Invertebrate Abundance and Community Composition on a Split Organic/Conventional Farm in Northern England: the Effects of Management, Crop Type and Field Boundary

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General Abstract

Invertebrates form a key component of agro-ecosystems, with a broad range of life-histories, and include crop pests and natural enemies. To understand the main drivers of invertebrate abundance and community composition, studies are required at the whole-farm level, and across several years, to encompass the entire cycle of agricultural management. This thesis investigates these drivers at Nafferton Farm, Northumberland, UK, which is a split organic-conventional farm, and thus also provides an opportunity to compare management regime on invertebrate ecology.

Invertebrates were sampled via two complementary methods, pitfall and yellow-pan traps, across the farm, together with associated records of crop and field boundary types, vegetation community composition and vegetation structure. Samples were collected in field boundaries (0 m), field edge (5 m) and within the crop (40 m). Invertebrates were usually identified to the taxonomic level of at least family or sub-family, whilst Carabidae were identified to tribe. Invertebrates were classified into three broad functional groups reflecting both their life-histories and sampling method: epigeal predators; foliar predators/ parasitoids; herbivores / pollinators. Taxonomic richness and total invertebrate abundance were analysed using linear models and linear mixed-effects models. Invertebrate community composition and its response to environmental and spatial-temporal factors were analysed via unconstrained, constrained and partial ordinations (CA, CCA and pCCA).

Across the whole farm, both invertebrate biodiversity and abundance were greater in organic compared with conventional management. Abundance was affected by crop type, with invertebrates particularly abundant in spring beans (organic), winter barley (conventional) and oilseed rape (conventional). Invertebrates were most abundant in field boundaries that comprised short grass, but had greatest biodiversity along woodland edges.

Major differences in invertebrate community composition over time were observed on the 5-year conventional rotation compared to the 8-year organic rotation. The latter had less soil disturbance, which disrupted the invertebrate community, and whilst crop type was the main driver, there was also a significant 'lag effect' from the preceding year's crop. Vegetation structure, cover and traits (measured according to the Competitor, Stress-tolerator, Ruderal system) all had major effects on the invertebrate community composition, with CSR patterns particularly important. Overall, more of the most abundant invertebrate taxa in field boundaries were found in the field edge (5 m) and crop (40 m) in the organic than conventional system. For some invertebrate taxa, associations between their relative abundance in the field boundary, edge and crop were related to their life-history traits, especially dispersal ability and body size.

The research demonstrates that a wide-range of environmental and agronomic factors affect invertebrate communities, and that these are best understood when analysed at the landscape-scale at multiple spatial and temporal scales.

Acknowledgements

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Chapter 1. **Introduction**

1.1 Invertebrates in agroecosystems and long-term changes

Insects are amongst the most taxonomically diverse group of animal (Ødegaard, 2000; Mora *et al.*, 2011). A conservative estimate by (UN, 2003.) suggested that there were approximately 30 million insect species worldwide, of which beetles (Coleoptera) account for the vast majority, approximately 40% of described species (Stork *et al.*, 2015). Many insects play important roles in the agro-ecosystem. For example, they act as pollinators for both wild plants (Khan and Yogi, 2017) and crops including oilseed rape, orchard fruits etc. (Kremen *et al.*, 2002; Calderone, 2012). Insect pollination is very important to crop production, which is estimated to provide £130 billion per annum to global economy (Gallai *et al.*, 2009). In the UK insect pollinated crops covered 20% of agricultural land by area, and about £400m per annum or 19% by value (Breeze *et al.*, 2011). In addition to pollinators, insects can act as crop pests, and have negative effects on agricultural production. In contrast, some insect species are predators of other invertebrates (Rusch *et al.*, 2010) and may therefore be beneficial in agroecosystems to reduce crop pests (Symondson *et al.*, 2002; Ives *et al.*, 2004). Others form key parts of the diet for taxa such as farmland birds (Holland *et al.*, 2006) especially chicks (Southwood and David, 2002), small mammals, and bats (Freeman, 1979; Wickramasinghe *et al.*, 2004).

There is evidence of declines in some insect populations both globally (Dirzo *et al.*, 2014) and within Europe (Habel *et al.*, 2016). Long-term samples of predominantly aerial invertebrates at the world's longest running survey, The Rothamsted Insect Survey, UK (Storkey *et al.*, 2016) and more recently by The Krefeld Entomological Society, Germany (Hallmann *et al.*, 2017) have both suggested that insect total biomass and abundance may have declined by over 50% in the past 50 years. Other long-term studies in cereal fields over 42 years (The Sussex Study) have highlighted the influences of extreme weather events, long-term climate and pesticide use, with predatory invertebrates such as Araneae and Coleoptera particularly sensitive to pesticide use (Ewald *et al.*, 2015). The abundance of both taxa are important in integrated pest management (IPM). These authors also found that the abundance of other groups of invertebrates, including Collembola and Aphididae, increased, possibly in response to climate change, and it is clear that the interplay between climate, weather and crop management is not simple. See Leather (2018) for comprehensive assessment of long-term studies.

Another useful source of historical data is from established annual monitoring schemes or citizen science surveys. For example, data from the UK Butterfly Monitoring Scheme, using data since the 1970s, has reported fluctuating butterfly abundance for generalist species, but significant declines in more specialised species (Brereton *et al.*, 2011). A number of other studies have reported declines in carabid beetles (Kotze and O'Hara, 2003; Brooks *et al.*, 2012), moths (Groenendijk and Ellis, 2011; Fox, 2013), and butterflies (Thomas, 2005). In 2004 the Royal Society for the Protection of Birds (RSPB) undertook a citizen science survey, in which drivers used their vehicles as mobile “field stations” to collect insect “splats” to assess insect numbers, but their results were inconclusive especially as the study was not repeated subsequently. Nevertheless, the implications of insect decline have raised concern amongst government bodies, policy-makers and the general public to investigate possible causes (Hole *et al.*, 2005; Alignier, 2018).

1.2 Agricultural policies and effects on invertebrates

A number of different agricultural changes may have contributed to invertebrate abundance and community composition: increased pesticide usage (Stoate *et al.*, 2001), increased mechanization (Kladivko, 2001) and loss of non-crop habitats (Robinson and Sutherland, 2002). In the UK many of these changes were initiated by the Ministry of Agriculture, Fisheries and Food's (MAFF) aim of increasing food production after 1945, and more recently the European Union's Common Agriculture Policy (CAP).

1.2.1 Increased pesticides use

Farming practice has become more intensive post world war two, with increased use of insecticides (Carvalho, 2006) and herbicides (Young, 2006). The use of herbicides changes the crop microclimate and reduces the numbers of host plants (crop weeds) on which herbivorous insects can feed, with knock-on effects higher up the food chain. Broad-spectrum insecticides, usually applied via sprays, have direct effects on all the invertebrates in a crop, as well as the risk of spray-drift into non-crop habitats (Longley *et al.*, 1997). Neonicotinoid insecticides are usually applied as seed dressings (Sparks, 2013) and were originally thought to cause few non-target problems, but are now known to affect non-target insects such as pollinators (Rundlöf *et al.*, 2015) and beetles (Cloyd and Bethke, 2011). Neonicotinoids are systemic chemicals that travels within crop plants and persist for long periods in soil and water; their effects can therefore cascade through the food chain by reducing amounts of available prey for other taxa such as birds (Hallmann *et al.*, 2014).

1.2.2 Increased mechanization

Agricultural intensification with more powerful tractors and mouldboard ploughs allows heavier soils to be cultivated more frequently (Kladivko, 2001). Tillage affects soil-dwelling invertebrates (Witmer *et al.*, 2003), due to change in soil temperature, water content and micro-topography of the soil. In general, smaller invertebrates appear to be less sensitive to disturbance by tillage, than larger organisms (see review Kladivko, 2001). Shearin *et al.* (2007) found that rotary tillage and mouldboard ploughing had negative effects on four carabid species which was attributed to direct tillage-induced mortality, whilst more carabids are associated with no-till methods (Lalonde *et al.*, 2012). Agricultural intensification associated with increased mechanization has seen a change in crop varieties, with a major shift in the UK from spring to autumn-sown crops (Robinson and Sutherland, 2002). The latter provides fewer over-wintering habitats and fewer host plants for many species of invertebrate (Marshall *et al.*, 2003). Mechanical ploughs, harvesters and high precision seed drills have let improvements in efficiency (Weiner, 2001) including larger field sizes, but smaller areas of non-crop habitat and field boundaries. The Agricultural Act of 1947 provided incentives for farmers to cultivate more grain through more efficient mechanization, which resulted in larger simplified crop landscapes (Robinson and Sutherland, 2002; Geiger *et al.*, 2010). Increased investment in bigger and more efficient farm machinery resulted in consolidation of smaller mixed farm into larger monoculture fields, devoid of plant diversity (Ekroos *et al.*, 2010a).

1.2.3 Replacement of non-crop habitats

The consequences of agricultural intensification on insect communities are exacerbated by the replacement of non-crop areas such as woodlands, field margins, hedgerows etc. which provide habitats for many invertebrates (Bianchi *et al.*, 2006; Verburg *et al.*, 2006). Consequently, important semi-natural habitats crucial to biodiversity were replaced with intensive crop fields (Robinson and Sutherland, 2002). Non-crop habitats serve as overwintering sites for beneficial invertebrates (Frank and Reichhart, 2007), alternate food sources (Goulson *et al.*, 2008), nesting and breeding sites (Holland and Luff, 2000), hibernation sites (Wamser *et al.*, 2011) and a link between the agricultural landscapes (Schmidt-Entling and Döbeli, 2009). Invertebrate abundance in field boundaries can be influenced by habitat quality (Dennis and Fry, 1992), hedge orientation (Maudsley *et al.*, 2002), structural diversity and shelter (Maudsley, 2000) in addition to boundary age and maturity (Burgio *et al.*, 2006). Increased floral diversity in field margins has been shown to enhance biological control (Winkler *et al.*, 2010), however, their ability to influence invertebrate community is predicated on their local environmental conditions (Poggio *et al.*, 2013). The organic system generally consist of a greater total area of semi-natural habitats and more diverse plant communities, which includes woodlands, field margins and hedgerows (Gibson *et al.*, 2007b), possibly due to a lack of herbicide drift and inorganic fertilizer usage (Aude *et al.*, 2004) which can provide cascading effect higher up the food chain (Chamberlain *et al.*, 1999). Habitat manipulation, for example wildflower strips (Blaauw *et al.*, 2014) and beetles banks (MacLeod *et al.*, 2004), have been used to provide food and shelter from adverse conditions for beneficial invertebrates (Landis *et al.*, 2000) in an attempt to provide pest control to adjacent crop fields (Firbank *et al.*, 2013).

1.3 Ecological processes and their relationship to biodiversity

Farm management affects invertebrates directly through pesticide use, soil tillage and choice of crops grown, and indirectly through effects on non-crop habitats especially the vegetation in the field boundaries. Conventional management with higher fertiliser inputs may affect the structure and traits of plants growing in non-crop habitats, and weeds within the crops themselves, with subsequent effects on the invertebrate communities.

1.3.1 Organic and Conventional Farming Systems

Organic management avoids pesticides and inorganic fertilizers usage (Mäder *et al.*, 2007; Tuck *et al.*, 2014) and in the UK and Europe generally grow spring- rather than autumn-sown cereals (Rinaldi and Vonella, 2006) to avoid weed flushes. Many organic farms utilize a holistic management (Baudry *et al.*, 2000), in which biodiversity conservation is at the whole farm scale. A number of sources have shown a strong organic market approximated to be: US$11 billion/annum globally (Robins. *et al.*, 2000), US$5 billion/annum Europe and US$1 billion/annum UK (Willer and Yussefi, 2000). Increased organic production in Europe (UN, 2003.) is driven partly by retailers (Maeder *et al.*, 2002) responding to consumers concern for human health and wildlife (Huber *et al.*, 2011).

A number of studies have investigated organic farming influences on flora and fauna biodiversity, with the majority of these showing positive benefits. The absence of pesticides, herbicides and inorganic fertilizers increased overall biodiversity (Geiger *et al.*, 2010). A broad range of taxa increase in both their abundance and species richness under organic agriculture including vascular plants, predatory arthropods, birds and bats (Wickramasinghe *et al.*, 2003; Gabriel *et al.*, 2006; Frank and Reichhart, 2007). The larger numbers of predatory arthropods in organic systems provides the potential for biocontrol of crop pests. More predators do not necessarily translate into better pest control. Farmers would need to create suitable habitats to ensure predator populations can be sustained over time (Landis *et al.*, 2000) and that the predators can move from non-crop habitats into the crop to provide optimal biocontrol (Kleijn *et al.*, 2001; Tscharntke *et al.*, 2005b).

1.3.2 Plant cover, structure and traits

In organic systems, crops are sown in the spring to limit the duration of the resurgence of weeds, whilst conventional fields are sown in the autumn (Gabriel *et al.*, 2005). Organic fields contain greater numbers of plant species (Gabriel *et al.*, 2006; Öberg, 2007) and a more complex physical structure of all the vegetation, including weeds, within the crop (Unwin and Smith, 1995). This provides a more continuous supply of food and habitat for invertebrates over the duration of the growing season. Grass/ clover leys in organic systems, generally cultivated for nutrient enrichment to the soil (Rasmussen *et al.*, 2013) result in less disturbed ground cover for invertebrates, due to the lack of annually cultivation by ploughing between years 3 and 4 in the crop rotation. Plant cover is positively correlated with activity-density of beneficial predators such as Coleoptera-Carabidae (O'Sullivan and Gormally, 2002; Navntoft *et al.*, 2006; Eyre *et al.*, 2016a), due to microclimate and available prey (Norris and Kogan, 2000).

Vegetation structure influences invertebrate communities. For example, sometimes tall vegetation supports more invertebrate species at higher densities (Morris, 2000) which may provide protection to escape from predatory arthropods (van Klink *et al.*, 2015). Mowing is sometimes used to manage grasslands along field boundaries and this changes the structure and vegetation microclimate. Less-mobile arthropods (including eggs, larvae and pupae) are more susceptible to high mortality partly due to direct contact with the cutting blades and lack of protection (Gardiner *et al.*, 2002). Management that consistently results in relatively short or tall vegetation is likely to alter the traits of the plant species, particularly the relative proportions of competitor species compared to ruderals or stress-tolerators in agroecosystems (Grime, 1988).

1.4 Rationale for this thesis

Invertebrates in agroecosystems are important as crop pests, beneficial predators, parasitoids and pollinators. Previous studies have compared organic and conventional management effects on invertebrate communities. Interpretation of data is difficult, partly due to environmental (site) dissimilarities that are associated with organic and conventional farms at different locations. A further complication is that different crops are grown in organic and conventional management, to the extent that the time-periods for completion of a complete rotation cropping cycle do not match. Long-term studies, with data collected across multiple years, are required to understand the effects of these different rotations. Invertebrate patterns at small spatial scales requires sampling not only from within the crop, but also the field edge and non-crop habitats. These typically differ between and within farms. The life-history traits and physical structure of the vegetation in the two management systems may differ, with subsequent effects on abundance, species composition and possibly life-history of the invertebrates. The structure of Nafferton Farm, managed as independent conventional and organic units at the same geographical location provides an ideal opportunity to investigate these issues, using both historical and recently collected field samples.

1.4.1 What are the effects of management on invertebrate abundance and composition*?*

Since organic and conventional systems use different management (chemicals, tillage etc.) crops, and rotation it is therefore not simple to distinguish between these three separate factors and their effects on the invertebrates. In addition, field edges and boundaries are affected by the farm management and crop, which may have additional effects on invertebrates. Finally, invertebrate functional groups, specifically epigeal predators, foliar predators/parasitoids, and herbivores/pollinators may respond differently. Several studies were undertaken, with invertebrates collected across the whole farm to compare the organic and conventional in combined analyses (Chapter 4). Long-term datasets were used to assess the impacts of the two different rotation systems (Chapter 5). Differences and similarities within the crop, field edge and boundary/non-crop areas were determined via individual analyses of the invertebrates from each half of the farm (Chapter 3, Chapter 6). Analyses were subdivided into the three invertebrate functional groups.

1.4.2 How does plant species composition (cover), structure and traits affect invertebrate composition and life-history traits*?*

Vegetation cover and composition is known to affect invertebrate communities, but most studies on vegetation structure have focussed on spiders, and less work has been done in agroecosystems. Whilst plant life-history traits have been well-documented for many years, there have been few attempts to relate plant life-histories to invertebrate community composition. Finally, very little research has been undertaken on the relationships between invertebrate life-history traits and their wider environment. Vegetation composition and structure was surveyed across the farm (Chapter 2) and compared with the invertebrates. The established Competitor-Stress Tolerator-Ruderal (CSR) method of Grime (1988) was used as a framework to measure the plant traits (Chapter 6). A customised invertebrate life-history trait database was developed for this project and related to the habitats in which the invertebrates were sampled (Chapter 3).

1.5 Schematic summary of each data chapter

1.5.1 General Methods

A detailed description of the study site, Nafferton Farm in Northumberland, UK, is provided in Chapter 2, including an explanation of the split-farm management into conventional and organic agriculture, and farm maps. The invertebrate and vegetation sampling techniques are described, plus the rationale behind the main univariate and multivariate analyses.

1.5.2 Relationship between agricultural management, crops and boundaries with invertebrate functional groups on a split organic/conventional farm

The influence of management system, crop and boundary type on invertebrate abundance and taxa richness within three functional invertebrate groups across the whole farm is described in Chapter 4. These univariate analyses were undertaken using conventional linear models. Within each management system differences in community composition as a result of crop and boundary type were assessed by unconstrained multivariate analyses. Invertebrate samples collected in 2015 from the field boundary and within crop were used in these analyses. The major role of management regime and the importance of crop and boundary type on agroecosystem invertebrates are discussed in this chapter.

1.5.3 Invertebrate communities are affected by both crop rotation and soil tillage

Different crop rotations are used in organic and conventional management systems, and the effects of these on the invertebrates, particularly in the context of soil tillage, is explored in Chapter 5. A five-year rotation is in place on the conventional part of the farm, and an eight-year rotation on the organic. Historical invertebrate data, collected from 2005-2012, using the same sampling protocols as implemented elsewhere in the thesis, were analysed. Weather data were also collected during this period. Changes in abundance of individual taxa in response to the current year's crop type were analysed via linear mixed effects models. Changes in invertebrate community composition over time in response to both the current and preceding year's crop were analysed through partial constrained ordinations, and their relative contributions quantified via variation partitioning.

1.5.4 Invertebrate functional groups in relationship to plant cover, structure and traits

The influence of plant cover, structure and traits on the abundance and composition of the invertebrates in organic and conventional systems is described in Chapter 6. Vegetation structure and cover were measured at each invertebrate sampling location whilst vegetation traits were collated according to (Grime, 1988) Competitor, Stress-tolerator and Ruderal system (CSR) plus annual or perennial life-history. The effects of these vegetation measures on invertebrate composition were analysed using CCA (using 2015 field data) with invertebrate data from the crops, field edge and field boundaries. The relative importance of plant cover, structure and traits on the invertebrate community was quantified using variation partitioning (VP).

1.5.5 Management practices, field boundary type, and invertebrate life-history, all affect both the abundance and taxonomical composition of invertebrates

The relationship between the most abundant invertebrate taxa in the field boundaries and the same taxa in the field edge and crop is described in Chapter 3. The main aim was to investigate the changes in abundance and composition of these taxa with increasing distance from the field boundary, and relate these the life history traits of these taxa. The ten most abundant taxa for each functional group were analysed, using multivariate generalised linear models via the R mvabund package (Wang *et al.*, 2012); this provides greater statistical power for small, skewed datasets, and model fit can be assessed in a similar manner to that in univariate GLMs. Additional analyses using partial CCA was also employed to remove effects due to boundary type and crop, via separate constrained ordinations of invertebrates in the field boundary, edge and crop. These separate ordinations were then compared via Procrustes analysis, to produce summary statistics to quantify the relationships between boundary vs field edge, and boundary vs crop invertebrates. Where possible, results were interpreted in the context of the known life-history traits of the invertebrates.

Chapter 2. **General Methods**

2.1 Site Description

2.1.1 Survey Area and Management

Nafferton Farm is located approximately 20 km west of Newcastle-upon-Tyne in Northumberland, UK (54°59', 09"N; 1°43', 56"W). The farm operates as a commercial and research/teaching facility of Newcastle University in northern England. Prior to 2001, the whole of Nafferton farm operated as a 320 ha commercial mixed farm, which included dairy and arable farming. Since 2001, however, Nafferton Farm commenced conversion of 160 ha to conventional farming and the other half to certified organic farming, completed in 2004.

Since conversion to a split organic-conventional system, Nafferton Farm operates two different crop rotational systems Figure 2.1. In the organic half of the farm, crop rotation follows an 8-year cycle of spring barley, grass/clover, spring wheat, potatoes and beans (see Figure 2.2). All organic crops are spring sown, usually until the end of May. Barley is undersown with grass / clover which provide cover and increase soil nitrogen (Hansen *et al.*, 2005) but spring wheat is not undersown. In the organic management the soil is not always annually cultivated by ploughing (e.g. between grass/clover leys in Rotation Years 3 and 4. These grass/clover leys are, however, subjected to three silage cuts each year to provide fodder for dairy cattle. Soil disturbance is highest in the potatoes with ploughing prior to planting and earthing-up around the developing crop. No artificial pesticides or fertilisers are applied in the organically managed half, and cow slurry from the dairy units is used to improve soil nutrients. Field boundaries on the organic managed farm consist of short herbaceous (up to heights of 0.5 m: *Agrostis stolonifera*, *Taraxacum officinale* and forbs), tall herbaceous (up to heights of 1.5 m: *Urtica dioica*, *Cirsium arvense* and forbs*)* and hedges (greater than 1.5 m: *Crataegus monogyna)* as classified in Eyre *et al.* (2013b).

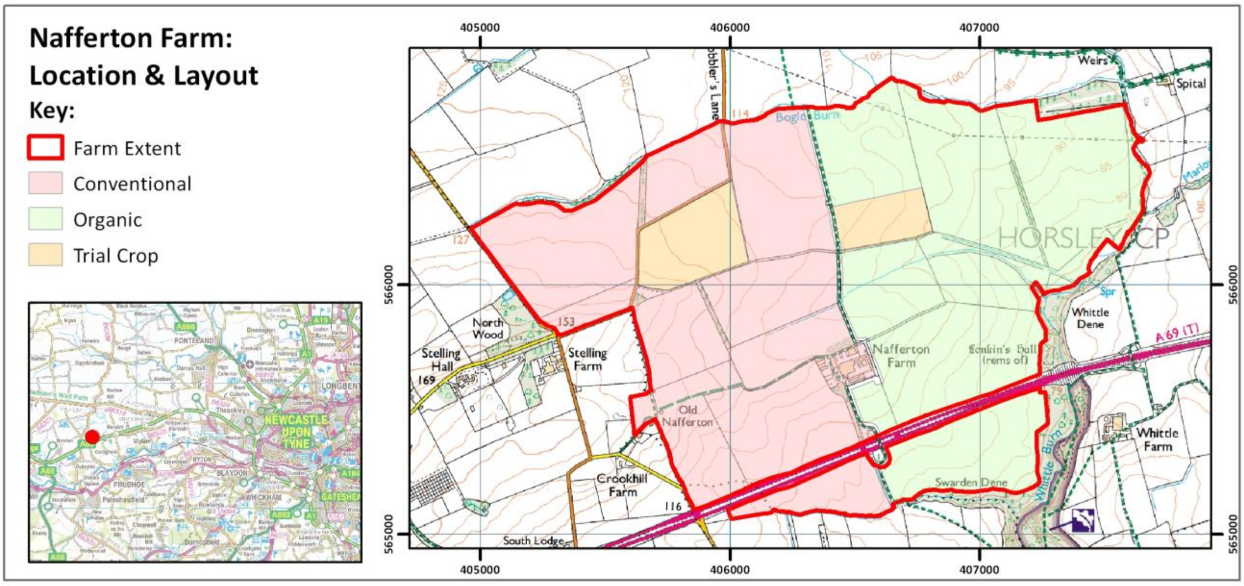


Figure 2.1 Basic layout of Nafferton split organic/ conventional farm.

