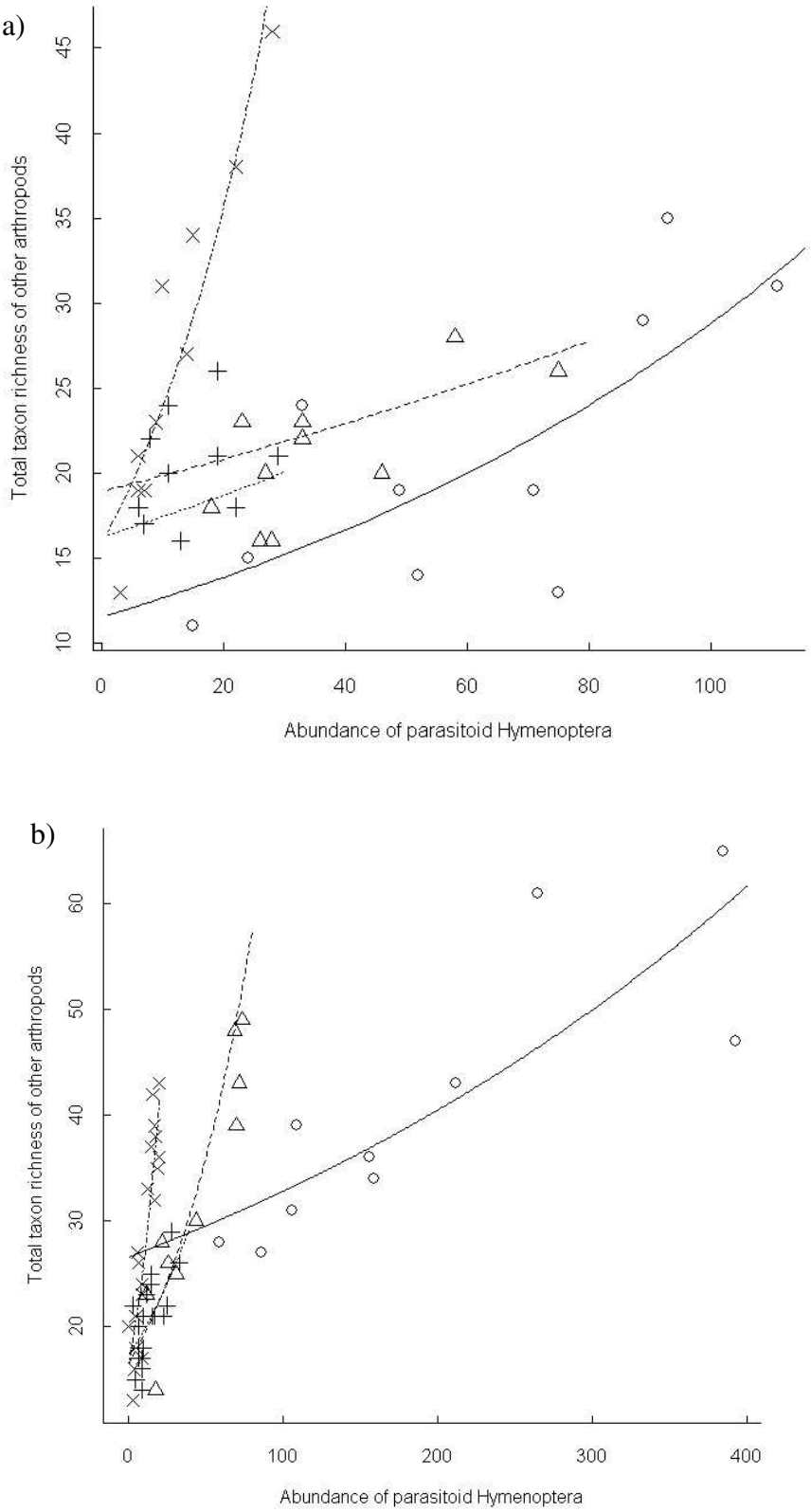

Figure 1: Model prediction of the relationship between the abundance of parasitoids and the total taxon richness of all other arthropods (excluding parasitoids) collected in suction samples from agricultural grassland swards over four seasons in 1976 (a) and 1977 (b). Fitted lines indicate the predicted relationships in May (x), June (+), July (triangles) and August (circles) respectively.

Appendix 1. List of botanical species recorded within swards sampled on dairy and non-dairy (drytsock) farms within the commercial farm survey and their total number of occurrences. PF indicates percentage frequency in a quadrat

	Sward			
	Drystock		Dairy	
	PF	No of farms	PF	No of farms
Achellia millefolium	3.07	4	0.00	0
Agrostis spp	67.47	15	40.91	30
Alopecurus geniculatus	0.67	2	0.86	4
Alopecurus pratensis	0.67	1	0.11	2
Anthoxanthum odoratum	0.27	1	0.00	0
Bellis perennis	0.67	3	0.46	7
Capsella bursa pastoris	0.00	0	0.17	1
Cardamine flexuosa	0.53	4	0.06	1
Carex sp.	0.40	1	0.00	0
Cerastium fontanum	4.93	11	0.80	10
Cirsium arvense	5.73	6	1.09	9
Cirsium vulgare	0.40	1	0.00	0
Crepis vesicaria	0.13	1	0.00	0
Cynosurus cristatus	7.33	5	0.06	1
Dactylis glomerata	1.87	3	2.34	7
Festuca rubra	1.73	4	0.06	1
Holcus lanatus	44.27	14	8.86	12
Juncus effusus	0.93	3	0.00	0
Lolium perenne	92.93	15	99.83	35
Lotus corniculatus	0.80	2	0.00	0
Matricaria recutita	0.00	0	0.06	1
Plantago major	0.27	2	0.17	3
Poa annua	1.87	6	3.31	10
Poa pratensis	1.60	4	3.26	10
Poa trivialis	12.40	9	6.97	21
Potentilla reptans	0.67	1	0.11	1
Ranunculus acris	0.13	1	0.23	2
Ranunculus repens	18.53	14	9.03	20
Rosa canina	0.00	0	0.06	1
Rumex acetosa	2.53	4	0.17	1
Rumex obtusifolius	3.07	5	3.71	23
Senecio jacobaea	0.40	2	0.11	2
Stellaria holostea	0.13	1	0.00	0
Stellaria media	0.13	1	0.97	5
Taraxacum off. agg.	1.07	4	1.49	9
Trifolium repens	51.73	15	34.57	34
Urtica dioica	0.53	4	0.23	4
Veronica serpyllifolia	0.53	0	0.23	1