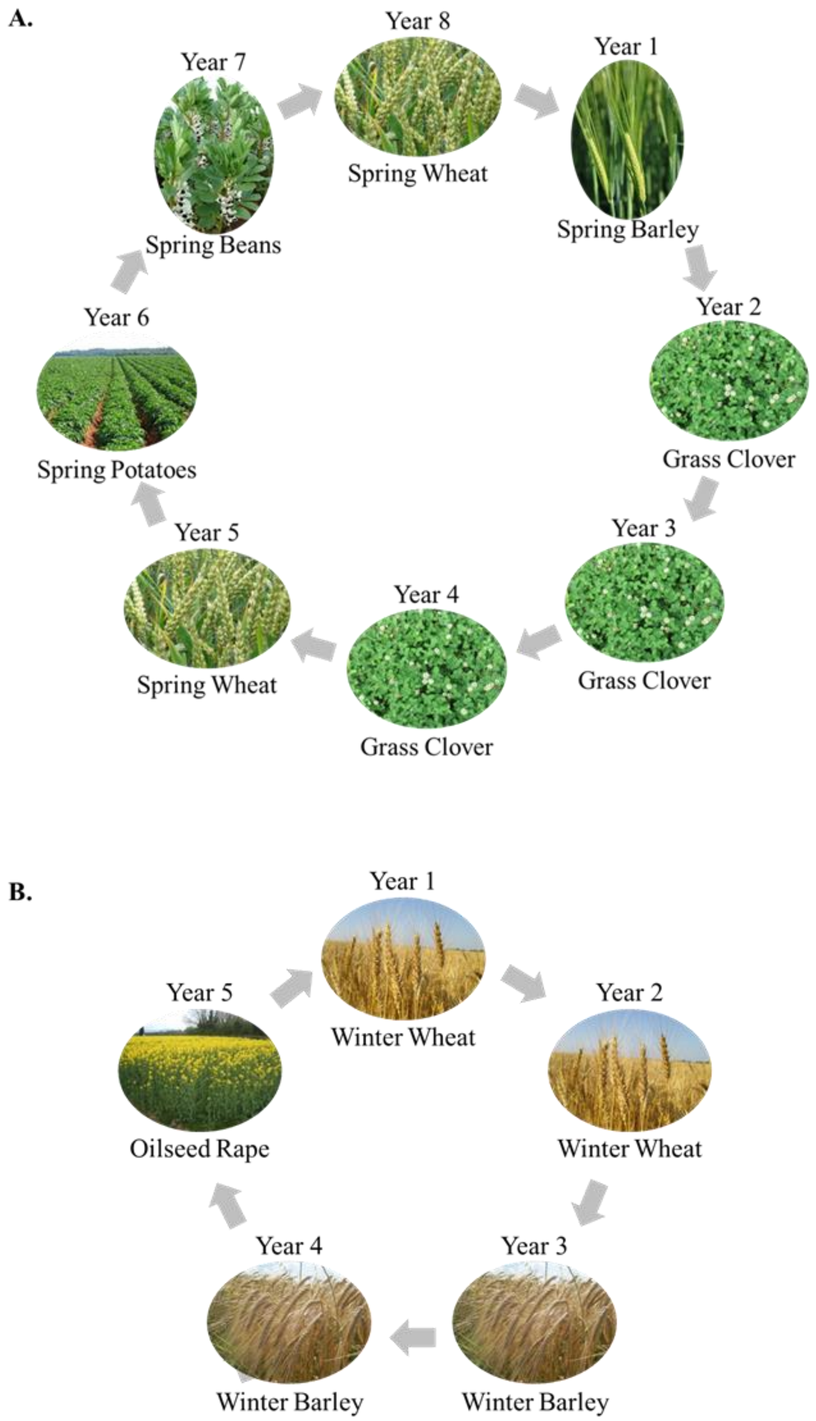


Figure 2.2 Basic crop rotational cycle for the eight years A) organic system, and five years B) conventional system.

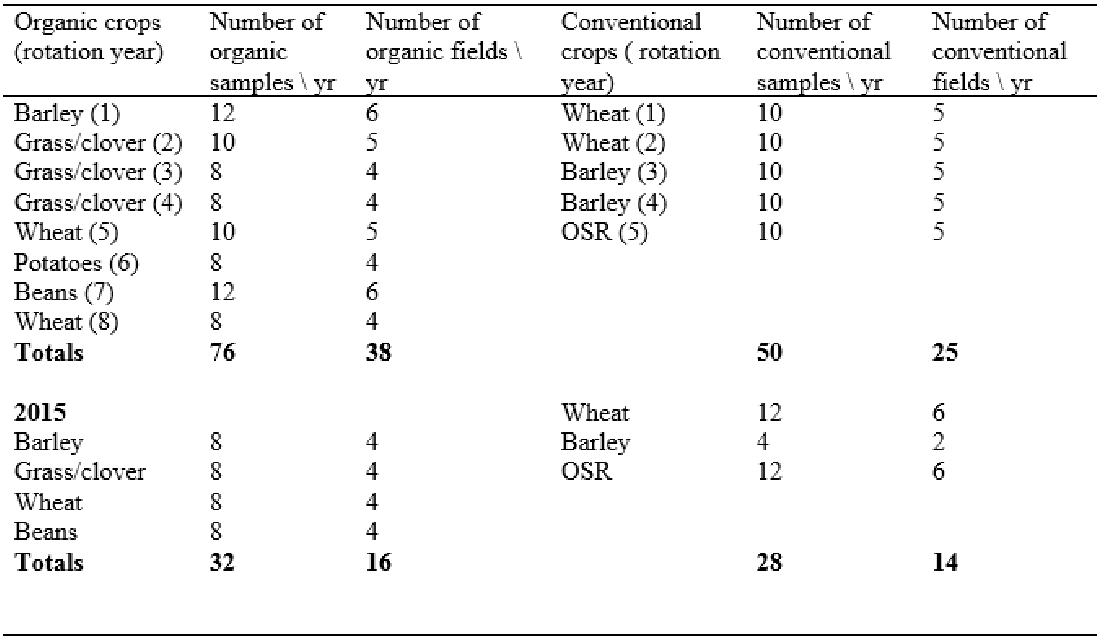
The crop rotation in the conventional managed system follows a sequence of: winter wheat, winter barley and oilseed rape over a 5-year period. Figure 2.2. Conventional crops are sown in the previous year autumn and provide vegetative cover throughout the winter seasons. The conventional system had fewer arable crops grown, with more monocotyledons (cereals: barley, wheat) than dicotyledons (oilseed rape) fields. In the conventional half of the farm, the soil is ploughed/tilled each year and herbicides, fungicides and inorganic fertiliser applied annually. Weeds are generally absent in the conventional fields. Field boundaries on the conventional half of the farm consist of short herbaceous (up to heights of 0.5 m: *Agrostis stolonifera*, *Taraxacum officinale* and fobs), tall herbaceous (up to heights of 1.5 m: *Urtica dioica*, *Cirsium arvense* and fobs*)* and woodland, mainly *Pseudotsuga menziesii*). Field boundaries are mowed annually and hedges are trimmed once or twice biannually on both the organic and conventional parts of the farm.

2.2 Sampling Methods

2.2.1 Invertebrates

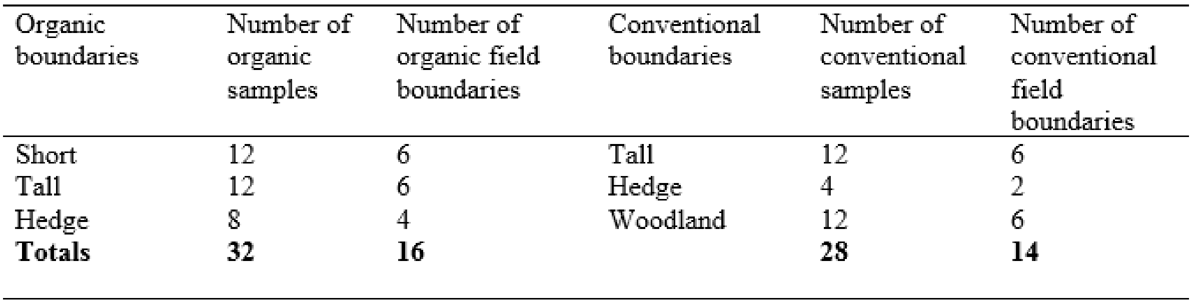
Invertebrates were sampled from both the organic and conventional systems, at two locations approximately 20 m apart within each field under study (see Table 2.1). At each location, invertebrates were collected at three points: one in the non-crop field boundary (0 m), one in the field edge 5 m from the boundary, and the third at least 40 m into the crop itself, Figure 2.3. At each sampling point, invertebrates were sampled using both pitfall traps and yellow pan traps. Pitfall traps (8.5 cm diameter, 10 cm deep clear polypropylene cups) were placed in holes made by a soil auger and placed flush with the soil surface causing minimal disturbance to the surrounding crop or weed vegetation. Invertebrates were sampled using a line of 10 pitfall traps, 0.5 m apart, plus one yellow pan trap (yellow plastic boxes 30 cm x 22 cm, 20 cm deep), containing a solution of concentrated salt (NaCl), water and three drops strong detergent (Siitonen, 1994). Materials and methods used in 2015 invertebrate sampling were similar to protocols used by Dr M.D. Eyre sampling between 2005 and 2012 for consistency. Pitfall traps are a standard method for recording epigeal (surface-active) invertebrates whilst pan traps are useful to sample aerial or foliar invertebrates, both groups being important in agroecosystems (Duelli and Obrist, 2003). Pitfall and pan traps were placed in the fields at the beginning of May, (traps were temporarily removed when required during silage cuts) and samples were collected from 2005 to 2012 and 2015.

Five monthly samples were collected from each field site, following the protocols described in Eyre *et al.* (2013b). Both pitfall and yellow pan traps were emptied and replaced with new salt solution mixture monthly to aid preservation of invertebrates. A total of 108 organic, 78 conventional sites were sampled between 2005 - 2012 rotation years and 2015 (Table 2.1). The major field boundary categories for the 32 samples (organic) and 28 samples (conventional) collected in 2015 are summarised in Table 2.2. See Figure 2.4 for a schematic outline of the study design.



Organic crops (rotation year)	Number of organic samples \ yr	Number of organic fields \ yr	Conventional crops (rotation year)	Number of conventional samples \ yr	Number of conventional fields \ yr
Barley (1)	12	6	Wheat (1)	10	5
Grass/clover (2)	10	5	Wheat (2)	10	5
Grass/clover (3)	8	4	Barley (3)	10	5
Grass/clover (4)	8	4	Barley (4)	10	5
Wheat (5)	10	5	OSR (5)	10	5
Potatoes (6)	8	4			
Beans (7)	12	6			
Wheat (8)	8	4			
Totals	**76**	**38**		**50**	**25**
2015			Wheat	12	6
Barley	8	4	Barley	4	2
Grass/clover	8	4	OSR	12	6
Wheat	8	4			
Beans	8	4			
Totals	**32**	**16**		**28**	**14**

Table 2.1 Total number of samples, aggregated across all months, collected per crop per year, and number of fields sampled per year, between 2005 to 2012 and in 2015 on the organic and conventional rotations at of Nafferton farm.



Organic boundaries	Number of organic samples	Number of organic field boundaries	Conventional boundaries	Number of conventional samples	Number of conventional field boundaries
Short	12	6	Tall	12	6
Tall	12	6	Hedge	4	2
Hedge	8	4	Woodland	12	6
Totals	**32**	**16**		**28**	**14**

Table 2.2 Total number of samples, aggregated across all months, and number of fields boundaries sampled in 2015 on the organic and conventional halves of Nafferton farm.

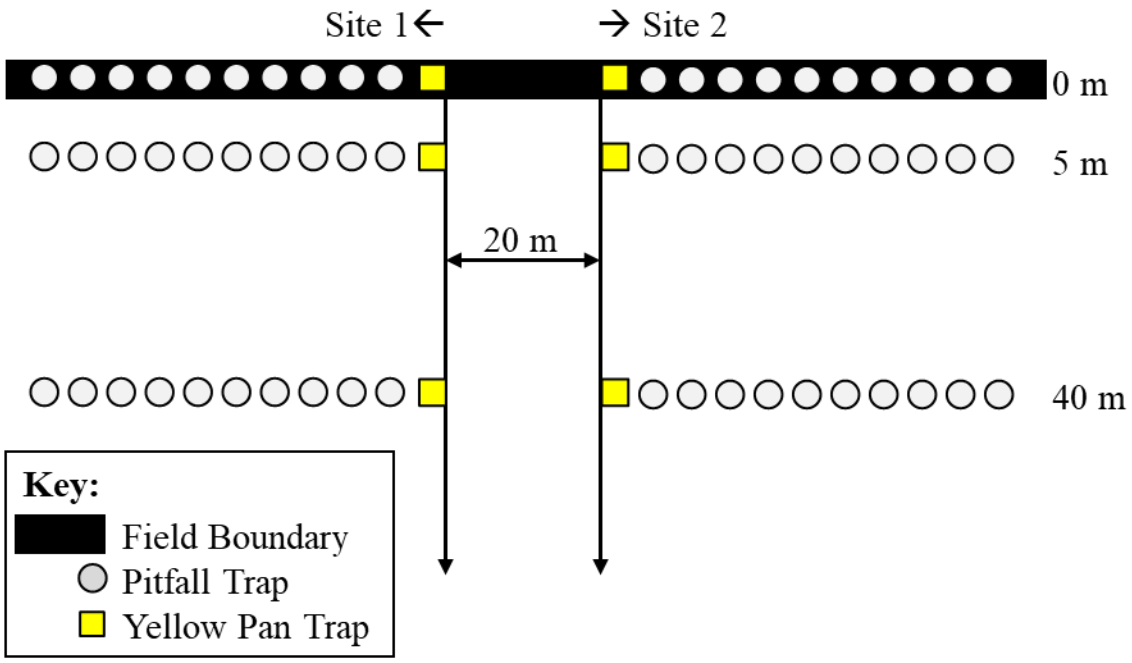


Figure 2.3 Basic layout of sampling sites at Nafferton farm

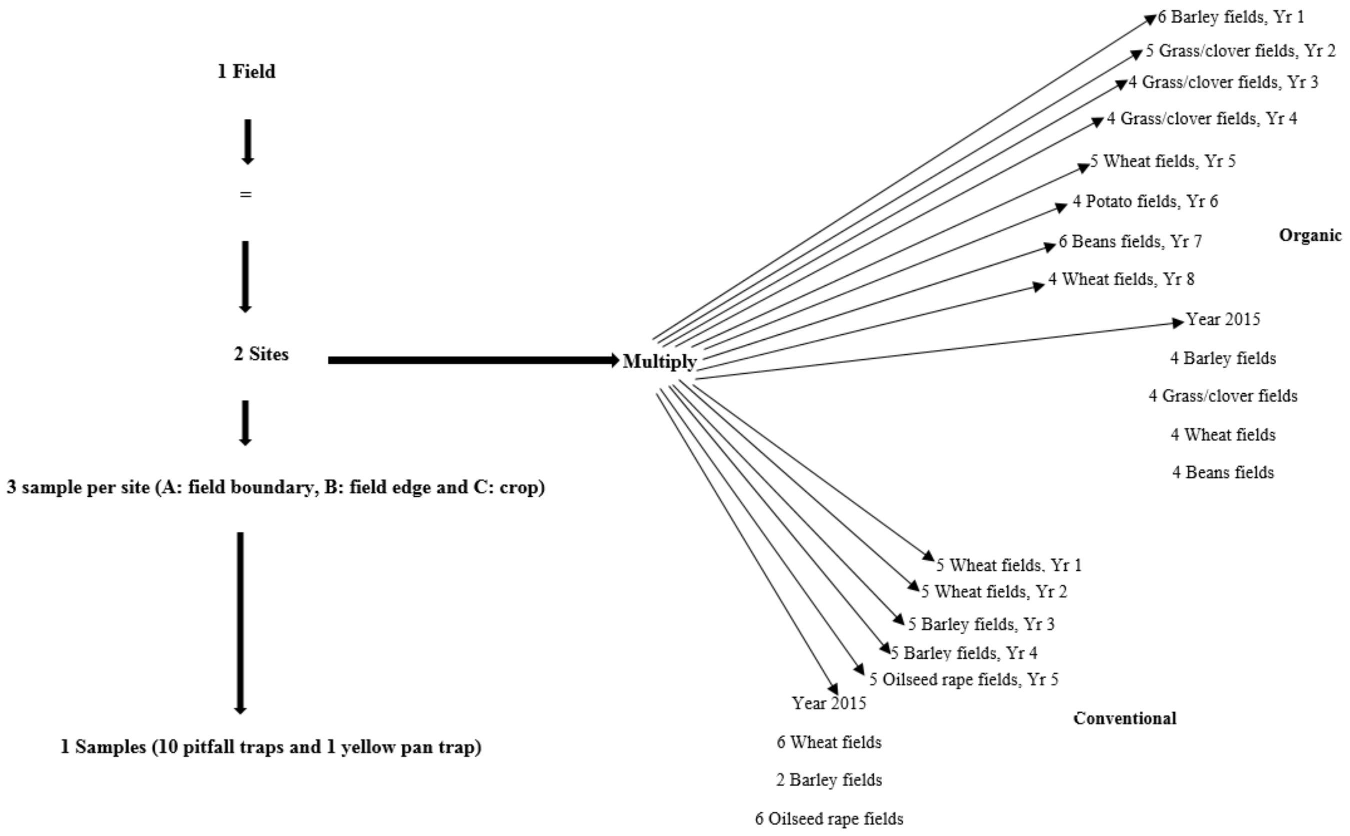


Figure 2.4 Schematic outline of invertebrate sampling at Nafferton farm from 2005 to 2012 and 2015.

All sampled invertebrate specimen were pre-sorted and stored in 70 % industrial methylated spirit (IMS) prior to identification. Invertebrates were identified to family, sub-family and tribe, according to Chinery (1993); Roberts (2001); Luff (2007) and confirmed by expert entomologist Dr M.D. Eyre, depending on functional group, and counted. Most individual research studies into invertebrates of agroecosystems have focussed on a small number of taxonomic groups (e.g. a single order or family), but identifying all specimens to species-level. For example Diekötter *et al.* (2010) studied 5 broad groups (Carabidae, Araneae, Collembola, Diplopoda, Oniscidea), whilst Rösch *et al.* (2015) studied 3 groups of invertebrates (Heteroptera, Auchenorrhyncha, Gastropoda-snails), all identified to species-level. Whilst this provides high taxonomic resolution for one family or order, it does not provide an adequate representation of the wide range of invertebrates present, with contrasting life-histories, within an agroecosystem. The main limitation on the use of a broad range of invertebrate species is not sampling *per se* but the time, technical ability and cost required to identify the considerable number of species sampled, together with taxonomical complexity in a number of groups (e.g. parasitic Hymenoptera). This has led to the advocacy of identification to higher taxonomic rank, for example, family or subfamily, rather than genus and species in agroecosystem research (Báldi, 2003). Broader taxonomic classification levels have therefore been used to assess biodiversity in landscape (Sauberer *et al.*, 2004) and land use studies (Biaggini *et al.*, 2007).

Three functional groups were defined for the purposes of this research: epigeal predators (23), foliar predators/parasitoids (18) and herbivores/pollinators (Table 2.3). This method of division into broad functional groups has been used in previous similar studies Ford *et al.* (2013) and Witmer *et al.* (2003); some functional groups are preferentially sampled by particular methods, whilst all three have important roles within the agroecosystem. Note that some invertebrates do not fit neatly into a single functional group (e.g. some Syrphidae have predacious larvae but nectar-feeding adults etc.) but allocation was based on the adult life-stage as this was the stage identified in the study. Groups were identified to family, sub-family or tribe based on previous similar research. Tribe-level is recommended by Luff and Turner (2007) and Arnett Jr and Thomas (2001) for Carabidae, whilst family-level in the taxonomic hierarchy has been recommended in previous similar research (Woodcock *et al.*, 2005b). Collembola abundance at each site was tallied, and was used generally as a bio-indicator to help explain collembolan-feeders trends (Magoba and Samways, 2012).

Mean air temperature per month and total monthly rainfall were calculated from data collected via the Delta-T Weather Station (Type WS01) located at Nafferton for each year in this study Table 2.4.

Epigeal predators (n=23)	**Foliar predators/parasitoids (n-18)**	**Herbivores/pollinators (n=25)**
Carabidae	Cantharidae	Anthicidae
Bembidini	Cerambycidae	Apionidae
Carabini	Coccinellidae	Byrrhidae
Cychrini	Anthocoridae	Elateridae
Elaphrini	Nabidae	Lathridiidae
Harpalini	Pentatomidae	Leiodidae
Lebiini	Conopidae	Melyridae
Loricerini	Syrphidae	Nitidulidae
Lucanidae	Forficulidae	Alticinae
Nebriini	Chrysopidae	Chrysomelinae
Notiophilini	Hemerobiidae	Criocerinae
Platynini	Panorpidae	Galerucellinae
Pterostichini	Vespidae	Ceuthorhynchinae
Scaritini	Braconidae	Entiminae
Sphodrini	Ichneumonidae	Molytinae
Trechini	Platygasteridae	Scolytinae
Zabrini	Proctotrupidae	Lygaeidae
Staphylinindae	Pteromalidae	Miridae
Aleocharinae		Saldidae
Omalinae		Cercopidae
Oxytelinae		Cicadellidae
Paederinae		Delphacidae
Staphylininae		Apidae
Steninae		Cynipidae
Tachyporinae		Tenthredididae

Table 2.3 List of taxa for the three functional groups sampled at Nafferton Farm.

Year	Total rainfall (mm)	Average temperature °C
2005	233	13.16
2006	247	14.04
2007	297	12.61
2008	443	12.98
2009	316	13.31
2010	185.2	12.65
2011	205.2	12.5
2012	238.5	13.89
2015	350	12.4

Table 2.4 The total rainfall and mean temperature recorded over the eight year sampling period at Nafferton fam from 2005 to 2012 and 2015.

2.2.2 Vegetation sampling

Plant species composition (cover) and structure are both reported to affect invertebrate communities (Lassau *et al.*, 2005; Schaffers *et al.*, 2008) and were therefore recorded. Plant community composition within the organic and conventional sample sites were assessed over the summer, (mid-July 2015), using 86 quadrats. Quadrats (1 m^2) were placed adjacent to each invertebrate sample at 0 m, 5 m, and 40 m from the field boundaries. From these quadrats, the percentage cover of all vascular plants and bryophytes was estimated by eye and confirmed by an independent sampler. Cover was estimated to the nearest 5%, or 1% for rare species. Where vegetation layers overlapped within in a quadrat the percentage cover exceeds 100%. Plants were identified to species according to Hubbard (1954), Grasses and wildflowers: A guide to their structure, identification, uses and distribution in the British Isles; Rose (1981), The Wild Flower Key: British Isles-N.W. Europe.

Vegetation structure was measured at all invertebrate sample sites, with the aid of a 1.4m height x 7cm diameter wooden pole with height intervals marked every 5cm. This was placed in the centre of each quadrat and all vegetation touching the pole was recorded including species and height interval at which the touch occurred.

2.2.3 Plant traits

On completion of the vegetation survey, a list of the major plant traits was generated using the scheme outlined in (Grime, 1974; Grime, 1988; Hodgson *et al.*, 1995). Grime's scheme provides plant trait data based on life history, established strategies, life form, canopy structure and height, lateral spread, leaf phenology, flowering time, regenerative strategies and seed bank Table 2.5.

Trait type	**Defined traits**	**Code**
Life History	**1. Annual**	**Lh_annu**
Established strategy	**2. Perennial**	**Lh_pere**
	1. Competitor	**Es_comp**
	2. Ruderal	**Es_rude**
	3. Stress Tolerator	**Es_stre_tol**
Life-form	1. Chamaephyte (buds > 250 mm above soil)	Lf_cham
	2. Hemicryptophyte (buds at soil level)	Lf_hemi
	3. Therophyte (seeds in unfavorable season)	Lf_ther
Canopy structure	1. Rosette	Cs_rose
	2. Semi-rosette	Cs_semi_ros
	3. Leafy	Cs_leaf
Canopy height	1. Foliage < 100 mm	Ch_<100mm
	2. 101-599 mm	Ch_101-599 mm
	3. 600 mm or more	Ch_>600 mm
Lateral spread	1.Therophytes, spread limited	Ls_ther
	2. Rhizomes or tussocks to 250 mm diameter	Ls_rhiz
	3. Tussocks > 250 mm diameter	Ls_tuss
Leaf phenology	1. Seasonal canopy	Lp_seas
	2. Evergreen canopy	Lp_ever
Flowering time	1. March/April	Ft_March/April
	2. May	Ft_May
	3. June	Ft_June
	4. July	Ft_July
Regenerative strategies	1. Vegetative	Rs_vege
	2. Seed bank	Rs_seed_bank
	3. Wind dispersal	Rs_wind
Seed bank	1. Rapid germination	Sb_rapi_germ
	2. Limited persistence in soil	Sb_limi_soil
	3. Long-term persistent seed bank in soil	Sb_long_soil

Table 2.5 Plant trait variables used to describe CCA ecological functioning in organic and conventional analyses with reference to Grime (1974); Grime (1988). Bolded traits were used in CCA community composition whilst the remainder in variation partitioning analyses (VP).

2.3 . Data analysis

2.3.1 Linear models (LM) and Linear Mixed -effects models (LME)

Linear models (LM) provided a simple method of comparing e.g. invertebrate abundance in all samples in the organic vs conventional parts of the farm. Linear models are equivalent to one-way analysis of variance (with one categorical explanatory variable), and *post hoc* test such as TukeyHSD can be used to compare different levels within the categorical explanatory variable if it contains 3 or more levels. Linear models were used in Chapter 4 to provide a broad initial overview of the effects of farm management system, crop type or boundary across the whole farm. Combined analyses of whole-farm datasets via LM indicated major differences between the organic and conventional invertebrate abundance, their separate analyses on each farm system were also undertaken in some chapters.

Mixed-effects models (Pinheiro and Bates, 2000) differ from conventional linear models in that they partial the variation into fixed-effects (e.g. organic vs conventional, different crops), and random effects (e.g. year of survey, temperature, rainfall, boundary type), thus improving their statistical power. The aim of the linear mixed-effects models (LME) was to determine the role of farming system or crop type on overall invertebrate abundance, having corrected for variability associated with temperature, rainfall, field boundary type and year of survey.

Invertebrate counts were transformed by log10(n + 1) in similar way to (Crawley, 2007; Ives, 2015) to stabilize the variance and to reduce the influence of extreme values; invertebrate data are often zero-inflated, and count-based. These analyses were undertaken in R environment, version 2.12.1 (Pinheiro *et al.*, 2011b).

2.3.2 Canonical Correspondence analysis (CCA) and Partial Canonical Correspondence analysis (pCCA)

A wide range of multivariate methods are now available to ecologists to compare the community composition of different samples. Here the aim is to analyse multiple species simultaneously, and measure changes in the relative contribution of species between samples. Unconstrained ordination methods utilise only the species data, with principal components analysis (PCA) and correspondence analysis (CA) amongst the most widely used. PCA is a 'linear' technique, suited for when there is relatively low species 'turnover' between samples. PCA transform and plot response data to find new coordinates to determine the principle axes of variation. CA is more widely used in ecological studies, as it assumes a 'unimodal' variation in species abundances, characteristic of sparse datasets with a few common species and many rare ones. In both PCA and CA, results are typically summarised by ordination plots for samples or species. In samples ordination plots, samples close to each other have relatively similar species composition, whilst those far apart are dissimilar in species composition. Likewise, in species ordination plots, species close together in ordination space are found in similar samples. See Gower (1987) for an overview of ordination techniques.

Constrained ordination methods incorporate explanatory environmental variables into the analysis with ordination axes scores forming linear combinations of the predictors (environmental variables). The most widely used method amongst ecologists is canonical correspondence analysis (CCA) which like CA assumes a unimodal species response curve (ter Braak, 1986; Ter Braak and Prentice, 1988). Both continuous (e.g. temperature, rainfall) and categorical (e.g. crop type) variables can be used as constraints in CCA. The result are displayed via biplots with continuous variables displayed by arrows and categorical variables using centroids (points). Like PCA or CA, sample scores plotted close together have similar species composition in common whilst scores far apart have dissimilar composition. The longer a biplot arrow from the origin, the more important the environmental variable is in determining the species composition of the samples, and similarly for centroids, whilst short arrows are less important. In addition, arrows pointing in the same direction suggest positive correlation between the environmental constraints, whilst arrows pointing in opposite directions are negatively correlated to each other. Finally arrows at 90° in relation to each other are considered uncorrelated. The statistical significance of the environmental variables can be determined via permutation tests.

Partial canonical correspondence analysis (pCCA) is performed in a similar manner as CCA, however the effects of confounding variables are removed or "partialled out" in the analysis so that the analysis can focus on the primary environmental variables of interest. For example, differences in community composition as a result of the crop and boundary type can be more readily measured if potential confounding variables such as rainfall, pH, temperature etc. are partialled out. Both CCA and pCCA were carried out using the CANOCO package (Ter Braak and Smilauer, 2002) and vegan R package (Oksanen J, 2015); separate analyses were done for each of the three functional groups on both management systems.

2.3.3 Variance Partitioning (VP)

Variance partitioning (also known as variation partitioning or variance decomposition) can be used to quantify (individual taxa-environmental relationships) and / or joint effects of multiple sets of explanatory variables on community composition (see Borcard *et al.* (1992); (Dray *et al.*, 2012). The aim of these analyses was to quantify the unique and joint effects on an invertebrate community of different sets of explanatory variables, and the relative contribution of each explanatory variables and the joint effect (if any) of both. This was done using a series of CCA and separate pCCAs. This requires three separate analyses for each variance partitioning if there are two types of explanatory variables. For example, as was used in Chapter 1, see below procedures.

- CCA1: Inverts ~ Current crop + previous crop
- pCCA1: Inverts ~ Current crop + partial (Previous crop)
- pCCA2: Inverts ~ Previous crop + partial (Current crop)

In the above, the variance explained by CCA1 measures the effects of the current crop and/or previous crop; pCCA1 is the effect from only the current crop; pCCA2 is the effect from only the previous crop. VP is also used to calculate the shared (or combined) effect of both the current crop and the previous crop using the inertia (a measure of the total variance in CCA and pCCAs). This can be calculated as:

- a = pure (independent) effect of current crop = pCCA1
- b = pure (independent) effect of previous crop = pCCA2
- c = joint effect of both current crop and previous crop = CCA1 - pCCA1 - pCCA2
- d = unexplained variation = Total inertia - CCA1

The above values can then be converted into percentages for ease of interpretation by division of a, b, c, or d by the total inertial. The significance of the three individual components (a, b or c) was tested by Monte Carlo permutation tests (999 permutations); separate sets of VP analyses were done for the different functional groups on both management systems. The most important crop types that contribute to the unique effect of current or previous year's crop can be identified via Monte Carlo permutation tests, but this cannot be done reliably for the joint effect (Buttigieg and Ramette, 2014).

To calculate VP for an analysis containing three explanatory variables, a more complex series of CCAs and pCCAs needed to be done. This method of calculation via three explanatory variables were used in Chapter 6. VP results can readily be displayed as table or Venn's diagram (Cushman and McGarigal, 2002) for ease of interpretation, with two circles (not drawn to scale) representing the current or previous crop, placed within an enclosing rectangle. The larger the area of the circle, the more important is that variable in explaining variation within the invertebrate community. Where the circles representing the current and previous crop overlap, this indicates the joint effect of both variables on the invertebrate community. The area outside of the circles within the enclosing rectangle represents the unexplained variation. In this thesis however, due to the complexity of some of the VP analyses, results were presented in tables for clarity.

Chapter 3. Invertebrate life-histories and the relationships between invertebrates in the boundary, field edge and crop

3.1 Abstract

Agricultural intensification has led to a reduction of field boundaries, but how boundary habitats, and invertebrates within them, affect invertebrates in the field edge and crop is unclear. We assessed the effects of boundary type on the abundance of the ten most common taxa in the boundaries (in three functional groups: epigeal predators; foliar predators / parasitoids; herbivores / pollinators). Boundary types were short and tall grassland, hedgerow and woodland. Sampling was by pitfall traps and pan traps in the field boundary (0 m) and field edge (5 m) and crop (40 m). Multiple generalized linear models (via mvabund) were used to directly assess the effects of boundary habitat type on individual taxa within the boundaries. Relationships between boundary taxa and the same taxa in the field edge or crop were assessed with a combination of partial CCA and Procrustes analyses. These latter analyses were also used to assess whether the relationships between boundary and field edge or crop taxa differed according to boundary habitat type, or amongst individual taxa.

Analysis of taxa via mvabund indicated that epigeal predators were most responsive to boundary habitat type, often being most abundant in hedgerows or along woodlands. In the organic system, whilst some taxa showed a response to boundary type, patterns were less consistent. Under both management systems, pCCA plus Procrustes indicated stronger associations between the boundary invertebrates and those in the field edge (5 m) than in the crop (40m). The relationship between boundary and field edge invertebrates was particularly strong for epigeal predators in the conventional system with hedgerow boundaries. Univoltine taxa with moderate dispersal abilities (in epigeal predators and foliar predators / parasitoids) also showed stronger links between abundance in boundary and field edge, but no consistent patterns with life-history traits were found for herbivores / pollinators.

3.2 Introduction

There has been a big change in the UK over the past 50 years towards larger fields, fewer hedgerows and mechanical management of hedgerows (thin, open hedges, rather than traditional 'layered' dense hedgerows). This has resulted in decreased biodiversity as a result of fragmented semi-natural habitats, and a more homogeneous landscape in part due to an increase in field size (Brooks *et al.*, 2012; Teja *et al.*, 2012). Consequently, European governments have established agricultural environmental schemes in order to help mitigate the biodiversity loss (Jenni *et al.*, 2014).

In a broader context, field boundaries provides shelter, food source, breeding sites and overwintering habitats (Denys and Tscharntke, 2002; Wamser *et al.*, 2011). The ability of field boundaries and associated invertebrate communities to influence neighboring invertebrates in crops (field edge - 5m or crop centre - 40m) can however be affected by herbicides and fertilizer drifts (Aude *et al.*, 2004). Moreover, relatively undisturbed perennial grassland boundaries tend to maintain higher invertebrate abundance of natural enemies (Collins *et al.*, 2003). The influence of “field boundary habitats”, has led to the investigation of invertebrate movement between crops and field boundaries and *vice versa*, assessed with Coccinellids (Rand and Louda, 2006) and parasitic wasps (Macfadyen and Muller, 2013). See reviews by Rand *et al.* (2006) and Blitzer *et al.* (2012).

At the farm-scale, studies of invertebrate habitats thought to increase invertebrate natural enemies developed from weed strips and margins (Lys, 1994; Marshall and Moonen, 2002) into the creation of ‘beetle banks’ (MacLeod *et al.*, 2004). These concepts were incorporated into agri-environment schemes (Whittingham, 2006; Aviron *et al.*, 2009), with sown field margins introduced to enhance both invertebrate and bird activity (Pywell *et al.*, 2012). However, the effectiveness of these schemes is disputed (Kleijn *et al.*, 2001; Herzog, 2005). Changes at the farm-scale have been advocated to provide more ecosystem services and to reduce the impact of agricultural intensification (Bommarco *et al.*, 2013).

The extent to which the field boundaries and their associated invertebrates affect invertebrates found in crop fields depends on their foraging distance, dispersal abilities and available food (Kremen *et al.*, 2007; Hof and Bright, 2010). For example, butterflies are able to disperse at greater distance (Zimmermann *et al.*, 2011) than carabids, which mainly disperse by walking or short flights. Smaller size ground beetle species are associated with highly managed agricultural sites (Ribera *et al.*, 2001). Plant cover and structure influences ground beetle distributions (Eyre *et al.*, 2016b), with small, flying species on arable land and larger, poorer-flying species after conversion to willow with a preference for less disturbed habitats.

Holland *et al.* (2005) advocated studies of arthropod communities across different habitats in agroecosystems; they noted that most studies were based on single field, crop and primarily Carabidae, but that a broader range of both crops / habitats and taxa should be studied. This chapter addresses this issue through a study of a wide range of invertebrate taxa in field boundaries, field edge, and a variety of crops under both organic and conventional management. The primary aims are to:

1) Field boundary types can influence the composition of the most abundant taxa in the field boundary
2) The relationship between the invertebrate taxa in the field boundary with similar taxa in field edge (5 m) and crops (40 m) is affected by the type of field boundary
3) Differences in the relative abundance of field boundary taxa at 5 m or 40 m is related to their life history

Unlike previous chapters, the analyses describes in this chapter focus primarily on the ten most abundant taxa in the field boundaries, and relate these to the same taxa in the field edge and crop.

3.3 Methods and Materials

3.3.1 Study area and management

Research was conducted at Nafferton Farm, Newcastle university teaching and research commercial farm in northern England, Northumberland, UK in 2015. Full details of the farm and invertebrate sampling methods are provided in Chapter 2, section 2.1.1. Invertebrates were identified to family, sub-family and tribe, according to Chinery (1993); Roberts (2001); Luff (2007) and confirmed by expert entomologist Dr M.D. Eyre, depending on functional group, and counted. A detailed account of sampling sites can be found in Table 2.1 and Table 2.2, whilst Figure 2.3 and Figure 2.4 provides a practical outline.

3.3.2 Life history traits (dispersal potential)

Four important life history traits that best represent morphology and behaviour were collated for individual taxa. For the body length (small (<5 mm), medium (5-9 mm) and large (>10 mm); locomotion (generally fly, generally crawl); dispersal potential (short distance (<10 m), medium (1- 100 m), long (>101); voltinism (one generation per year), (> one generation per year). Invertebrate trait data were obtained from multiple peer-reviewed literature, especially den Boer (1977); Forsythe (1983); Castella and Speight (1996); Schweiger *et al.* (2005); Tauber *et al.* (2009); Katharina *et al.* (2014); Amici *et al.* (2015); Carola *et al.* (2015) and expert advice (Dr M.D. Eyre).

3.4 Data Analyses

Data analyses were restricted to the 10 most abundant taxa within each of the three functional groups that were sampled in the field boundaries in each management system. In all three functional groups in both farm management systems the top 10 taxa in the boundaries comprised more than 95% of individuals sampled. The relative abundance of these same taxa in the field edge and crop were compared to those in the boundaries for further analysis.

3.4.1 Aim 1: Changes in invertebrate abundance as a result of the type of field boundary

The manyglm function from the R package mvabund (Yi *et al.*, 2012) was used to determine the relationship between taxa abundance and field boundary type. The manyglm function fits separate univariate, generalized linear models to the abundance of each taxon (response) to the boundary habitat type (explanatory) taking into account the possible correlations between the taxa. It is particularly useful where the variance is relatively low for an individual taxon, or the data are sparse (Alistair *et al.*, 2000). Initially the Poisson error model was used for the analysis, but as this was over-dispersed (probably due to the sparse data) a negative-binomial distribution was used. Likelihood ratio tests (LRT) are used to determine significance for each taxon via resampling (Yi *et al.*, 2012).

3.4.2 Aim *2*: Effect of field boundary type on relationships between boundary invertebrates and those in the field edge or crop

Three sets of ordinations were undertaken to characterize the composition of the most abundant invertebrates in the boundary, field margin and crop. Note that the same set of taxa in each functional group was analyzed in all three ordinations, i.e. the 10 most abundant taxa found in the boundaries. To eliminate the effects of crop type affecting invertebrate composition partial canonical correspondence (pCCA) was used, with crop type as a conditioning variable. Thus the form of the ordinations were:

Invertebrates in boundary ~ Condition (crop type)

Invertebrates in edge ~ Condition (crop type)

Invertebrates in crop ~ Condition (crop type)

Any two ordinations with the same number of sites, as in this study, can be compared via Procrustes rotation (Gower, 1975). As the name suggests, the analysis rotates and rescales the site scores in the two ordinations that are being compared until the fit between them is maximized. The relationship between them is summarized via the m^2 statistic (on a scale between 0 and 1), whose interpretation is analogous to that of a convention regression R^2 statistic. The significance of the m^2 statistic can be tested via permutation tests; we used the implementation of the 'protest' function in the R package 'vegan' (Oksanen J, 2015). The significance of overall similarity of the boundary vs field edge, and boundary vs crop invertebrate communities was assessed by comparing their pCCA scores through Procrustes tests. In addition to the overall m^2 statistic and significance test, Procrustes analysis calculates a residual for each pair of sites being compared. The size of the residuals from a Procrustes analysis indicate the degree to which the invertebrates for each pair of sites were similar. In other words, a site with small Procrustes residuals corresponds to high similarity in the invertebrate species composition between the boundary vs field edge or boundary vs crop, and *vice versa*. The Procrustes residuals for each site were summarized according to the boundary type, to determine whether boundary type had any effects on the similarity between boundary vs field or crop invertebrate communities.

3.4.3 **Aim** *3:* **Assess effects of boundary invertebrate life histories on their relative abundance in the field edge or crop**

The first part of this analysis was to make a comparison of the boundary vs field edge or crop invertebrate communities having accounted for any effects of both boundary and crop type. Therefore the separate pCCAs were expanded so that both boundary and crop type were used as partial (constraining) variables:

Invertebrates in boundary ~ Condition (boundary type) + Condition (crop type)

Invertebrates in edge ~ Condition (boundary type) + Condition (crop type)

Invertebrates in crop ~ Condition (boundary type) + Condition (crop type)

Site scores were compared as before, and the Procrustes m^2 statistic tested for significance.

It is usually not possible to investigate individual taxa via Procrustes rotation, as typically each matrix of sites x taxa being compared has different numbers of taxa present. However, in our study analyses were restricted to the same 10 taxa in all cases, which meant that the taxa pCCA scores could also be compared via Procrustes rotation. The advantage this approach is that the Procrustes residuals for individual taxa can then be extracted. Taxa with very low Procrustes residuals indicate a close correspondence in their relative abundance in the boundary vs field edge, or boundary vs crop, and *vice versa*.

3.5 Results

3.5.1 Organic management: Changes in invertebrate abundance as a result of the type of field boundary

Overall, taxa composition of epigeal predators in the organic system differed significantly between habitat types in the field boundaries that they were found in (LRT=85.92, P=0.005 - Table 3.1). Most predatory taxa (e.g. Bembidiini and Staphylininae*)* were significantly more abundant in short grass boundaries or showed other responses to boundary type (Table 3.1 A). In contrast, the taxonomic composition of foliar predators/parasitoids did not significantly differ between the field boundaries (LRT=32.96, P=0.256 - Table 3.1 B). Overall herbivore/pollinator composition differed significantly between the field boundary habitats in the organic system (LRT=72.64, P=0.013 - Table 3.1 C). The two most abundant taxa in this group, flea beetle Alticinae and sap beetle Nitidulidae (both small size, plant or pollen feeders) were most abundant in tall grass boundaries.

Functional groups	**Totals**	**Hedge**	**Short**	**Tall**	**Boundary LRT/p-value**
A. Epigeal predators					**85.92/0.005**
Bembidiini	2807	109	520	85	**20.15/0.019**
Harpalini	248	60	23	6	**22.71/0.013**
Loricerini	232	19	29	13	3.74/0.564
Nebriini	552	34	61	40	1.21/0.936
Platynini	596	60	72	31	4.33/0.520
Pterostichini	4780	409	367	416	0.10/1.000
Zabrini	249	21	21	21	0.00/1.000
Aleocharinae	131	2	22	7	**24.02/0.011**
Staphylininae	1097	54	157	61	9.53/0.148
Tachyporinae	339	26	28	30	0.089/1.000
Total	**11031**				
B. Foliar predators/parasitoids					32.96/0.256
Braconidae	255	12	38	13	2.81/0.779
Ichneumonidae	450	46	34	37	0.649/0.972
Platygasteridae	9	1	0	1	5.61/0.533
Proctotrupidea	50	11	4	2	4.38/0.702
Pteromalidae	2	0	1	0	4.39/0.702
Forficulidae	13	1	1	2	0.65/0.972
Panorpidae	45	1	1	7	6.54/0.461
Syrphidae	46	3	3	5	0.792/0.972
Cantharidae	464	20	31	51	3.51/0.779
Coccinellidae	43	2	7	2	3.59/0.779
Total	**1377**				
C. Herbivores/pollinators					**72.64/0.013**
Alticinae	2807	15	14	43	8.62/0.353
Ceutorhynchinae	641	39	31	16	15.02/0.073
Chrysomelinae	249	17	18	13	2.51/0.829
Elateridae	188	21	8	7	7.92/0.377
Entiminae	574	21	14	17	3.60/0.829
Nitidulidae	2157	41	21	57	14.38/0.079
Cicadellidae	40	18	7	1	13.05/0.096
Miridae	68	6	4	17	3.37/0.829
Apidae	174	22	15	37	1.51/0.829
Tenthredididae	265	20	5	18	2.63/0.829
Total	**7163**				

Table 3.1 Relative abundance and mean number of individuals together with significances obtained from Mvabund analyses for, A) epigeal predators, B) foliar predators/parasitoids and C) herbivores/pollinators in the organic system.

3.5.2 Organic management: Effects of field boundary type on relationship between boundary invertebrates and those in the field edge or crop

When only crop type was partialled-out, in the organic system (Figure 3.1), Procrustes analysis revealed a significant relationship between epigeal predator assemblage in the field boundary and field edge (59%, m^2=0.648, P=0.045 - Figure 3.1 A) but not for assemblage in the crop (47%, m^2=0.778, P=0.160- Figure 3.1 B). There was a closer association in the taxonomic composition of epigeal predators in the field boundary and field edge when the field boundary comprised hedge or short grassland, but a poorer association between the communities when the boundary was tall grassland. This is indicated by the smaller Procrustes residuals for hedge and short grassland in compared to tall grassland.

Overall, foliar predator/parasitoids composition in the field boundary were not similar to those in the field edge and crop (26%, m^2=0.931, P=0.756; m^2=0.882, P=0.443 respectively) when crop type was partialled-out (Figure 3.2 A). For both field edge and crop the relationships between taxonomic compositions was best in short grass boundaries, as these had the lowest Procrustes residuals.

Procrustes analyses revealed a significant association between herbivore/pollinator assemblages in the field boundary habitats and their assemblages in field edges (63%, m^2=0.695, P=0.016) when crop type was partialled-out (Figure 3.3 A). The boundary vs field edge residuals were least with tall boundaries, suggesting a stronger association between the boundary and edge invertebrates next to that type of boundary. The relationship was non-significant further into the field (21%, m^2=0.956, P=0.814 - Figure 3.3 B). There was no obvious differences between the boundary habitats.

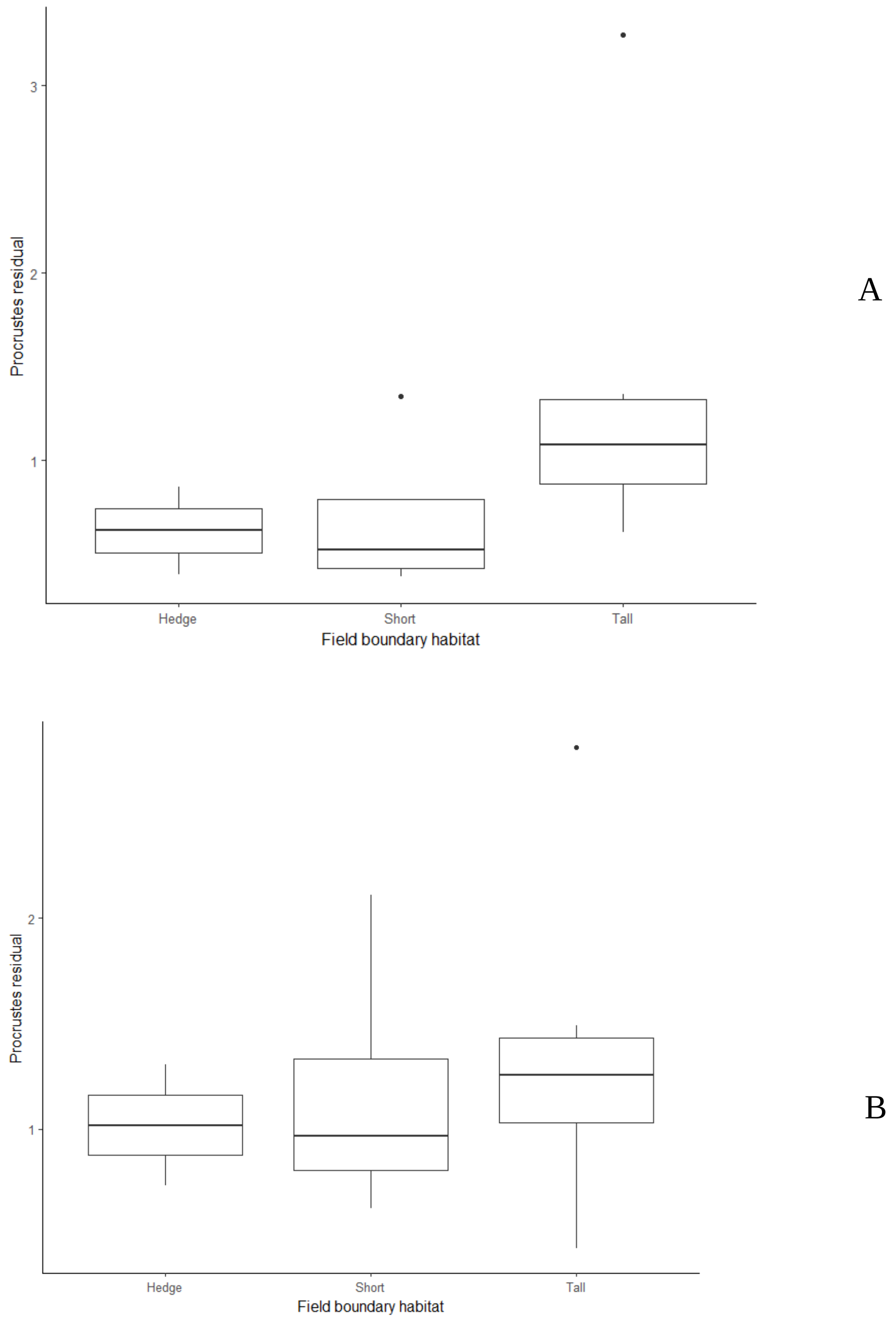


Figure 3.1 Procrustes rotation residuals plot, showing the similarities in the pCCA configuration of ten most abundant epigeal predators between: A) field boundary and field edge (59%, m^2=0.648, P=0.045); B) field boundary and crop (47%, m^2=0.778, P=0.160) in the organic system.

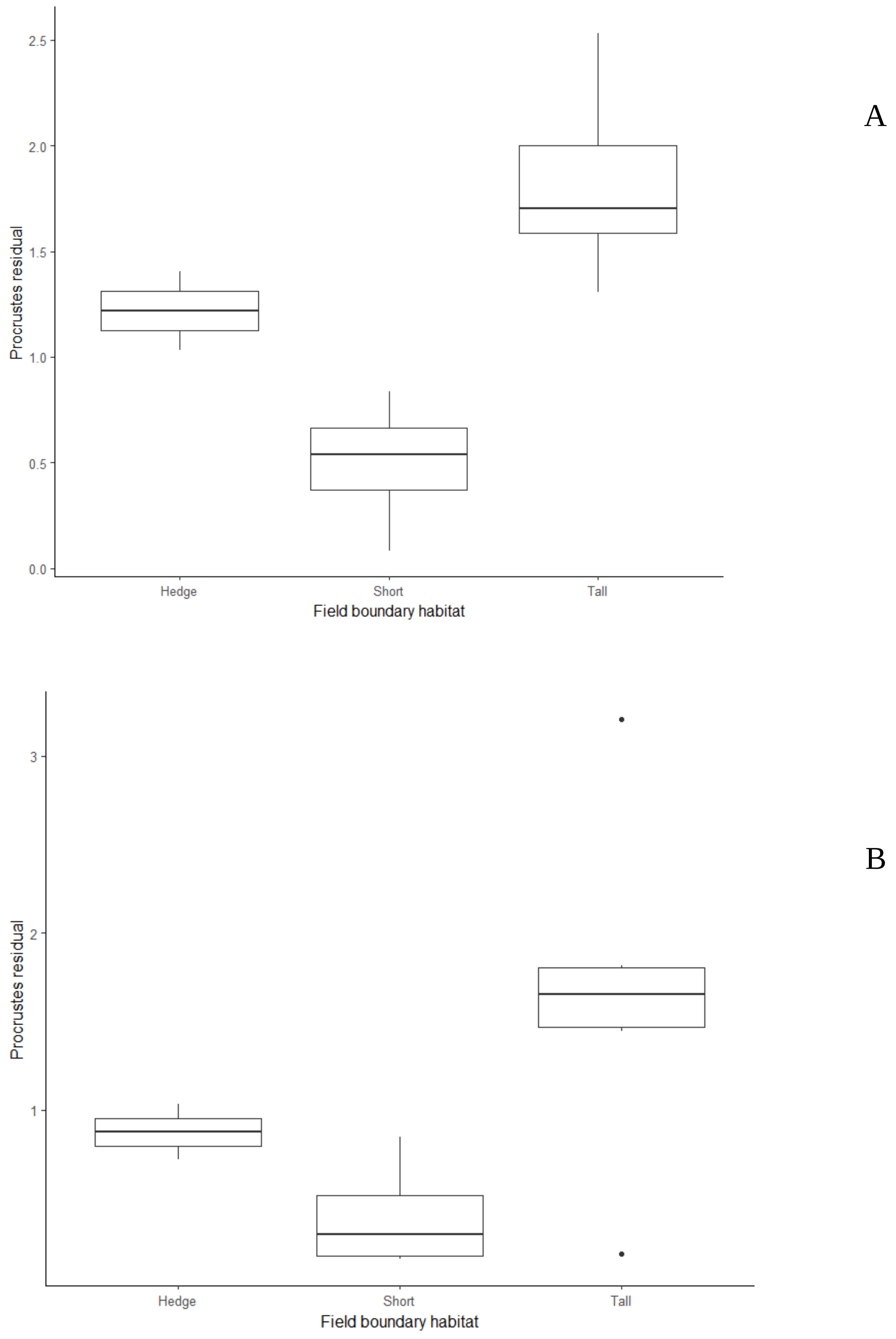


Figure 3.2 Procrustes rotation residuals plot, showing the similarities in the pCCA configuration of ten most abundant foliar predators/parasitoids between: A) field boundary and field edge (26%, m^2=0.931, P=0.756); B) field boundary and crop (34%, m^2=0.882, P=0.443) in the organic system.

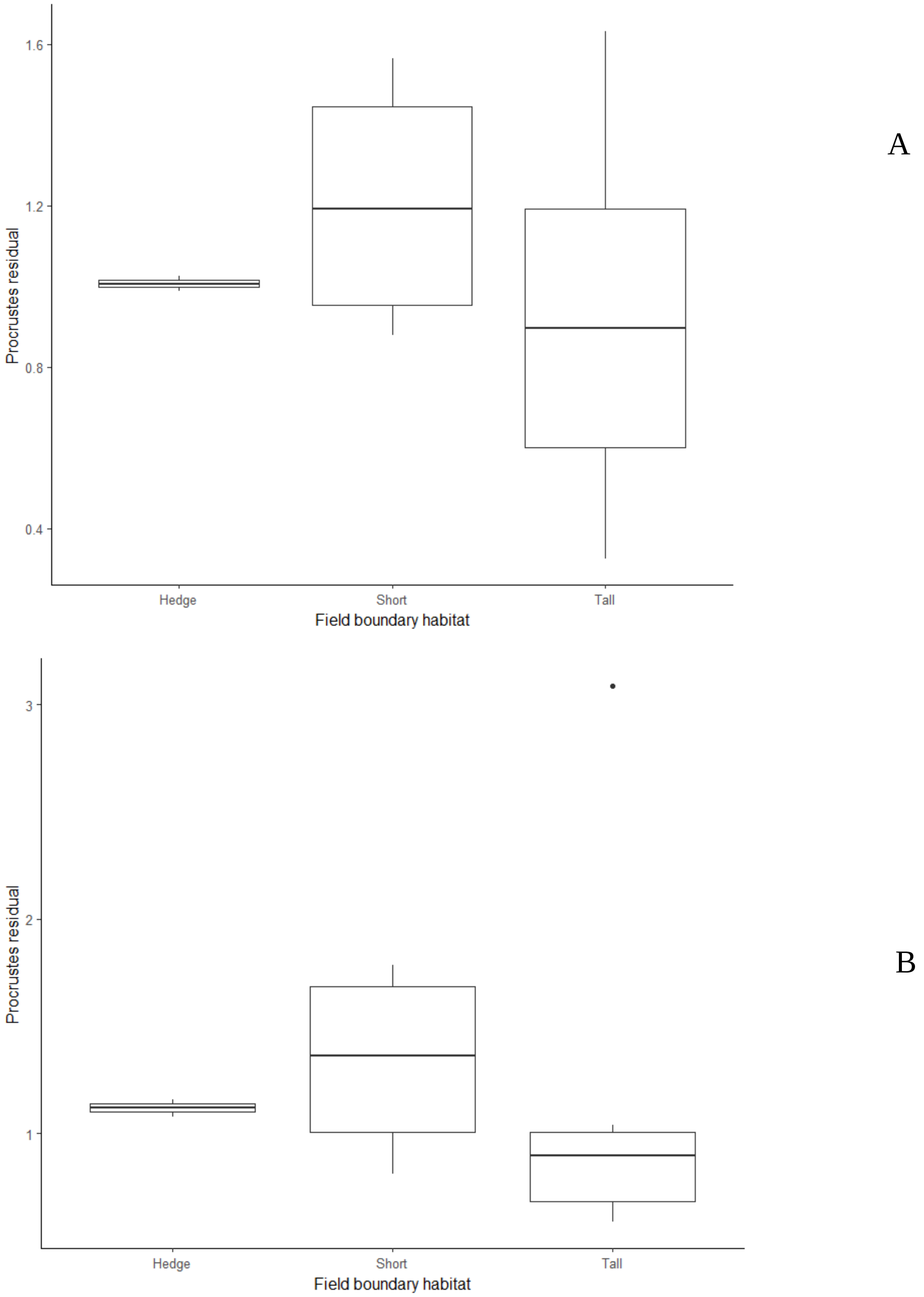


Figure 3.3 Procrustes rotation residuals plot, showing the similarities in the pCCA configuration of ten most abundant herbivores/pollinators between: A) field boundary and field edge (63%, m^2=0.597, P=0.016); B) field boundary and crop (21%, m^2=0.956, P=0.814) in the organic system.

3.5.3 Organic management: Effects of boundary invertebrate life histories on their relative abundance in the field edge or crop

Epigeal predator community composition had significant similarity between field boundary and field edge when both boundary type and crop type were partialled-out (71%, m^2=0.500, P=0.014 - Figure 3.4 A). The best fits between field boundary and field edge (lower residual scores) were observed for univoltine predatory taxa Aleocharinae and Nebriini, both relatively good flying groups. There were poorer fits (larger residuals), for large size Pterostichini and Staphylinidae between field boundary and field edge. Overall there was not a relationship between epigeal predators in the field boundary and crop (55%, m^2=0.695, P=0.087 - Figure 3.4 B). At 40 m away from the field boundary, lower residual scores were observed amongst univoltine generalist feeders Platynini and Zabrini whilst high scores was found for large univoltine Pterostichini. The most abundant taxa, Pterostichini, had high residual score in both field edge and crop.

Foliar predator/parasitoids relationships between boundary and field edge and crop are summarized in Figure 3.5. These were non-significant at both 5 m and 40 m (37%, m^2=0.863, P=0.502; 26%, m^2=0.930, P=0.625; respectively). Procrustes residuals were lower for medium size Coccinellidae at both distances see Table 3.2.

As with earlier analyses of herbivores/pollinators, when both crop and boundary type were partialled-out, significant relationships were detected between boundary and field edge communities (64%, m^2=0.596, P=0.043- Figure 3.6 A), but not 40 m into the crop (49%, m^2=0.758, P=0.166 - Figure 3.6 B). The closest relationships between the boundary and field were observed for medium size, sap feeders Ceutorhynchinae (weevils, low residual scores) whilst poor fits (high residual scores) were detected for Elateridae at both field distances see Table 3.2).

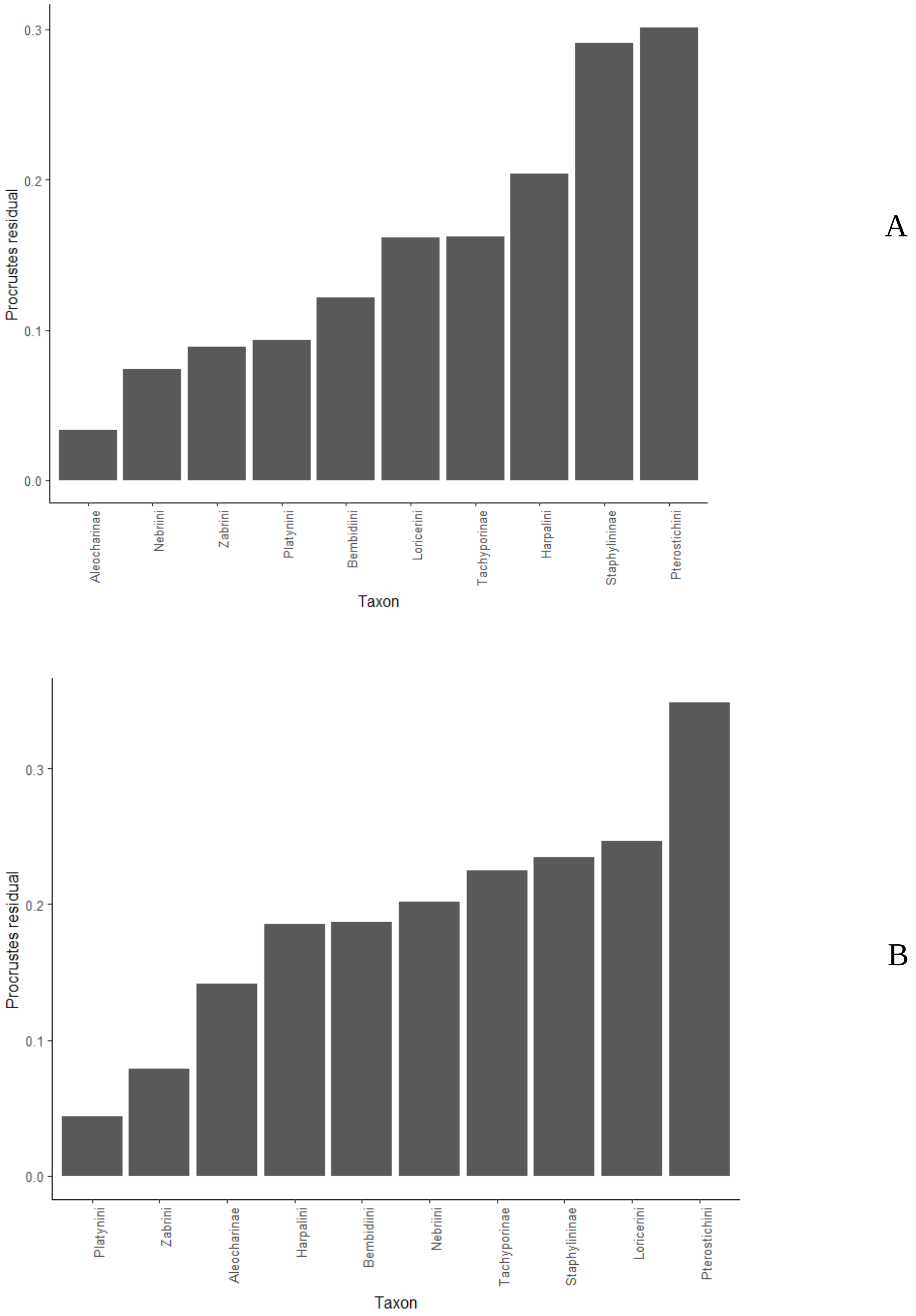


Figure 3.4 Procrustes residuals plot, showing the similarities in the pCCA configuration of ten most abundant epigeal predators between A) field boundary and crop (71%, m^2=0.500, P=0.014); B) field boundary and field center (55%, m^2=0.694, P=0.087) in the organic system.

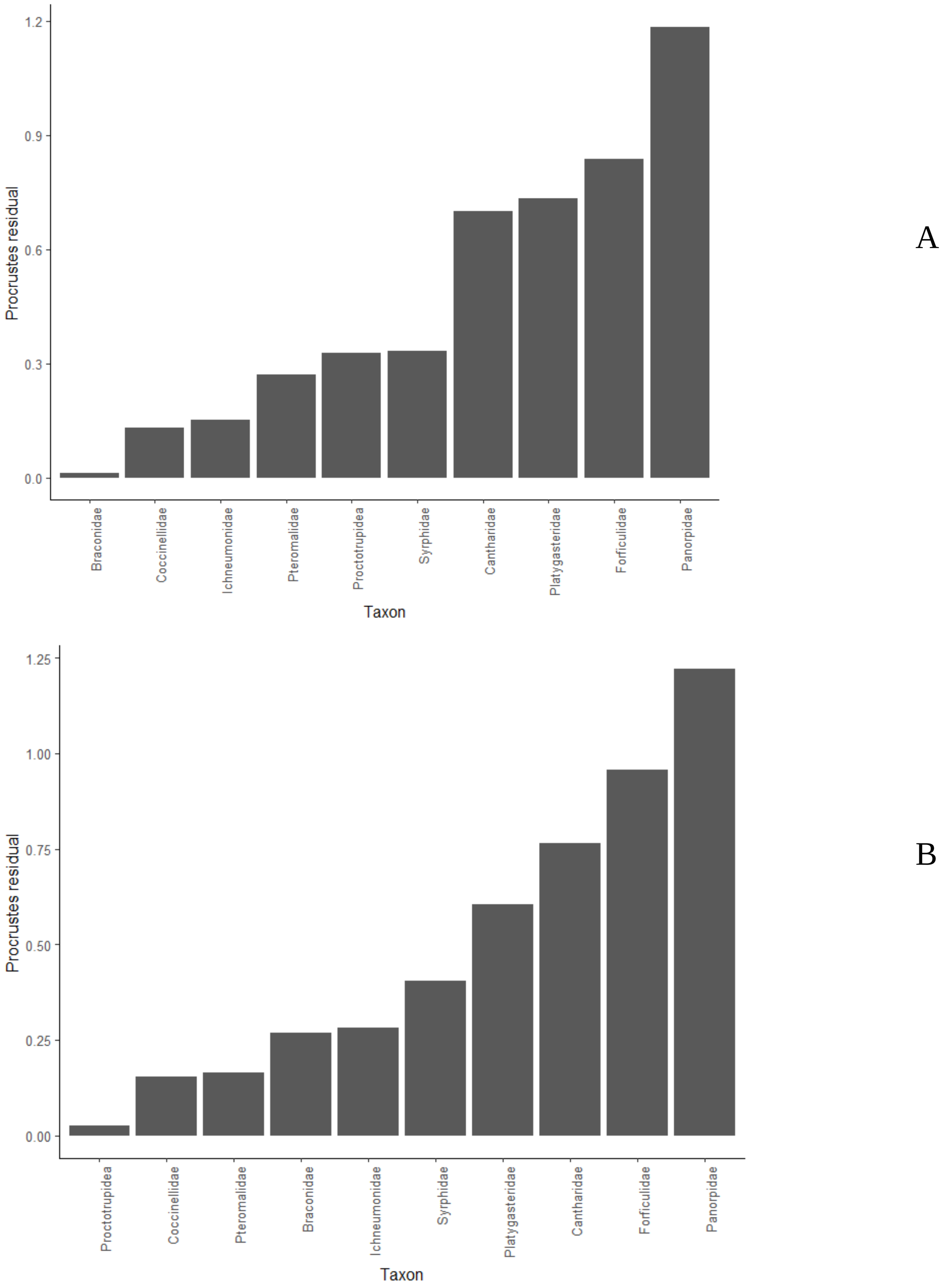


Figure 3.5 Procrustes residuals plot, showing the similarities in the pCCA configuration of ten most abundant foliar predators/parasitoids between A) field boundary and field edge (37%, m^2=0.863, P=0.502); B) field boundary and crop (26%, m^2=0.930, P=0.625) in the organic system.

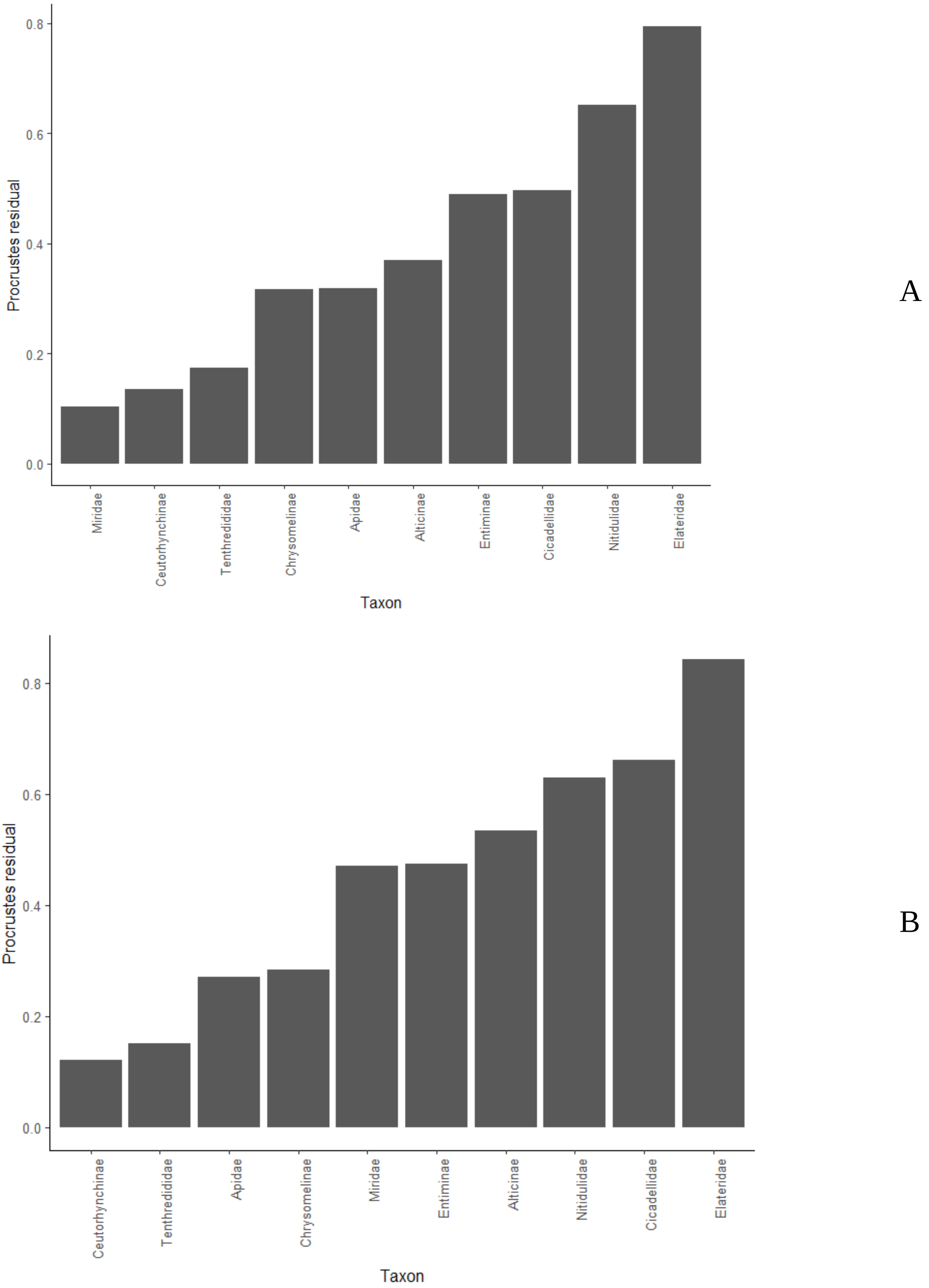


Figure 3.6 Procrustes residuals plot, showing the similarities in the pCCA configuration of ten most abundant herbivores/pollinators between A) field boundary and field edge (64%, m^2=0.596, P=0.043); B) field boundary and crop (49%, m^2=0.758, P=0.166) in the organic system.

Taxa	**Field boundary(0m)**		**Field edge(5m)**		**Crop(40m)**	
	Abundance	%	Abundance	%	Abundance	%
A. Epigeal predators						
Bembidiini	2807	25.4	2668	30.9	2415	24
Harpalini	248	2.2	123	1.4	179	1.8
Loricerini	232	2.1	298	3.4	285	2.7
Nebriini	552	5.1	286	3.3	449	4.5
Platynini	596	5.4	727	8.4	683	6.8
Pterostichini	4780	43.3	2780	32.1	3549	35.2
Zabrini	249	2.3	186	2.2	202	2
Aleocharinae	131	1.2	187	2.2	211	2.3
Staphylininae	1097	9.9	1214	14	1918	19.1
Tachyporinae	339	3.1	179	2.1	173	1.6
Total	**11031**		**8648**		**10064**	
B. Foliar predators/ parasitoids						
Braconidae	255	18.5	257	21.7	623	36.9
Ichneumonidae	450	32.7	385	32.5	545	32.3
Platygasteridae	9	0.7	6	0.5	32	1.9
Proctotrupidae	50	3.6	26	2.2	45	2.7
Pteromalidae	2	0.1	7	0.6	1	0.1
Forficulidae	13	0.9	3	0.3	2	0.1
Panorpidae	45	3.4	17	1.3	13	0.8
Syrphidae	46	3.3	41	3.4	48	2.8
Cantharidae	464	33.7	358	30.2	285	16.8
Coccinellidae	43	3.1	86	7.3	95	5.6
Total	**1377**		**1186**		**1689**	
C. Herbivores/ pollinators						
Alticinae	2807	39.2	2118	23.7	3749	32.8
Ceutorhynchinae	641	8.9	1326	14.8	1382	12.1
Chrysomelinae	249	3.5	168	1.9	125	1.1
Elateridae	188	2.6	44	0.5	18	0.2
Entiminae	574	8	609	6.8	485	4.2
Nitidulidae	2157	30.1	4046	45.2	5003	43.7
Cicadellidae	40	0.7	15	0.2	19	0.2
Miridae	68	0.9	155	1.7	302	2.5
Apidae	174	2.4	191	2.1	169	1.5
Tenthredididae	265	3.7	273	3.1	193	1.7
Total	**7163**		**8945**		**11445**	

Table 3.2 The relative abundance and percentage abundance (0m, 5m and 40m) for the three functional groups: A) epigeal predators, B) foliar predators/parasitoids and C) herbivores/pollinators in the organic system.

3.5.4 Conventional management: Changes in invertebrate abundance as a result of the type of field boundary

Overall, taxa composition of epigeal predators in the conventional system differed significantly between habitat types in the field boundaries (LRT=94.73, P=0.003 - Table 3.3). Five epigeal predators varied significantly across boundary types Notiophilini (LRT=11.62, P=0.009), Nebriini (LRT=17.06, P=0.017), Platynini (LRT=17.04, P=0.017), Zabrini (LTR=7.68, P=0.045) being most abundant along woodland boundaries. Overall foliar predator/ parasitoid abundance differed significantly between field boundary habitats (LRT=81.56, P=0.002), although there were no consistent patterns amongst taxa with regard to their life histories. Herbivores/pollinators did not significantly differ between the field boundaries in which they were sampled (LRT=2.44, P=0.103).

Functional groups	Totals	Hedge	Tall	Woodland	Boundary LRT/p-value
A. Epigeal predators					**94.73/0.003**
Bembidiini	2087	80	134	205	7.33/0.240
Loricerini	383	9	52	23	**11.59/0.050**
Nebriini	790	23	27	102	**17.06/0.017**
Notiophilini	107	3	5	13	**11.62/0.009**
Platynini	1079	16	22	155	**17.04/0.017**
Pterostichini	3896	326	134	343	2.96/0.327
Zabrini	457	17	26	48	**7.68/0.045**
Aleocharinae	158	20	7	8	5.24/0.327
Staphylininae	789	38	34	83	**9.02/0.045**
Tachyporinae	896	75	24	84	4.87/0.327
Total	**10642**				
B. Foliar predators/parasitoids					**81.56/0.002**
Braconidae	455	41	3	46	16.47/0.014
Ichneumonidae	622	71	28	38	4.79/0.611
Platygasteridae	12	2	1	1	1.06/0.878
Proctotrupidea	15	2	1	2	1.17/.0878
Pteromalidae	20	2	0	2	4.18/0.666
Forficulidae	100	1	1	16	**16.63/0.014**
Panorpidae	40	4	8	1	3.69/0.666
Syrphidae	168	4	3	24	**23.33/0.002**
Cantharidae	261	20	25	14	2.48/0.771
Coccinellidae	30	1	3	3	7.76/0.248
Total	**1723**				
C. Herbivore/pollinators					**2.44/0.103**
Alticinae	372	15	14	47	6.29/0.554
Ceutorhynchinae	376	39	31	16	2.57/0.824
Chrysomelinae	215	17	18	13	0.49/0.973
Elateridae	158	21	8	7	4.56/0.693
Entiminae	243	21	14	17	0.37/0.973
Nitidulidae	585	41	21	57	3.77/0.696
Cicadellidae	370	18	7	1	8.20/0.374
Miridae	138	6	4	17	5.76/0.597
Apidae	209	23	15	37	4.01/0.696
Tenthredididae	106	21	5	18	8.02/0.374
Total	**2772**				

Table 3.3 Relative abundance and mean number of individuals together with significances obtained from Mvabund analyses for, A) epigeal predators, B) foliar predators/parasitoids and C) herbivores/pollinators in the conventional system.

3.5.5 Conventional management: Effects of field boundary type on relationship between boundary invertebrates and those in field edge or crop

When only crop type was partialled-out (Figure 3.7), in the conventional system, Procrustes analyses revealed a significant relationships between epigeal predators assemblage in the field boundary and field edge (51%, m^2=0.743, P=0.050 - Figure 3.7 A) but not for assemblage in the crop at 40 m (39 %, m^2=0.844, P=0.259- Figure 3.7 B). There was a closer association in the taxonomic composition of epigeal predators in the field boundary and field edge when the field boundary comprised of hedge, but a poorer association between communities when the boundary was tall grassland. This was indicated by the small Procrustes residuals for hedge in compared to tall grassland.

There was a significant association between foliar predator/parasitoid assemblages in field boundaries and field edges (72 %, m^2=0.470, P<0.001 - Figure 3.8 A) but the relationship was non-significant at greater distances into crop fields (41 %, m^2=0.828, P=0.217 - Figure 3.8 B). There was a closer taxonomical association for foliar predators/parasitoids in the field boundary and field edge when field boundary comprised of tall and woodland boundaries, but poor association between communities when the boundary was hedge. However, there was no obvious differences between the boundary habitats for invertebrates common to both boundary and crop.

Overall, herbivore/pollinator composition in the field boundary were not similar to those in both field edge and crop (18 %, m^2=0.967, P=0.902; 35 %, m^2=0.875, P=0.406 respectively - Figure 3.9) when crop type was partialled-out. Nevertheless, for both field edges and crop the relationship between taxonomical composition was best in hedge boundaries, indicated by the lower Procrustes residual scores.

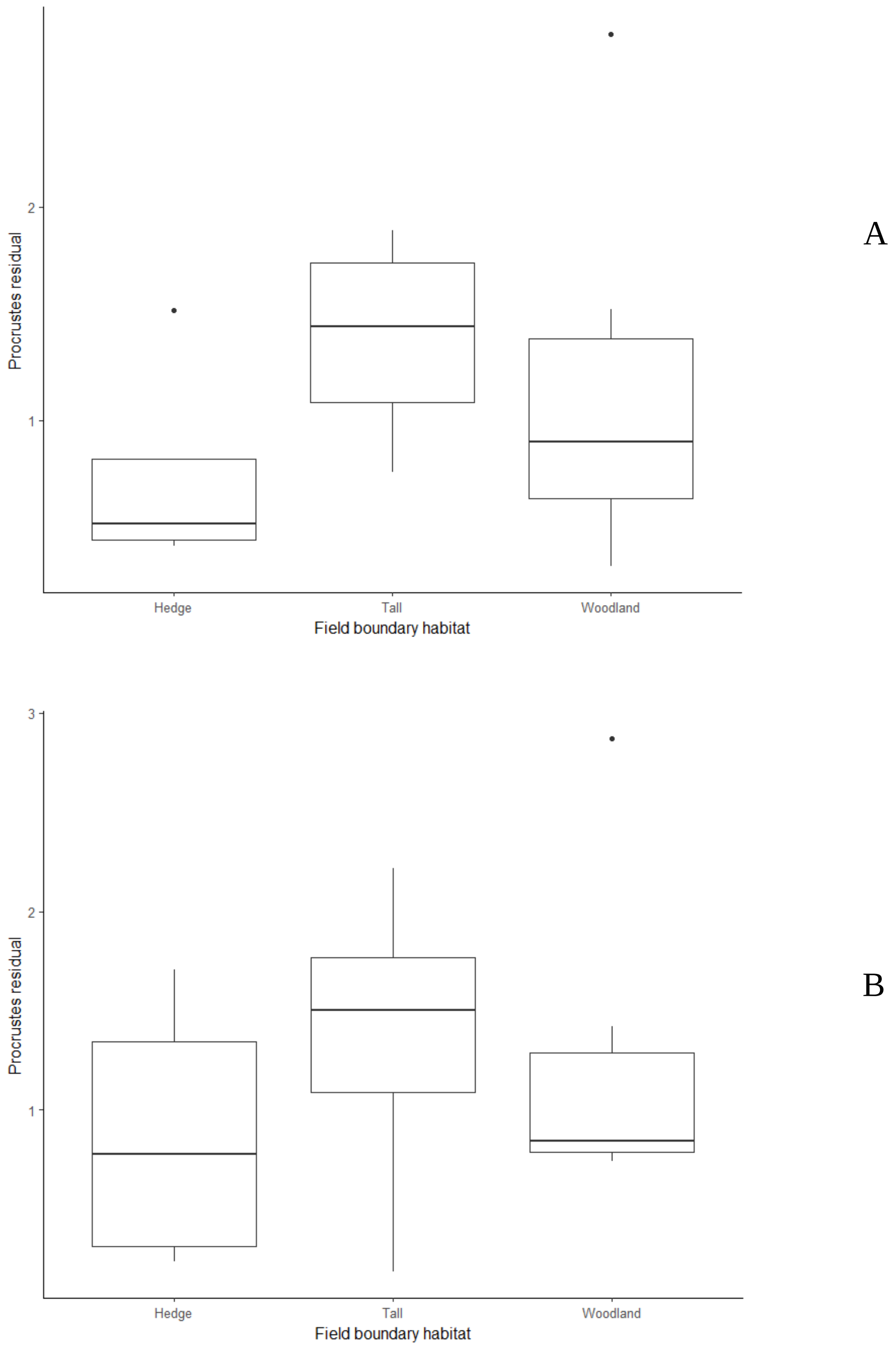


Figure 3.7 Procrustes rotation residuals plot, showing the similarities in the pCCA configuration of ten most abundant epigeal predators between: A) field boundary and field edge (51%, m^2=0.743, P=0.050); B) field boundary and crop (39%, m^2=0.844, P=0.259; Figure 2) in the conventional system.

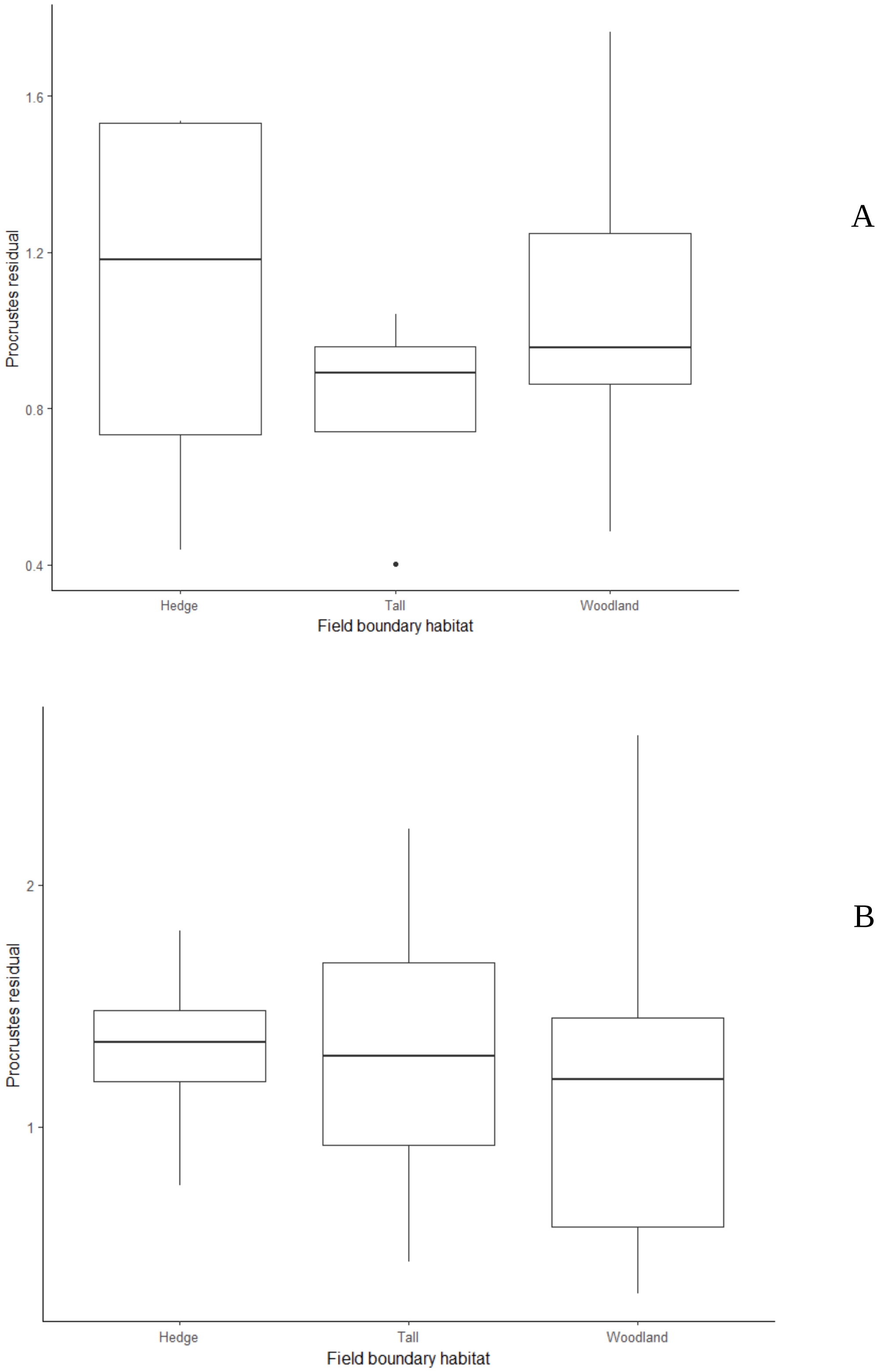


Figure 3.8 Procrustes rotation residuals plot, showing the similarities in the pCCA configuration of ten most abundant foliar predators/parasitoids between: A) field boundary and field edge (72%, m^2=0.470, P<0.001); B) field boundary and crop (41%, m^2=0.828, P=0.217) in the conventional system.

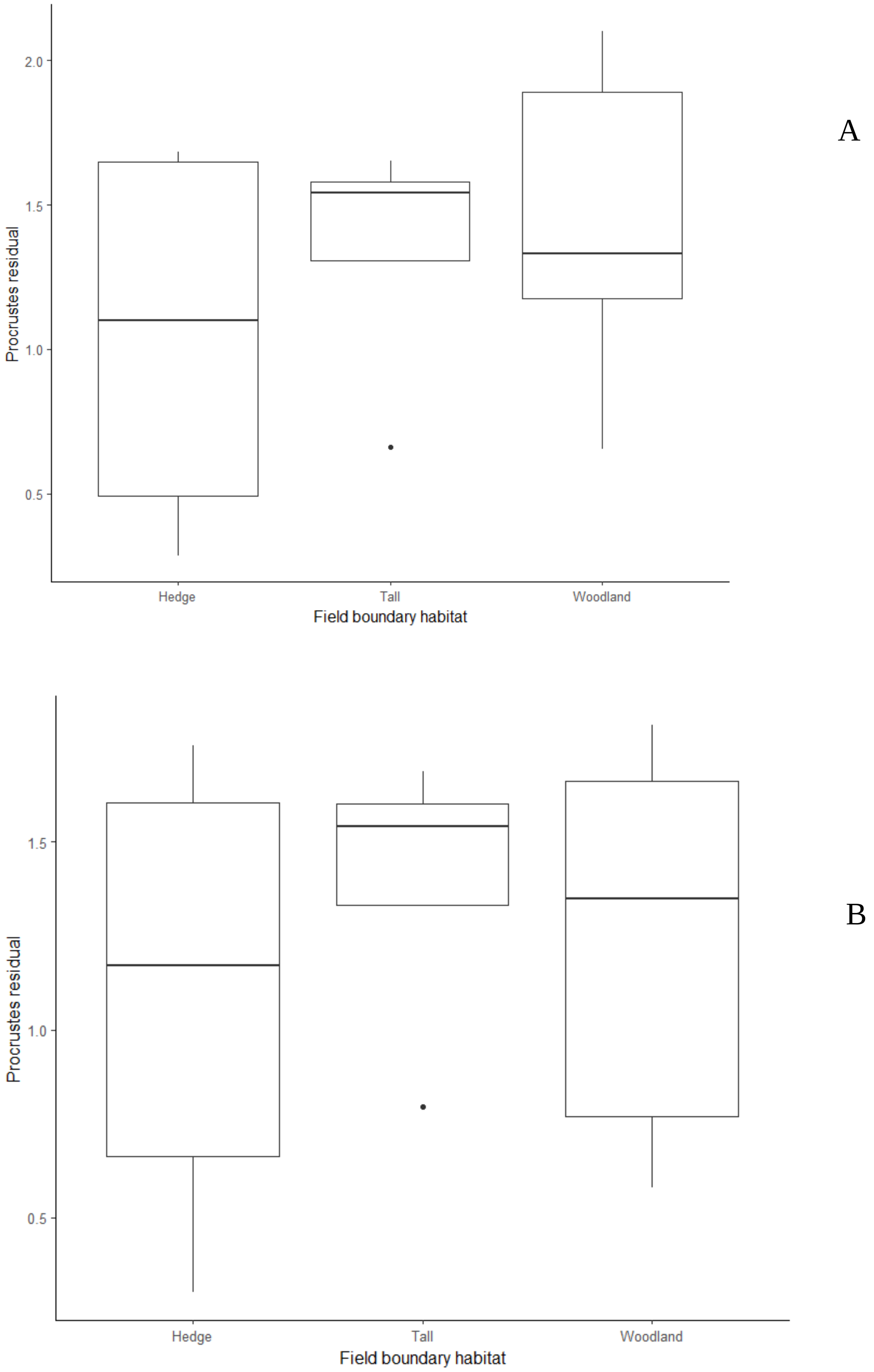


Figure 3.9 Procrustes rotation residuals plot, showing the similarities in the pCCA configuration of ten most abundant herbivores/pollinators between: A) field boundary and field edge (18%, m^2=0.967, P=0902); B) field boundary and crop (35%, m^2=0.875, P=0.406) in the conventional system.

3.5.6 Conventional management: Effects of boundary invertebrate life histories on their relative abundance in field edge or crop

When both boundary and crop type were partialled-out (Figure 3.10), epigeal predator composition in the field boundary had non-significant similarity between field boundary and assemblages in field edge and crop (45%, m^2=0.794, P=0.254; 35%, m^2=0.875, P=0.523 respectively - Figure 3.10 A and Figure 3.10 B). The strongest association (low residual scores) between field boundaries and field edge or crop habitats were Zabrini and Staphylininae, generally strong flying dispersers. Weak association (large residual scores) between boundary invertebrates and the two other habitats occurred in Nebriini (generally disperse by flight) and large-bodied Pterostichini (some species mainly disperse by walking). Pterostichini was the most abundant epigeal predator in all three field position Table 3.4.

Overall, foliar predator/parasitoid communities in the field boundary were not similar to those in the field edge (39 %, m^2=0.843, P=0.385 - Figure 3.11 A). However, foliar predator/parasitoid in crop at 40m were associated with those in the field boundaries (66%, m^2=0.556, P=0.014 - Figure 3.11 B). Association were best (low Procrustes residual scores) for predatory- Cantharidae and Ichneumonidae between field boundary and field edge. At 40m into the field, lower residual scores were observed amongst abundant parasitoid-Braconidae and predator- Syrphidae Table 3.4.

Herbivore/pollinator communities in the conventional system showed weak association between boundaries and both distances into the field (26 %, m^2=0.930, P=0.821; 21%, m^2=0.956, P=0.927; respectively - Figure 3.12 A and Figure 3.12 B). The closest relationship between the boundary and the crop field was observed with the abundant taxa Nitidulidae (pollen beetle; See Table 3.4 taxa percentage in the three positions).

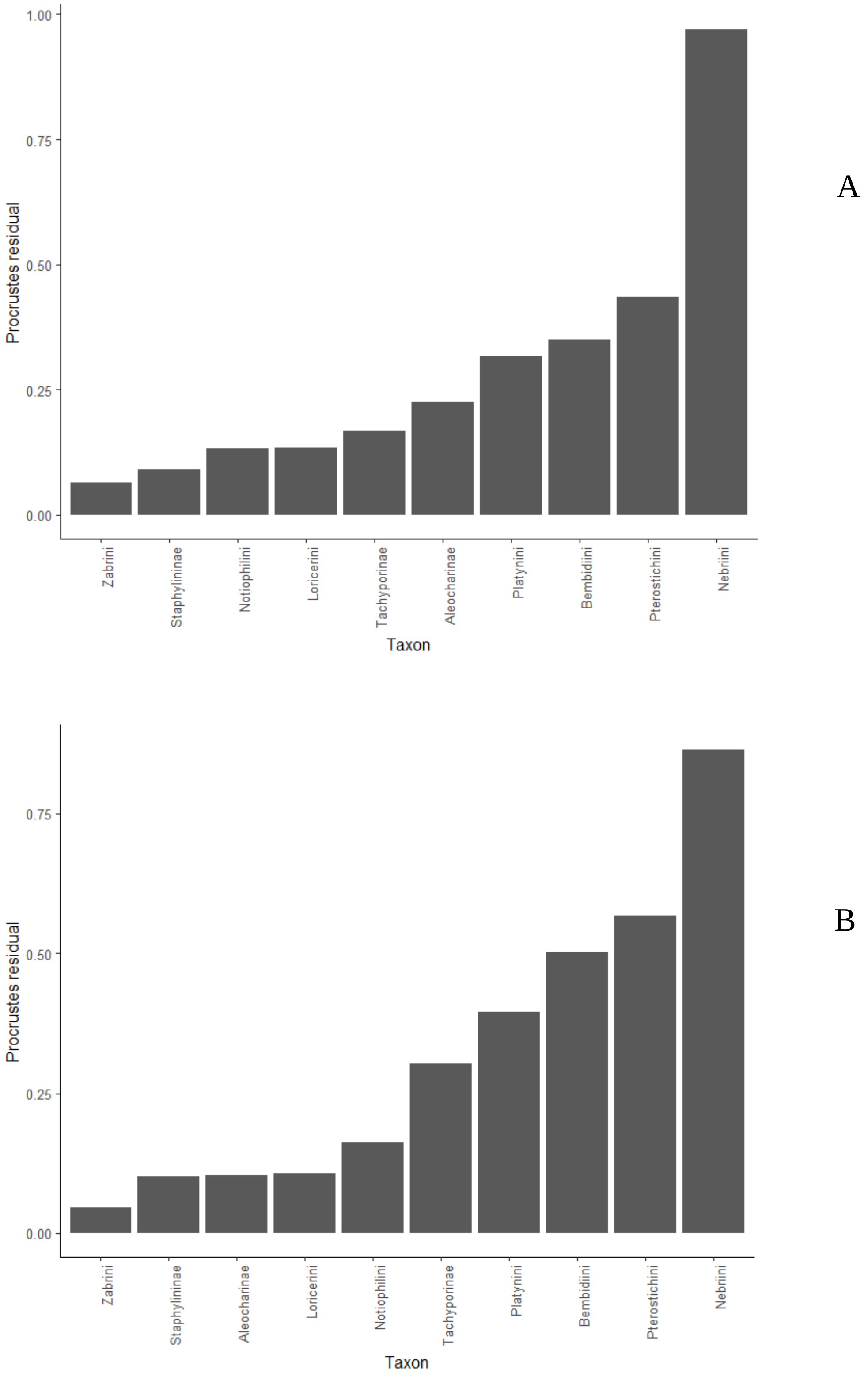


Figure 3.10 Procrustes residuals plot, showing the similarities in the pCCA configuration of ten most abundant epigeal predators between A) field boundary and field edge (45%, m^2=0.794, P=0.254); B) field boundary and crop (35%, m^2=0.875, P=0.523) in the conventional system.

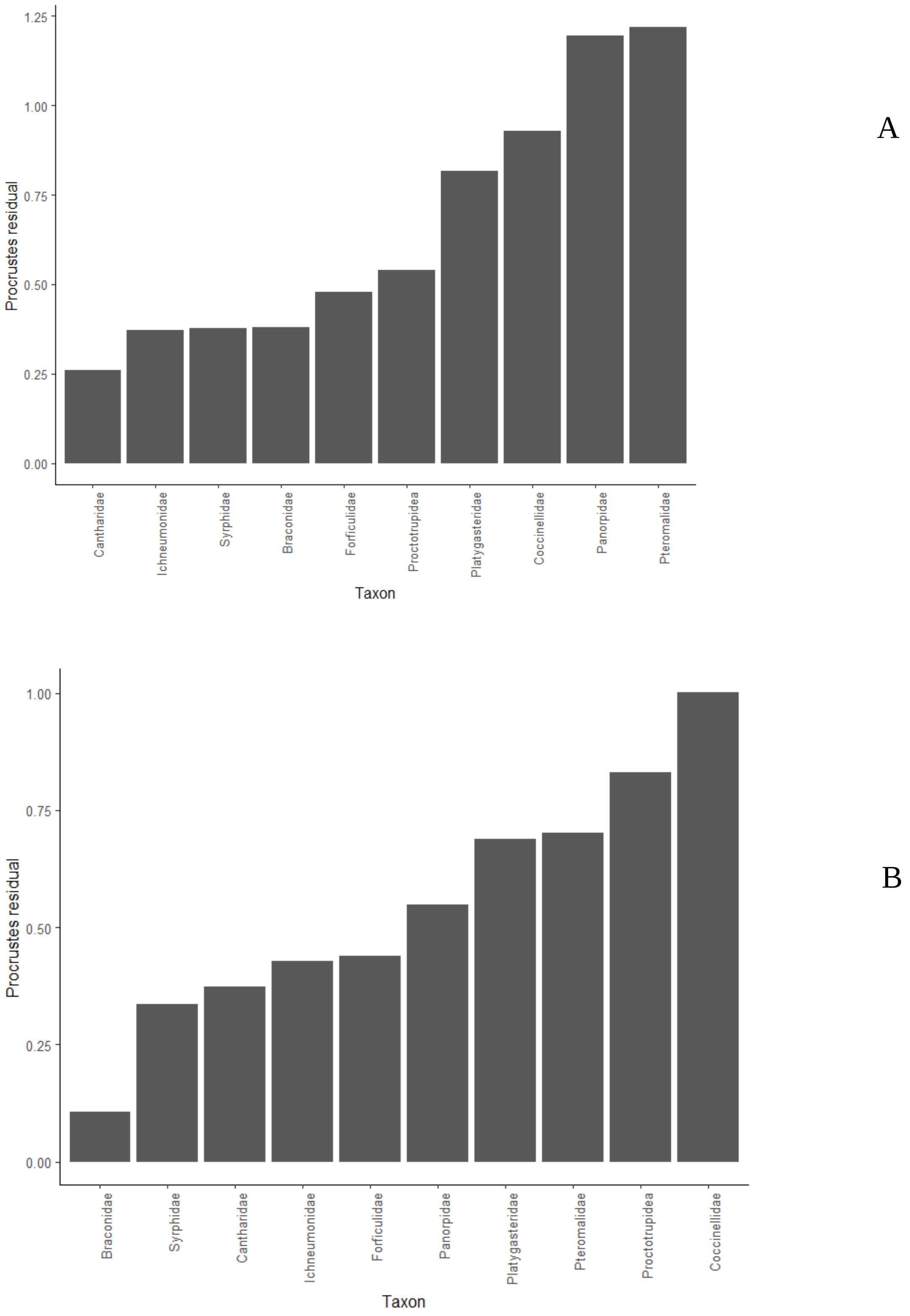


Figure 3.11 Procrustes superimposition residuals plot, showing the similarities in the pCCA configuration of ten most abundant foliar predators/parasitoids between: A) field boundary and field edge (39%, m^2=0.843, P=0.385); B) field boundary and crop (66%, m^2=0.556, P=0.014) in the conventional system.

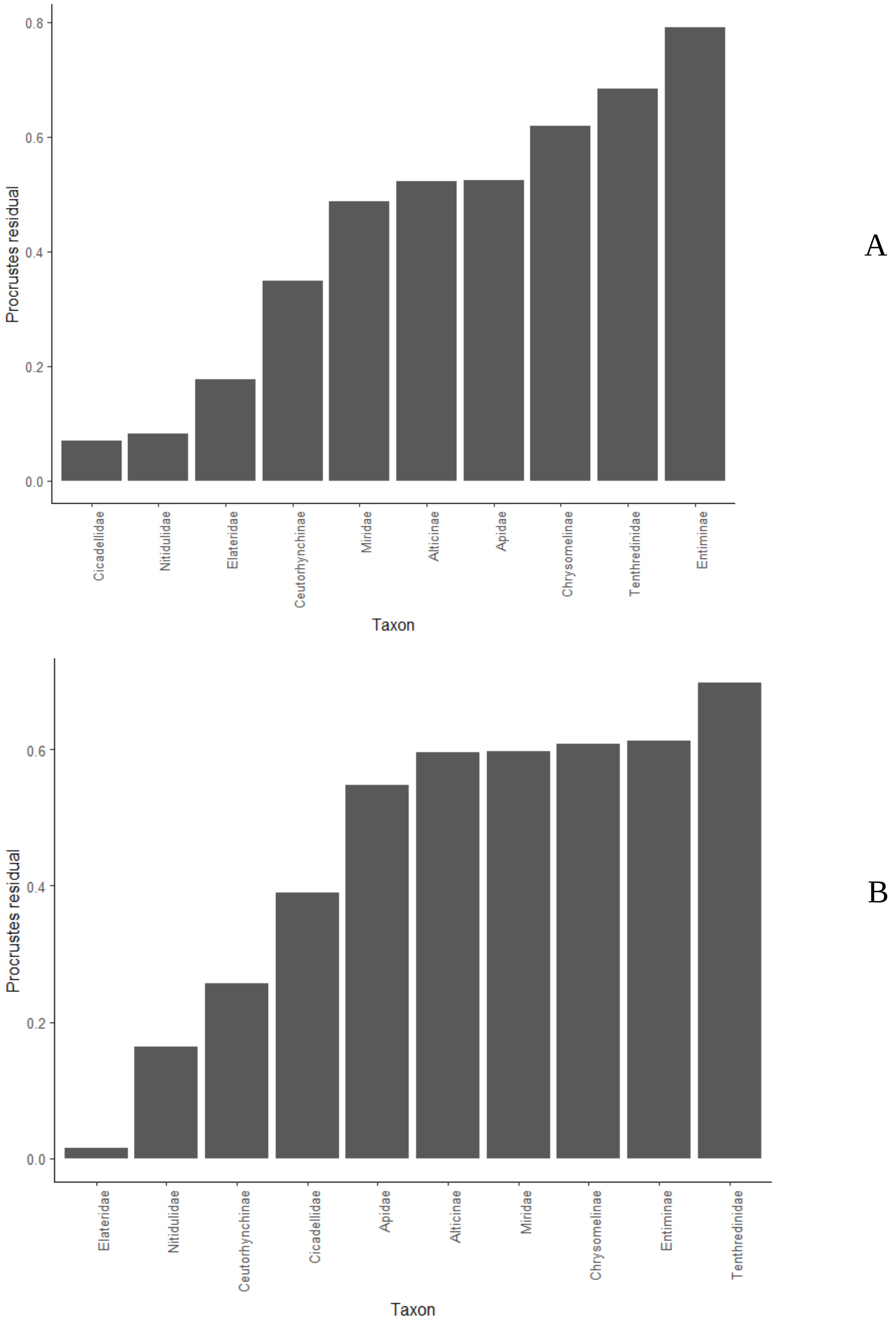


Figure 3.12 Procrustes superimposition residuals plot, showing the similarities in the pCCA configuration of ten most abundant herbivores/pollinators between A) field boundary and field edge (26%, m^2=0.930, P=0.821); B) field boundary and crop (21%, m^2=0.956, P=0.927) in the conventional system.

Taxa	Field boundary(0m)		Field edge (5m)		Crop (40m)	
	Abundance	%	Abundance	%	Abundance	%
A. Epigeal predators						
Bembidiini	2087	19.6	2746	25.7	2853	22.3
Loricerini	383	3.6	578	5.4	893	7
Nebriini	790	7.4	770	7.2	917	7.2
Notiophilini	107	1	194	1.9	69	0.5
Platynini	1079	10.1	1086	10.2	807	6.4
Pterostichini	3896	36.6	3245	30.4	4985	39.1
Zabrini	457	4.3	581	5.4	526	4.1
Aleocharinae	158	1.5	112	1	107	0.8
Staphylininae	789	7.5	982	9.2	1221	9.7
Tachyporinae	896	8.4	373	3.6	374	2.9
Total	**10642**		**10667**		**12752**	
B. Foliar predators/ parasitoids						
Braconidae	455	26.4	155	34	194	23.6
Ichneumonidae	622	36.1	80	17.6	485	58.9
Platygasteridae	12	0.7	1	0.2	11	1.3
Proctotrupidae	15	0.9	2	0.4	9	1.1
Pteromalidae	20	1.2	2	0.4	1	0.1
Forficulidae	100	5.8	35	7.8	1	0.1
Panorpidae	40	2.3	1	0.2	6	0.7
Syrphidae	168	9.8	85	18.6	29	3.6
Cantharidae	261	15.1	73	16	64	7.8
Coccinellidae	30	1.7	22	4.8	23	2.8
Total	**1723**		**456**		**823**	
C. Herbivores/ pollinators						
Alticinae	372	13.4	294	9.2	246	8.2
Ceutorhynchinae	376	13.6	225	7.1	302	10.1
Chrysomelinae	215	7.8	34	1.1	14	0.5
Elateridae	158	5.7	21	0.7	23	0.8
Entiminae	243	8.8	76	2.4	59	2
Nitidulidae	585	21.1	2339	73.7	2191	73.3
Apidae	370	13.3	131	4.1	86	2.8
Miridae	138	5	20	0.6	42	1.4
Tenthredinidae	209	7.5	31	1	24	0.8
Cicadellidae	106	3.8	1	0.1	3	0.1
Total	**2772**		**3172**		**2990**	

Table 3.4 The relative abundance and percentage abundance (0m, 5m and 40m) for the three functional groups: A) epigeal predators, B) foliar predators/parasitoids and C) herbivores/pollinators in the conventional system.

3.6 Discussion

This study has demonstrated that management practices and field boundary type had variable effects on the most abundant invertebrates occurring in the field boundary. The abundance of these invertebrates was affected by boundary type, although the effect was more pronounced and across a wider range of taxa in the conventional than organic system. The relationships between the invertebrates in the field edge and crop, and the same taxa in the boundaries, appeared to depend on the boundary type and management, with stronger associations with the invertebrates at 5 m than at 40m. When the effects of boundary and crop type were removed, this association was apparent in the organic system, but not the conventional. Some life-history traits appeared to be associated with stronger relationships between the boundary, edge and crop invertebrates, especially univoltine taxa with moderate dispersal abilities in epigeal predators and foliar predators / parasitoids. No consistent patterns with life-history traits were found for herbivores / pollinators. Note that the research described in this chapter cannot quantify the numbers of invertebrates moving from boundaries into field edges or crop, and those moving from field edges or crop into boundaries. This would require studies using marked individuals.

3.6.1 Boundary type

In the organic system, results showed that invertebrates in the field boundaries had no strong preference to a particular type of boundary, except for epigeal predators that were most abundant in short grassland boundaries. Vegetation in the organic field boundaries was more species-rich, possibly from lack of herbicide and artificial fertilizer applications (Aude *et al.*, 2003; Roschewitz *et al.*, 2005a; Ekroos *et al.*, 2010b). This resulted in field boundary habitats that are relatively similar to each other in vegetation structure, composition and local micro climate at the base of the vegetation structure (Egan *et al.*, 2014).

In contrast, in the conventional system, there was generally a greater abundance of invertebrates in hedge and woodland boundaries compared with grasslands. The exact causal mechanisms for this are unclear, but one possibility is that mature hedgerows reduce the amount of spray drift between adjacent fields (Davis *et al.*, 1994; Boutin and Jobin, 1998; Marshall and Moonen, 2002), leading to greater vegetation diversity along the base of the hedgerows (Boutin and Jobin, 1998; French and Cummins, 2001). For example, in two adjacent conventional fields separated only by a narrow short-grass boundary, spray drift may result in the grass boundary accidentally receiving a double-dose of pesticide. This risk might be reduced where two conventional fields are separated by hedgerows. Invertebrate and flora diversity is known to be positively correlated with more arthropods in hedges than crop edge (Thomas and Marshall, 1999). Burgio *et al.* (2006) reported that older and more mature weedy margins adjacent to hedgerows increased predatory Coccinellidae and Nabidae abundance, which then spillover into adjacent field edges. For more information on effects of hedgerows maturity see Deeming *et al.* (2010). Furthermore, Kremen *et al.* (2002) suggested that woodland habitat near farms can aid pollination services provided by native bees, which can produce a cascade effect higher up the food chain (Fuller *et al.*, 2001; Firbank *et al.*, 2013). In general however, field boundaries in the conventional systems have been shown to be negatively affected by herbicide drift, with subsequent effects on vegetation diversity and fewer herbivores / pollinators (Potts *et al.*, 2010; Oliver *et al.*, 2015).

3.6.2 Relationships between communities in boundary with field edge or crop

Overall, boundary invertebrate communities were more strongly associated with invertebrates in the field edge compared to those in the crop, in both management systems, when accounting for crop type. In many ways this result is unsurprising, given the foraging and dispersal patterns of invertebrates over the distances investigated. Crop fields become less hospitable for invertebrates due to annual disturbances (tillage, cutting and ploughing) compared to stable field boundary environment (William and Terry, 1982; Pfiffner and Niggli, 1996; Giller *et al.*, 1997; Poggio *et al.*, 2013), see Chapter 5 on crop rotation. Many species of beetles short distances forage by walking. There is also evidence of a cyclical foraging movement between boundary and nearby field edges, possibly diurnally (Duffield and Aebischer, 1994; Wissinger, 1997); for example Anjum-Zubair *et al.* (2010); Batáry *et al.* (2012) have shown that epigeal predators can invade field edge of arable crops.

In addition, the similarity between boundary invertebrates and those in the field edge was affected by the type of boundary habitat. This association was particularly pronounced for epigeal predators in hedge boundaries and the field edge, but not into the crop itself. This may be related to the grass and wildflower mix used adjacent to the hedge-bottom, which resulted in a species rich habitat and stable local micro-climate (Moonen and Marshall, 2001). In addition, the low frequency with which the hedges are cut at Nafferton, sometimes less than once a year, leads to more stable plant communities (Valtonen, 2006; Noordijk *et al.*, 2009) and thus have positive effects on invertebrates that require cover. The influence of field boundary habitats to provide 'ecosystem services' in the form of beneficial epigeal predators into the crop itself is limited (Firbank *et al.*, 2013). Previous attempts to enhance predator activity have included the provision of invertebrate habitats such as "beetle banks" (MacLeod *et al.*, 2004) in agri-environment schemes, but their practical utility is contentious (Kleijn *et al.*, 2001; Kleijn *et al.*, 2006).

3.6.3 Individual taxa and life-history traits

After accounting for both crop type and boundary type, positive associations between boundary invertebrates were, as expected, stronger for field edge invertebrates than crop invertebrates. The associations however were stronger for the organic than conventional system. One advantage of these analyses is the ability to compare individual taxa within each functional group. Under organic management, positive associations between boundary and field edge invertebrates were strongest for epigeal predators and herbivores / pollinators. Boundary-field edge associations were strongest amongst epigeal predators in univoltine taxa with moderate dispersal abilities, such as Aleocharinae and Nebriini (see Figure 2), both of which generally disperse by flight. The exact causal mechanisms for this are unclear, but one possibility is that flying insects may innately possess greater dispersal abilities and less likely to be affected by barriers between the boundary-crop divide than non-flying predators. However, for these epigeal predators to navigate between field boundary and the dense crop habitats, they often encounter different obstacles. This phenomenon was mentioned by den Boer (1977) where during flight invertebrates collided with obstacles (usually- plants) and fall to the ground, eventually reducing there dispersal distance. Fry and Main (1993) reports Lepidoptera (high dispersal abilities) as being impeded by hedgerows whilst Wratten *et al.* (2003) suggested Syrphidae dispersed further when there was no barriers between flowers and foraging site. In contrast, larger-bodied taxa such as Pterostichini usually disperse short distances by walking, and their abundance in field boundary was poorly associated with that in the field edges or crop. Trait patterns were less easy to interpret for herbivores / pollinators.

Chapter 4. **Relationships between agricultural management, crops and boundaries with invertebrate functional groups on a split organic/conventional farm**

4.1 Abstract

Invertebrate abundance and composition may be affected by factors across management systems at different spatial scales. These differences are partly related to the application of herbicides and pesticides, the availability of food source in crops and surrounding field boundary types. I investigated the influence of management, crop and field boundary types on invertebrate abundance and composition of 59 invertebrate taxa, mainly families and subfamilies/ tribes. Sampling was done using pitfall and pan traps in crops and field boundaries on a split organic/conventional farm in northern England in 2015. These were split into three functional groups, reflecting similar traits: epigeal predators, foliar predators/parasitoids, and herbivores/pollinators.

Overall, there was a significantly greater total abundance of invertebrates on the organic than conventional farm. Likewise, there were significantly more taxa, at both family and subfamily/tribe level, on organic management. In both management systems, invertebrate abundance, but not the number of taxa was affected by the type of crops cultivated. In the organic system, the activity of all three functional groups was affected by crop type, with greatest activity density in spring beans. Under conventional cropping, both epigeal predators and herbivores/pollinators were most abundant on winter barley and oilseed rape respectively.

Across the whole farm, in the field boundaries, invertebrate abundance was greatest in short grassland, although the largest number of taxa (at the subfamily/tribe level) was in woodland boundaries. When however invertebrate functional groups were assessed within each management system, only herbivores/pollinators in the organic system showed a significant response, being most activity density in short grassland.

Separate CCA analyses at either the family or subfamily/tribe level were undertaken to investigate the effects of crop type or field boundary in the two farming systems. Monte Carlo permutation tests indicated that both crop type and field boundary category had highly significant impacts on the overall community composition of the invertebrates.

Invertebrate abundance, functional group characteristics and community composition were all affected by farming system (organic versus conventional), crop type and field boundaries. Some of these effects are not unexpected, and accord with previous studies. We also detected evidence that levels of soil disturbance between different organic crops may have disproportionate effects on invertebrate abundance and composition.

4.2 Introduction

Invertebrates in agroecosystem have been studied at a range of spatial scales, from within one crop (Schmidt *et al.*, 2005) to a mosaic of crops within agricultural landscapes (Duelli *et al.*, 1999; Billeter *et al.*, 2008; Rusch *et al.*, 2013; Vasseur *et al.*, 2013). These investigations have highlighted differences in distribution patterns and interactions between different groups of invertebrates, depending on their life-histories, foraging behaviour, at various spatial scales (Kremen *et al.*, 2007). For example, at larger scales a greater abundance of natural enemies has been observed in complex landscapes, particularly herbaceous compared to wooded habitats (Bianchi *et al.*, 2006). The abundance and species richness of natural enemies and parasitoids is however partly dependent on the habitat type (Tylianakis *et al.*, 2006; Lacasella *et al.*, 2015), availability of food source in crops (Rand *et al.*, 2006) and management system (Holland and Luff, 2000).

At the smaller farm-scale, habitats thought to enhance invertebrate natural enemy relative abundance have included weed strips and margins (Lys, 1994; Marshall and Moonen, 2002) and ‘beetle banks’ (MacLeod *et al.*, 2004). Agricultural environmental schemes provides mixed benefits (Kleijn *et al.*, 2006; Carvell *et al.*, 2007; Olson and Wäckers, 2007) to enhance farmland biodiversity. Furthermore, their effectiveness to increase biodiversity may vary depending on the crops being grown in the field, and the vegetation structure and composition of other field boundaries (Cole *et al.*, 2002; Roschewitz *et al.*, 2005b; Eyre, 2006). Any patterns may be more difficult to observe if research is focussed on a single taxonomical group, in a single crop, or within a single management system (Woltz and Landis, 2014). A more holistic approach is needed to understand the effects of both crop and boundary types, ideally across contrasting farm management systems such as organic and conventional.

Research has indicated that both invertebrate abundance and biodiversity is greater on organic farming systems (Mäder *et al.*, 2002; Holzschuh *et al.*, 2007a), where inorganic chemicals are prohibited, than conventionally managed farms. In addition, organic farms enhances greater abundance and biodiversity of plants (Gabriel *et al.*, 2006; Norton *et al.*, 2009b), and more diverse habitat types(Gibson *et al.*, 2007a). In general, there is a tendency for beneficial taxa to be more abundant in organic farming systems (Landis *et al.*, 2000) which in theory should aid pest control (Geiger *et al.*, 2010), increase pollination and reduce crop damage (O'Sullivan and Gormally, 2002; Gabriel *et al.*, 2010a). The benefits of organic farming to biodiversity varies however amongst taxa (Fuller *et al.*, 2005) depending on the crops and spatial scale of the study. Inclán *et al.* (2015) found that landscape composition affects parasitoids species composition but not species richness whilst landscape heterogeneity increased butterfly species richness and abundance (Rundlöf and Smith, 2006).

These findings reiterated the need for invertebrate investigation at multiple spatial scales in both organic and conventional systems. The life-history traits of invertebrates also affects their response to crop management regime and field boundaries. For example, Eyre and Leifert (2011a) suggested foliar-dispersed invertebrates were most abundant under organic management, particularly in the field boundaries. Investigation of invertebrate biodiversity therefore requires surveys of both crops and non-crop habitat (especially field boundaries). Newcastle University's Nafferton Farm provided an ideal location to compare invertebrates on two halves of the same farm with different crop and management systems. Invertebrates within three functional groups (epigeal predators, foliar predators/parasitoids, herbivores/pollinators) were sampled to determine the impacts of management, crops and boundary types. Samples were collected from two management systems (organic/conventional), four boundary types (short herbaceous, tall herbaceous, hedge boundary, and woodland boundary) and seven crop types: winter wheat, barley, and oilseed rape; spring wheat, barley, beans, and grass/clover). We addressed three main questions:

1) Invertebrate abundance and taxa richness are affected by the local management system
2) Invertebrate abundance, taxa richness and community composition are affected by the type of crop cultivated
3) Invertebrate abundance, taxa richness and community composition are affected by the types of field boundaries

4.3 Methods and Materials

Samples were collected at Nafferton Farm, located approximately 20 km west of Newcastle upon Tyne in Northumberland, UK. Full details of the farm are provided in Chapter 1, with information on invertebrate sampling methods in Chapter 2, section 2.2.1. Invertebrates were sampled monthly from May to September 2015, with 28 samples from the conventional half of the farm: 12 in wheat fields, 4 barley, and 12 in oilseed rape; and 32 from the organic: 8 in wheat fields, 8 in barley, 8 in beans and 8 in grass/clover (samples at 40 m within the field – see Chapter 2, Figure 2.3, Figure 2.4). Invertebrates in field boundaries (0 m) were sampled, and boundary habitat classified according to the schema described in Chapter 2 (see Table 2.2 and Table 2.3). A small number of field boundaries were shared between fields. All pitfall and pan trap samples were sorted in the laboratory and invertebrates stored in 70% industrial methylated sprit. Invertebrates were identified to family, sub-family and tribe, according to Chinery (1993); Roberts (2001); Luff (2007) and confirmed by expert entomologist Dr M.D. Eyre, depending on functional group, and counted.

4.3.1 Influence of management system on taxa abundance and richness

Linear models (LM) were used to investigate the relative importance of management (conventional and organic) on invertebrate abundance and taxa richness, as well as the total numbers in each functional group. Analyses were done for individual taxa (family, subfamily or tribes as appropriate), broken down into the three life-history functional groups. Only samples taken from within the crop (i.e. at 40 m) were used in this analysis. The statistical analyses were performed to address two main questions. First, to determine the overall differences in invertebrates abundance between group (crop or boundary types), using multiple analyses of linear models (anova). Secondly, TukeyHSD was to determine pairwise differences in means between the explanatory variables (compared with each other) via anova. The analyses were restricted to simple LM as the ‘unbalanced’ design of the farm, with different crops and boundary types in the organic and conventional halves, meant that more advanced LME methods could not be implemented for whole - farm analyses.

Invertebrate counts were transformed by log10(n + 1) as recommended by Crawley (2007) to stabilize the variance and to reduce the influence of extreme values, and analyses undertaken in the R statistical environment, (Pinheiro *et al.*, 2011b). Management type (organic or conventional) was used a categorical explanatory variables, and number of individuals of each taxon, or overall taxa richness, used as the response, split by functional group. Individual taxa were omitted from the analysis if there was less than five individuals recorded in all the samples.

4.3.2 Influence of crop type within each management system on taxa abundance and richness

Linear models (LM) were used to determine the importance of crop types within and across both management systems on invertebrate abundance and taxa richness, and sub-divided for the three functional groups. This was done using three separate sets of LM models with invertebrate taxa abundance or richness as response variables and explanatory variables of 1) crop types across both management systems; 2) organic crop types only; 3) conventional crop types only.

Canonical correspondence analysis (CCA) was used to assess differences in invertebrate community composition as a result of crop types; separate in CCA analyses were undertaken for each management system. The matrix of taxa by samples was used as the response, constrained by the explanatory variables of crop types within either the organic or conventional system. The contribution of each crop-type was tested via automatic forward selection, and statistical significance estimated using Monte Carlo permutation tests (999 permutations). The CCAs were carried out using the CANOCO package (Ter Braak and Smilauer, 2002).

4.3.3 Effect of field boundary type on taxa abundance and richness within each management system

Linear models (LM) were used to determine the importance of field boundary type within each management system on invertebrate abundance and taxa richness for the functional groups. Only samples taken from within the field boundaries (i.e. at 0 m) were used in this analysis. This was done using three separate sets of LM models with invertebrate taxa abundance or richness as response variables, and explanatory variables of: 1: Field boundary types across both management systems; 2: organic field boundary types only; 3: conventional field boundary types only.

Canonical correspondence analysis (CCA) was used to assess differences in invertebrate community composition as a result of boundary type; separate CCA analyses were undertaken for each management system. The matrix of taxa by samples was used as the response, constrained by the explanatory variables of boundary type within either the organic or conventional system. The contribution of each boundary type was tested via automatic forward selection, and statistical significance estimated using Monte Carlo permutation tests (999 permutations).

4.4 Results

4.4.1 Influence of management system on taxa abundance and richness

Significantly more invertebrates occurred per site in organic than conventional management, which resulted increase abundance in organic, even though the number of sites were different plus more families and subfamilies Table 4.1. Although the differences between taxa richness of subfamilies were highly significant, mean numbers of taxa between organic and conventional regimes were relatively low.

	Organic	**Conventional**	**$F_{1,28}$**	**P-values**
Mean number of invertebrates	3335	2215	47.1	**<0.001**
Mean number of families	20	15	25.5	**<0.001**
Mean number of subfamilies/tribes	19	17	25.5	**<0.001**

Table 4.1 Mean number of individual invertebrate recorded from the four organic and three conventional crops, together with the mean number of family and subfamily taxa found in the two halves of the farm and the significance, degrees of freedom, derived from the linear models.

4.4.2 Influence of crop type within each management system on taxa abundance and richness

Differences in the abundance across all crops in both management systems were highly significant for the total invertebrates ($F_{6, 28}$=27.4, P<0.001) but not for the number of taxa in families ($F_{6, 28}$=5.70, P=0.265) and subfamilies ($F_{6, 28}$=5.70, P=0.262). Tukey tests showed that the mean abundance was significantly lower in spring wheat than in grass/clover (P<0.001), oilseed rape (P<0.001) and barley (P=0.028), whilst winter wheat had lower invertebrate abundance than grass/clover (P= 0.029). Most families and subfamilies were found in grass/clover, and all organic crops had slightly greater taxa richness, than the conventional crops. When crop type was analysed across both management systems, overall there were more invertebrates recorded from organic spring beans than other organic or conventional crops **Error! Reference source not found.**. Organic grass/clover had greater abundance than each of the three conventional crops, but the lowest mean total in any crop was for organic wheat.

Summaries from separate models of organic and conventional crops are presented in Table 4.3 There were significant differences in invertebrate abundance within the organic crops for the total invertebrates ($F_{3, 12}$=10.8, P<0.001), and also within the conventional crops ($F_{3, 12}$=4.10, P=0.044). No significant difference in the number of families and subfamilies were found within the four organic or within the three conventional crops.

Within the organic crops, all three functional groups showed differences in their abundance Table 4.4 epigeal predators ($F_{3, 22}$=7.00, P=0.005- 14866 individuals), foliar predators/parasitoids ($F_{3, 22}$=9.10, P=0.002- 1953 individuals) and herbivores/pollinators ($F_{3, 22}$=3.80, P=0.037- 14541 individuals). A *Post hoc* Tukey test indicated lower abundance of epigeal predators in spring wheat than grass/clover (P=0.028) or spring beans (P=0.005) and spring barley (P=0.004). Foliar predators/parasitoids were more abundant in grass/clover than spring barley (P=0.002), spring beans (P=0.041) and spring wheat (P=0.002). Herbivores/pollinators, were more abundant in spring beans than spring wheat (P=0.030). Most epigeal predators and herbivores/pollinators were in spring beans and fewest in spring wheat. Foliar predators/parasitoids had greatest abundance in grass/clover and least in spring wheat.

Within the conventional crops Table 4.5, only epigeal predators ($F_{2, 21}$=5.30, P=0.023- 13573 individuals) and herbivores/pollinators ($F_{2, 21}$=16.8, P<0.001- 3031 individuals) had significant differences in mean abundance as a result of crop type. Tukey HSD tests suggested that the mean abundance of epigeal predators was greater on winter barley than oilseed rape (P=0.052) whilst herbivores/pollinators were more abundant on oilseed rape than either winter barley (P=0.014) or winter wheat (P<0.001). Most epigeal predators were in the cereals (barley and wheat) whilst most herbivores/pollinators in oilseed rape.

	Grass clover	**Spring wheat**	**Spring barley**	**Spring beans**	**Winter wheat**	**Winter barley**	**Oilseed rape**	**F ratios**	**P-values**	**D.F**
Mean number of invertebrates	2882	1631	3253	5575	2175	2681	2101	27.4	**<0.001**	$6,_{28}$
Mean number of families	22	19	18	18	15	16	15	5.7	0.265	$6,_{28}$
Mean number of subfamilies	20	18	19	18	17	17	18	5.7	0.262	$6,_{28}$

Table 4.2 Mean number of individual invertebrate recorded from the four organic (grass/clover to beans) and three conventional (winter wheat to oilseed rape) crops, toge ther with the mean number of family and subfamily taxa found in each crop and the significance derived from the linear model.

Organic	**Totals**	**$F_{3,12}$**	**P-values**
Total invertebrates	53370	10.8	**<0.001**
Number of individual families	31360	2.3	0.126
Number of individual subfamilies/tribes	2210	3.2	0.060

Conventional	**Totals**	**$F_{3,12}$**	**P-values**
Total invertebrates	31019	4.1	**0.044**
Number of individual families	17439	0.1	0.840
Number of individual subfamilies/tribes	13580	0.3	0.700

Table 4.3 Significances derived from linear models of total number of individual, also total number of individuals in families and subfamilies/tribes recorded from the four organic and three conventional crops analysed separately.

Functional groups	**Epigeal predators**	**Foliar predators/parasitoids**	**Herbivores/ pollinators**
Grass clover	965	217	589
Spring barley	1043	65	687
Spring wheat	465	56	408
Spring beans	1242	150	1949
$F_{3,22}$	7	9.1	3.8
P-values	**0.005**	**<0.001**	**0.037**

Table 4.4 Mean number of individuals in each functional group recorded from the four organic crops sampled in 2015, together with the *P* values derived from the linear models, F ratios and total catch.

Functional groups	**Epigeal predators**	**Foliar predators/parasitoids**	**Herbivores/ pollinators**
Oilseed rape	737	92	452
Winter barley	1332	17	38
Winter wheat	1080	41	40
$F_{2,21}$	5.3	1.5	16.8
P-values	**0.023**	0.251	**<0.001**

Table 4.5 Mean number of individuals in each functional group recorded from the three conventional crops sampled in 2015, together with the significances derived from the linear models, F ratios and total catch.

Composition of invertebrate families and subfamilies/tribe in relation to organic crop type are summarised in biplots Figure 4.1. Figure 4.1A indicates that most variation was between the grass/clover and spring bean crops on axis 1, whilst axis 2 indicated differences between the two cereal crops (spring wheat/spring barley) compared to spring beans and grass/clover. A considerable number of families were found close to the origin, with no preference for any particular crop but two Hymenoptera - Parasitica wasp and one Coleoptera (Proctotrupidae, Braconidae; Nitidulidae) were associated with spring beans. The subfamilies/tribes biplot (Figure 4.1 B) differed from the family biplot in that the major variation axis 1 was between grass/clover and a cereal crop (spring barley) and other crops, whilst differences between spring beans and spring wheat were on axis 2. Neuroptera- Chrysomelinae and Coleoptera- Molytinae were associated with barley and grass/clover, whilst Coleoptera- Criocerinae and Coleoptera- Aleochorinae were associated with wheat/beans. Two Carabidae tribes, Coleoptera- Zabrini and Coleoptera- Notiophilini are along opposite ends of axis 2, but without a specific association to a particular crop.

Biplots in Figure 4.2 show the relationship between family and subfamily/tribes taxa with the conventional crops. Axis 1 (Figure 4.2 A) shows that the major variation with family taxa was between oilseed rape and winter wheat, with differences between winter wheat and winter barley providing secondary variation axis 2. Oilseed rape was especially positively associated with families such as Homoptera- Cercopidae and Hymenoptera- Cynipidae, with Dermaptera- Forficulidae and Diptera- Syrphidae abundance associated mostly in winter wheat and Hemiptera- Cicadellidae mostly in winter barley. The subfamily/tribe Biplot (Figure 4.2 B) shows the variation on both axes to be the same as that with family taxa. Coleoptera- Ceuthorynchinae and Coleoptera- Molytinae abundance were associated mostly with oilseed rape, with most ground beetle tribes more abundantly associated with the cereal crops. Variation along axis 2 was limited and most of the subfamilies/tribes were close to the origin having no distinct association with particular crop.

4.4.3 Influence of field boundary type within each management system on taxa abundance and richness

Field boundary types was analysed across both management systems, overall there were significant difference across all the boundary vegetation types for total invertebrates ($F_{3, 22}$ = 0.90, P=0.009)

	Short vegetation	**Tall vegetation**	**Hedges**	**Woodland**	**F ratios**	**P-values**	**D.F**
Mean number of invertebrates	**4024**	**1997**	**2178**	**2651**	**0.9**	**0.009**	**3,$_{22}$**
Mean number of families	**19**	**21**	**23**	**22**	**1.2**	0.319	**3,$_{22}$**
Mean number of subfamilies	**20**	**20**	**19**	**22**	**1.2**	0.128	**3,$_{22}$**

Table 4.6. Total abundance was significantly greater in short than tall field boundaries (P<0.001). Although more families were recorded from the two woody boundaries (hedge and wood) than herbaceous boundaries (short and tall vegetation), these were not statistically different. Differences in taxa richness across all boundary type in both management systems

was non-significant for families ($F_{3, 22}$ = 1.20, P=0.319), subfamilies/ tribes ($F_{3, 22}$ = 4.50, P=0.128). Nevertheless, most subfamilies were found in woodland and least in hedges.

	Short vegetation	**Tall vegetation**	**Hedges**	**Woodland**	**F ratios**	**P-values**	**D.F**
Mean number of invertebrates	**4024**	**1997**	**2178**	**2651**	**0.9**	**0.009**	**$3,_{22}$**
Mean number of families	**19**	**21**	**23**	**22**	**1.2**	0.319	**$3,_{22}$**
Mean number of subfamilies	**20**	**20**	**19**	**22**	**1.2**	0.128	**$3,_{22}$**

Table 4.6 Mean number of individuals and mean number of families and subfamilies recorded from the four field boundary types, together with the significance derived from the linear models.

When field boundary was analysed in the organic system Table 4.7 differences in the abundance across all boundary type was significant for herbivores/pollinators ($F_{2,\,9}$ =5.00, P=0.033- 7325 individuals) with more herbivores in short vegetation, least in hedges. *Post hoc* comparison using Tukey HSD test indicated that the mean for total abundance between tall and short was marginally non- significant (P=0.057). More epigeal predators were found in the short vegetation than hedges, whilst more foliar predators/parasitoids were in hedges than short vegetation, but not statistically different. In the conventional system Table 4.8, more epigeal and foliar predators/parasitoids were in woodland habitat and least in tall vegetation whilst more herbivores/pollinators were found in tall vegetation, with non-significant differences across boundary type.

Functional groups	**Epigeal predators**	**Foliar predators/parasitoids**	**Herbivores/pollinators**
Short vegetation	1244	97	948
Tall vegetation	930	113	390
Hedge vegetation	1001	173	242
$F_{2,9}$	1.1	6.3	5
P-values	0.351	0.550	**0.033**

Table 4.7 Mean number of individuals in each functional group recorded from the four boundary types sampled in 2015, together with the *P* values derived from the linear models, F ratios and total catch, organic boundaries.

Functional groups	**Epigeal predators**	**Foliar predators/parasitoids**	**Herbivores/pollinators**
Tall vegetation	637	95	215
Woodland vegetation	1156	158	208
Hedge vegetation	867	100	133
$F_{2,11}$	3.6	2.7	0.2
P-values	0.061	0.106	0.763

Table 4.8 Mean number of individuals in each functional group recorded from the four boundary types sampled in 2015, together with the *P* values derived from the linear models, F ratios and total catch, conventional boundaries.

Composition of invertebrate families and subfamilies/tribes taxa in relation to organic field boundary type are summarised in Figure 4.3. The major variation for invertebrate family (Figure 4.3 A) on axis 1 between the two herbaceous boundaries (short vegetation and tall vegetation), with Coleoptera- Coccinellidae and Araneae- Linyphiidae associated with short boundaries, compare to Coleoptera- Cicadellidae and Homoptera- Cercopidae, whilst axis 2 indicated differences between hedges and the herbaceous boundaries but none strongly associated with hedges. The subfamily/tribes (Figure 4.3 B) differed from the family biplot, in that the major variation axis 1 was between the short boundaries and hedges and tall boundaries, whilst differences between hedges and tall vegetation were on axis 2. The majority of the subfamilies were found close to the origin with no preference for any particular boundary type. Coleoptera- Aleochorinae and Coleoptera- Scartini were associated with short boundaries, while Coleoptera- Chrysomelinae and Coleoptera- Tachyporinae with the other boundaries (hedge and tall vegetation).

The biplots Figure 4.4 shows the relationship between families and subfamilies/tribes taxa with the conventional field boundaries. Axis 1 (Figure 4.4 A) shows the major variation with family taxa was between woodland and tall vegetation, with differences between hedges and the other two boundaries (woodland and tall vegetation) providing the secondary variation axis 2. Araneae- Tetragnathidae were associate with woodland, compare to Homoptera- Cercopidae and Cicadellidae in tall vegetation. None of the families or subfamilies were associated with hedges. The Subfamilies/tribes biplots (Figure 4.4 B) showed a spread of taxa across axis 1, with Coleoptera- Omalinae and Oxytelinae associated with woodland and Scartini and Harpalini positively associated with tall vegetation boundaries. Variation along axis 2 was limited and most of the subfamilies/tribes were close to the origin having no distinct association with particular boundary type.

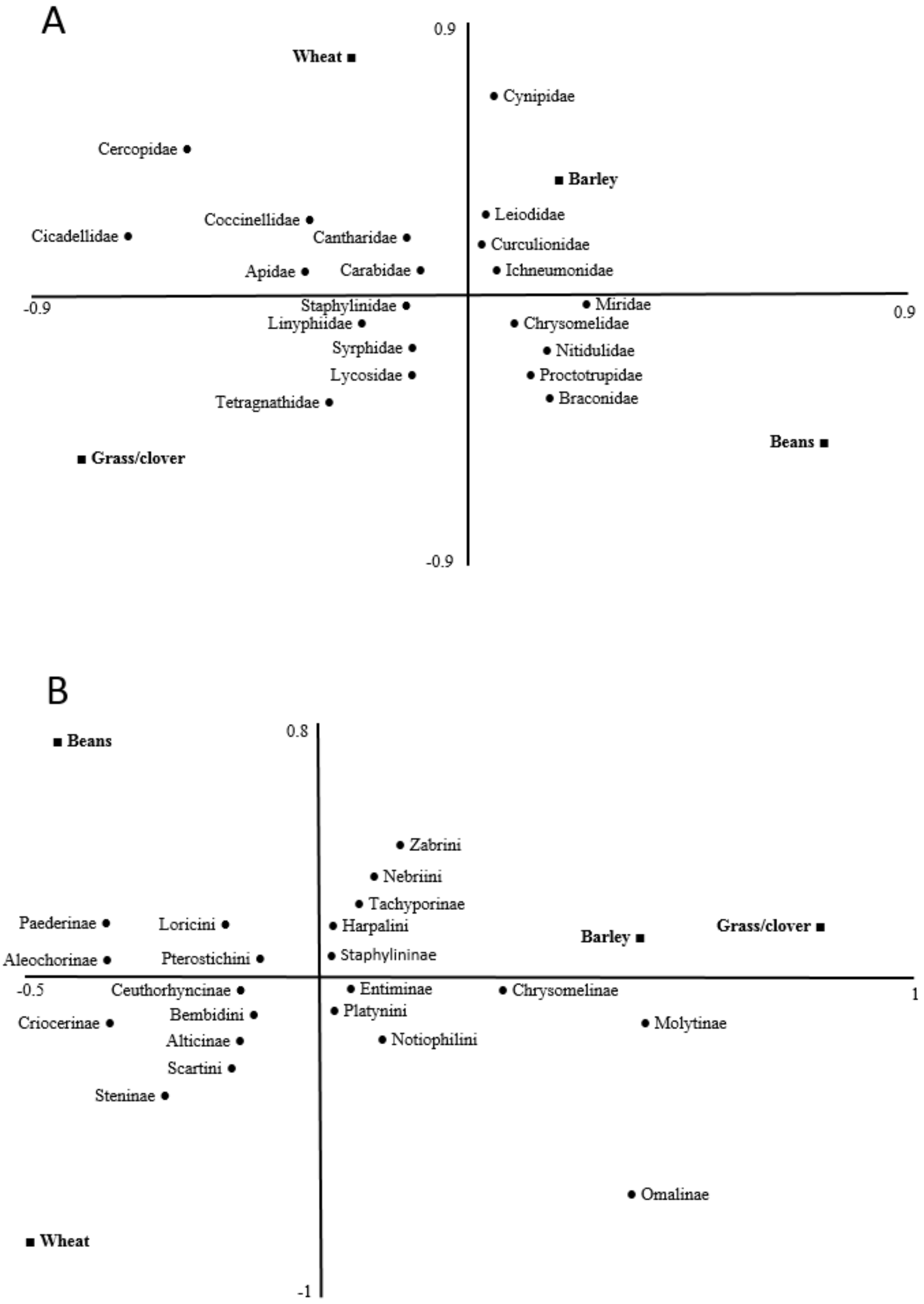


Figure 4.1 Biplots derived from constrained ordination of organic taxa; square symbols are centroids of the active explanatory variable, crop type, whilst circles are invertebrate taxa. A) twenty most abundant families, B) subfamilies and tribes in the four organic crops.

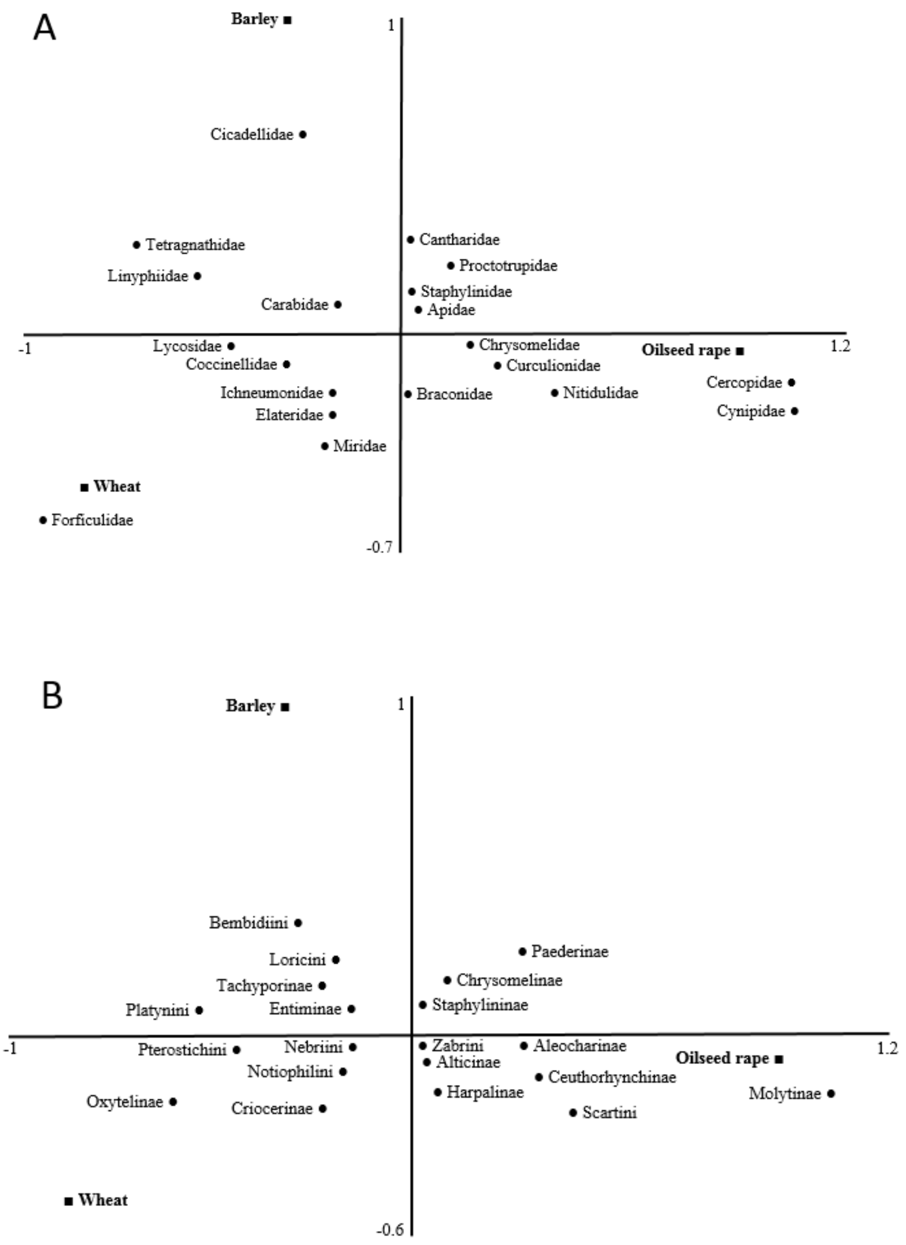


Figure 4.2 Biplots derived from constrained ordination of conventional taxa; square symbols are centroids of the active explanatory variable, crop type whilst circles are invertebrate taxa. A) twenty most abundant families, B) subfamilies and tribes in the three conventional crops.

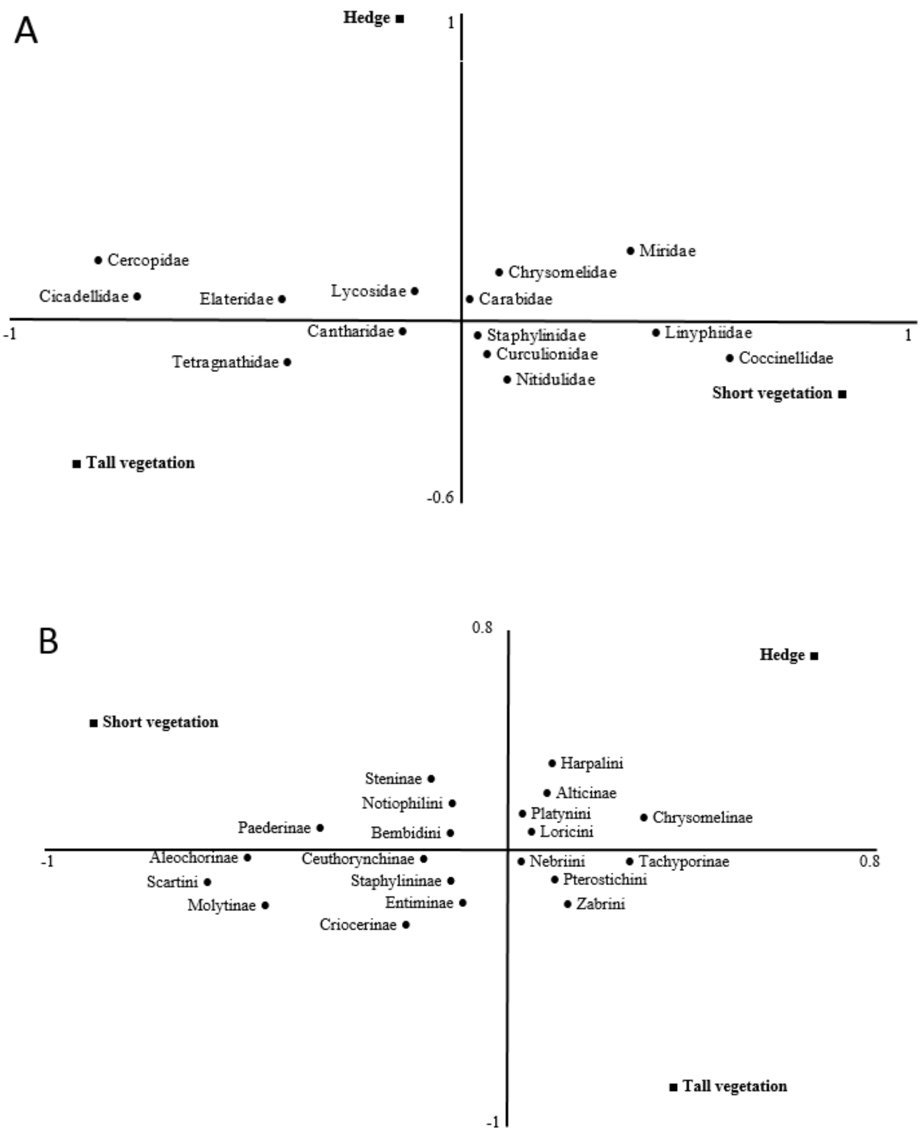


Figure 4.3 Biplots derived from constrained ordinations organic taxa; square symbols are centroids of the active explanatory variable, boundary type, whilst circles are invertebrate taxa. A) fourteen most abundant families (at least 20 in a family), B) and the twenty most abundant subfamilies and tribes in the three field boundary types on the organic half of the farm.

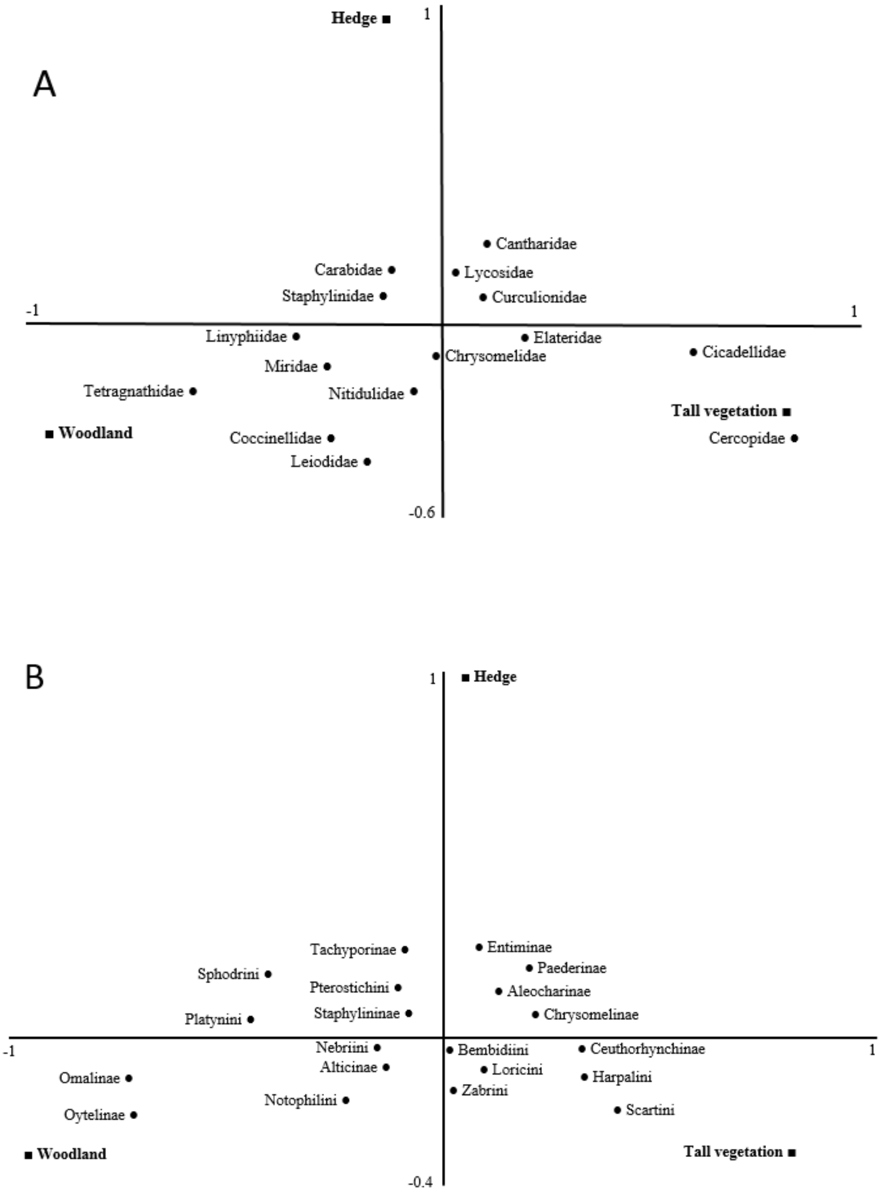


Figure 4.4 Biplots derived from constrained ordination conventional taxa; square symbols are centroids of the active explanatory variable, boundary type, whilst circles are taxa. A) fifteen most abundant families (at least 20 in a family), B) twenty most abundant subfamilies and tribes in the three field boundaries on the conventional half of the farm.

4.5 Discussion

4.5.1 Farm management influences

There were major differences in both invertebrate abundance and taxa richness in the organic compared to conventionally managed system in the samples collected over a four month period in 2015 (Table 4.1). This difference is consistent with finding from a comparative review by Shepherd *et al.* (2003) who suggested that there is up to six times more species within organic managed crops compared with conventional. Bengtsson *et al.* (2005) and Burgio *et al.* (2015) suggested an increase in invertebrate activity in organic crops rather than conventional management and differences were affected by the crops. This positive benefit to wildlife is mainly due to conservational management practices that benefits biodiversity and the more diverse habitat structure (Clough *et al.*, 2007; Öberg *et al.*, 2007). In general, invertebrates should benefit from the absence of chemical application (especially insecticides and herbicides) and organic fertilizer (Holland and Luff, 2000). A review by Hole *et al.* (2005) reported greater abundance for mammals, invertebrates and plants in organic systems, possibly due to both crop protection practices and fertility management (Eyre *et al.*, 2012). Whilst conventional farms use inorganic fertilizer to improve the soil, organic farms use slurry and farmyard manure/compost (Romero *et al.*, 2008; Sharma *et al.*, 2017). Whilst conventional crops are generally sown in the autumn, organic crops are sown in the spring, with crop debris on the soil surface during winter providing more overwintering habitats for invertebrates (Morris *et al.*, 1996). Whilst spring spring-sown organic crops develop later, a greater vegetation species richness (primarily weeds) present in the growing season (Roschewitz *et al.*, 2005b; Gabriel *et al.*, 2006).

Organic farming is known to lead to increased numbers of both individuals and taxa of ground beetles (Fuller *et al.*, 2005) and rove beetles (Maeder *et al.*, 2002). Tuck *et al.* (2014) reported that biodiversity levels in several invertebrate groups was generally higher in organic crops; however numbers varied between crop types, whilst Lüscher *et al.* (2014) showed that spider abundance was primarily affected by crop rather than management. The effects of crops and management are simultaneously intertwine making it more difficult interprete results. Therefore in subsequent analyses in this thesis the two management systems (organic/conventional) will be considered separately as obvious differences between the two management, such as sowing times confound results.

4.5.2 Crop influences

Recent investigations of invertebrate taxa and functional traits similar to those used in here have shown that predators are more affected by land use intensity than herbivores (Liu *et al.*, 2014). Molina *et al.* (2014) found that more complex landscapes provide greater exchange of invertebrates between crop and non- crop habitat. In similar work on ground beetles, Hanson *et al.* (2016) found smaller sized, more active beetles in arable crops than in grassland. This was similar to results at Nafferton Farm, with smaller ground beetles most abundant in spring arable and beans crops. This may reflect differences in crop productivity levels and disturbance within the agroecosystem, with more complex landscapes arising from less intensive farming, and grass-land being less soil-cultivated than arable fields. The productivity of the farm can be viewed as areas within the landscape which provides abundant food for invertebrates, and compared to boundaries, the crops tends to be more productive. However productivity differs amongst crops, whilst soil disturbance via cultivation in ploughing/tillage can affect the abundance and distribution of invertebrates (Eyre *et al.*, 2013b). While there were different preferences for crop, they were also a range of possible reactions to productivity and disturbance by both individual taxa groups. These differences is partly a result of the crop management system, for example grass/ clover on the organic farm is cut for silage. This level of disturbance is relatively different from disturbance that result from chemical application on the conventional farm. As a result, additional work done on both farm systems should be treated statistically separately.

4.5.3 Field boundary influences

Mean numbers of epigeal invertebrate were highest in short vegetation in organic boundaries, and highest in woody vegetation in the conventional boundaries. There was however an association of a number of groups with the least managed boundary (tall vegetation), for example Scartini, Cercopidae and Cicadellidae. The pattern of foliar predators showed no major differences between field boundary types, whilst most herbivores were found in short. Farm boundaries can be managed to increase ecosystem services, for example beetle banks, which aim to increase natural enemy abundance (Collins *et al.*, 2002). Wider field margins, larger hedges and woodland in the landscape may increase the numbers of beneficial invertebrates (Holland *et al.*, 2008; Macfadyen *et al.*, 2011; Haenke *et al.*, 2014) but does not necessarily lead to greater parasitism or predation in adjacent crops. Eyre *et al.* (2009) found no spillover of ground beetles that predate cabbage root fly eggs into Brassica crops from planted field boundaries. Jonsson *et al.* (2015) found that planted buckwheat strips produced more parasitism in adjacent kale crops in simple landscapes but not more complex ones, indicating that even with considerable management of donor strips and boundaries, any improvement in pest control is liable to be affected by other influences than management.

4.5.4 Conclusions

These results suggest that future analyses will be more informative if undertaken separately on the two halves of the farm because management system is confounded with crop type and sowing time (Purvis and Fadl, 2002), and whole-farm analyses risk obscuring patterns. The preliminary analyses undertaken in this chapter highlight the importance of crop type, but do not provide an understanding of casual mechanisms, especially in relation to soil disturbance over a rotation cycle. Similarly, these analyses have indicated that field boundaries have major effects on invertebrate composition and abundance, but do not allow us to infer the exact relationships between crop invertebrates and those in adjacent non-crop habitats. Finally, investigation is needed to determine the significance of plant composition and structure on invertebrate abundance and distribution.

Chapter 5. **Invertebrate communities are affected by both crop rotation and soil tillage in organic and conventional agriculture**

This chapter is being revised for submission as: Patterson E., Sanderson R., Eyre M. Effects of crop rotation and soil tillage on invertebrate communities in organic and conventional agriculture. *Journal of applied Entomology*.

5.1 Abstract

Crop rotation systems in organic and conventional management systems differ in crop types, management and duration. However, changes in invertebrate communities over the entire rotation system are however, poorly understood, as many studies have surveyed only single years or have not encompassed the entire rotation period. Here i describe changes in invertebrates in two contrasting systems: one an 8-year organically-managed rotation with five crops, the other a 5-year conventionally managed rotation with three crops. Invertebrates were classified into three functional groups, representing epigeal predators, foliar predators/parasitoids, and herbivores/pollinators.

Invertebrates were dominated by epigeal predators across all crops in both management systems. They were affected by soil tillage which occurred annually in the conventional rotation, but was intermittent in the organic, with much greater abundance of epigeal predators during years with low or no soil tillage. Significant changes in the abundance of individual taxa in all three functional groups of invertebrates in both rotation systems were strongly associated with both the crop type, and its sequence in the rotation. Overall, invertebrates were most abundant on the conventional rotation, but most taxonomically diverse on the organic.

In the conventional system, all three functional groups showed a cyclical change in their taxonomic composition that closely matched the crop rotation sequence, analysed via partial CCA. In contrast, on the organic rotation this pattern was only observed in herbivores/pollinators, as the cycle was disrupted by periods without soil tillage for both epigeal predators and foliar predators/parasitoids. Variation partitioning indicated that whilst the current year’s crop type was the major determinant of invertebrate community composition, there was a significant ‘lag effect’ for many taxa from the preceding year’s crop.

The results suggest that both reduced soil tillage (e.g. in no-till systems) and crop rotation order have major impacts on invertebrates in agroecosystems.

5.2 Introduction

A number of studies have indicated that invertebrate communities are higher in both abundance and species richness under organic systems (Wickramasinghe *et al.*, 2004; Fuller *et al.*, 2005; Holzschuh *et al.*, 2007a). This is partly due to lack of synthetic fertilizer and pesticides which promotes increase of weed species (Romero *et al.*, 2008), as well as potentially greater habitat heterogeneity from the field to farm and wider landscape (Clough *et al.*, 2007; Öberg *et al.*, 2007). Although many invertebrates are agricultural pests, organic farms also support higher numbers of beneficial invertebrates, especially predators, parasitoids and pollinators (Pfiffner and Niggli, 1996; O'Sullivan and Gormally, 2002; Power Eileen and Stout Jane, 2011).

In the UK, organic farms usually grow more types of crops than conventional (Norton *et al.*, 2009b), spring- rather than autumn-sown (Purvis and Fadl, 2002) plus nitrogen-fixers such as beans and clover to increase soil productivity (Maeder *et al.*, 2002). This means that the crop rotation patterns are longer than on conventional farms, sometimes up to 8 years. However, most invertebrate studies have been confined to trial plots lasting only 2 or 3 years (Honek and Jarosik, 2000; O’Rourke *et al.*, 2008; Bourassa *et al.*, 2010; Crotty *et al.*, 2015), with few at the farm-scale of sufficient duration to reflect realistic crop rotations. Other longer-term studies have been restricted to soil microbial invertebrates (Lupwayi *et al.*, 1998; Balota *et al.*, 2003) and soil enzyme activities (Balota *et al.*, 2004).

The grass-clover leys used in organic rotation result in periods of reduced soil cultivation (Watson *et al.*, 2002) compared to conventional systems, where annual tillage is more likely (López-Fando and Bello, 1995; Hatten *et al.*, 2007; Eyre and Leifert, 2011b). Soil tillage is known to affect invertebrates, with most studies indicating higher diversity and abundance in no-till, or reduced tillage systems (Kladivko, 2001; Sharley *et al.*, 2008). The impacts are variable, however, possibly depending on the life-history traits of different invertebrate species (Inclán *et al.*, 2014). For example, small, highly active species respond to more intensively managed systems (Cole *et al.*, 2005) whilst non-carnivorous beetles are common in crops such as wheat that have larger areas of bare ground (Batáry *et al.*, 2012). Many studies have utilised only a single trapping method (usually pitfall traps) in isolation which as an “activity-density” measure may not reflect the actual invertebrate population size (Topping and Sunderland, 1992).

To understand the different effects on the invertebrates of crop rotation, soil tillage, farm management, current and previous cropping history, it is necessary to study them over the entire crop rotation. Here i utilise eight and five-year invertebrate data from a split organic/conventional farm in northern England, respectively. We split the invertebrates into three broad functional groups: epigeal predators; foliar predators/parasitoids and herbivores/pollinators. I also employed two standard sampling methods, in an attempt to obtain more representative invertebrate data (Gibb and Hochuli, 2002; Ford *et al.*, 2012).

The primary aims were to:

1) Invertebrate abundance is affected primarily by the current year’s crop in both organic and conventional crop rotations
2) Temporal changes in a crop rotation will influence invertebrate assemblage composition in organic and conventional rotations
3) Quantify the relative importance of current and previous year’s crop on the invertebrate assemblage composition for the three functional groups, within each management system

5.3 Materials and Methods

5.3.1 Survey Area and Management

The research was undertaken at Nafferton Farm in Northumberland, UK (54°59', 09"N; 1°43', 56"W), and approximately half the farm (160 ha) is under organic management, with the remainder conventional. The crop rotations are summarised in Figure 5.1. The data analysed in this study covers an eight-year organic period from 2005 to 2012 inclusive, and five-year conventional period from 2005 to 2009, with individual fields in both management systems in different ‘Rotation Years’.

Arable crops on the conventional half were autumn-sown with annual ploughing and application of herbicides and fungicides where appropriate. Organic crops were spring-sown with no use of synthetic pesticides or fertilisers. In the organic rotation during grass-clover leys the soil was not cultivated but leys were cut three times/year for silage.

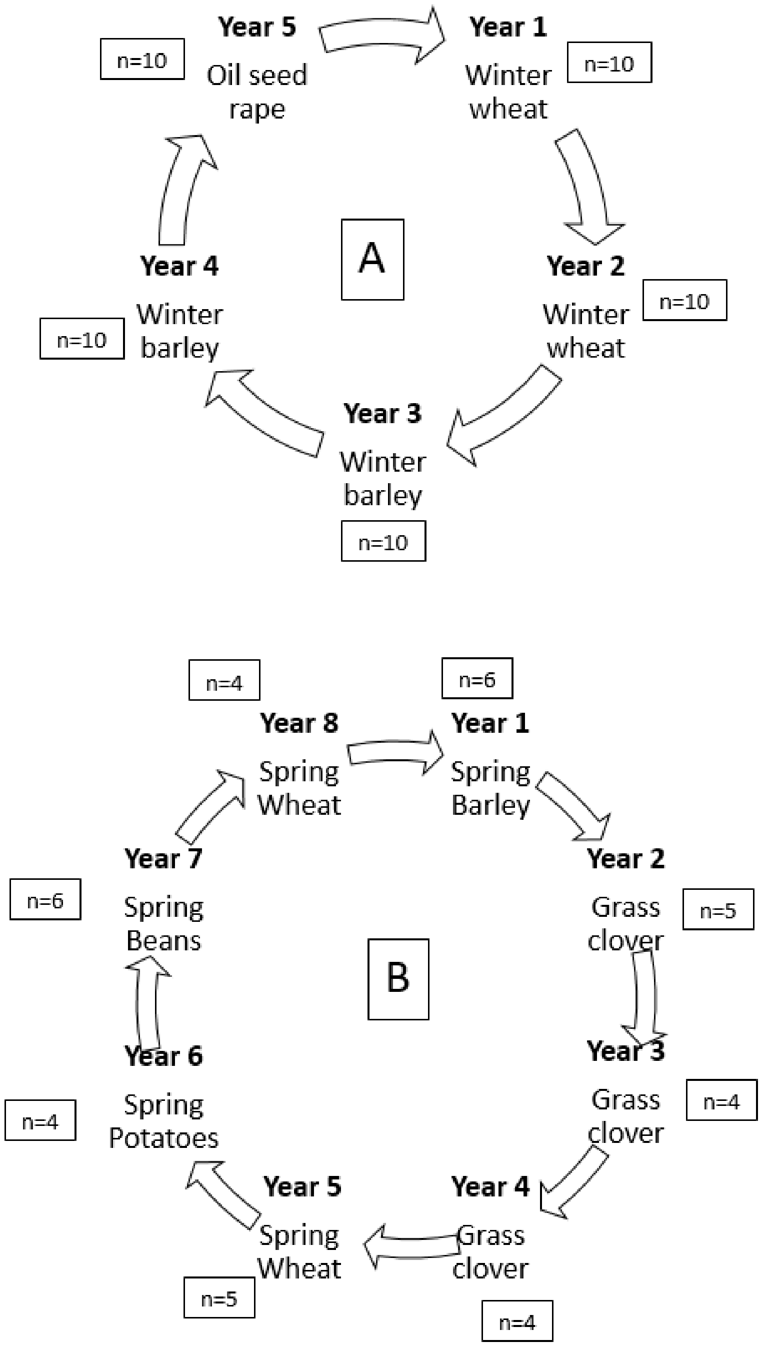


Figure 5.1 The five year crop rotation for the conventional farm A) and eight year rotation on the organic half of Nafferton B). n = numbers of fields sampled per year in each crop.

5.4 Sampling

5.4.1 Invertebrates

Invertebrates were sampled from a pair of sites approximately 20 m apart in each field, at least 40 m from the field boundary (within the crop). Invertebrates were trapped at each site with a line of 10 pitfall traps, 0.5 m apart (white polypropylene cups 8.5 cm diameter, 10 cm deep) and yellow pan traps (plastic box 30 cm x 22 cm, 20 cm deep, see Chapter 2, Figure 2.3 and Figure 2.4), all part-filled with saturated salt (NaCl) solution containing a small amount of detergent as a preservative and break the surface tension (Schmidt *et al.*, 2006). Samples were collected over the whole rotation period of both management systems (2005 – 2012), with traps set in the first week of May (traps temporarily removed during silage cuts) emptied monthly over a 20 week period (Menalled *et al.*, 2007; Eyre *et al.*, 2013b). Seventy-six samples were undertaken in the organic half of farm and fifty samples in the conventional (Table 5.1).

Organic crops (rotation year)	Number of organic samples \ yr	Number of organic fields \ yr	Conventional crops (rotation year)	Number of conventional samples \ yr	Number of conventional fields \ yr
Barley (1)	12	6	Wheat (1)	10	5
Grass/clover (2)	10	5	Wheat (2)	10	5
Grass/clover (3)	8	4	Barley (3)	10	5
Grass/clover (4)	8	4	Barley (4)	10	5
Wheat (5)	10	5	OSR (5)	10	5
Potatoes (6)	8	4			
Beans (7)	12	6			
Wheat (8)	8	4			
Totals	**76**	**38**		**50**	**25**

Table 5.1 Total number of samples, aggregated across all months, collected per crop per year, and number of fields sampled per year, between 2005 to 2012, on the organic and conventional rotations at of Nafferton farm.

Invertebrates were identified to family, sub-family and tribe, according to Chinery (1993); Roberts (2001); Luff (2007) and confirmed by expert entomologist Dr M.D. Eyre, depending on functional group, and counted, see Table 5.2. Invertebrates were classified into three functional groups, based primarily on their life-history as adults: epigeal predators, foliar predators/parasitoids and herbivores/pollinators, with taxa split according to the schema given by Ford *et al.* (2013). The characteristics of the nearest field boundary to each site were recorded according to the classification of Eyre and Leifert (2011b). Mean air temperature per month and total monthly rainfall were calculated from data collected via the Delta-T Weather Station (Type WS01) located on the farm.

	Organic totals		Conventional totals
Epigeal predators	**112790**	**Epigeal predators**	**113608**
Carabidae	74616	Carabidae	86931
Bembidiini	16883	Bembidiini	4894
Harpalini	520	Loricerini	6707
Loricerini	4815	Nebriini	11754
Nebriini	5867	Notiophilini	1219
Notiophilini	638	Platynini	2827
Platynini	2135	Pterostichini	50752
Pterostichini	35453	Sphodrini	180
Sphodrini	454	Trechini	4670
Trechini	6196	Zabrini	3840
Zabrini	1681	Staphylinidae	11919
Staphylinidae	12324	Aleocharinae	867
Aleocharinae	2391	Omalinae	122
Paederinae	585	Paederinae	410
Staphylininae	7327	Staphylininae	6481
Steninae	178	Steninae	134
Tachyporinae	1761	Tachyporinae	3883
Foliar predators/parasitoids	**35130**	**Foliar predators/parasitoids**	**20849**
Cantharidae	415	Cantharidae	176
Coccinellidae	1539	Coccinellidae	250
Anthocoridae	144	Syrphidae	366
Syrphidae	1302	Braconidae	2032
Braconidae	4416	Ichneumonidae	11310
Ichneumonidae	24920	Platygasteridae	1416
Platygasteridae	292	Proctotrupidae	4262
Proctotrupidae	3476	Pteromalidae	1126
Pteromalidae	434	**Herbivores/pollinators**	**8987**
Herbivores/pollinators	**26770**	Chrysomelidae	1650
Chrysomelidae	6215	Curculionidae	1865
Curculionidae	11108	Nitidulidae	1897
Nitidulidae	1517	Cercopidae	154
Cercopidae	147	Cicadellidae	359
Cicadellidae	1121	Apidae	361
Miridae	688	Cynipidae	1894
Apidae	514	Tenthredinidae	156
Cynipidae	1294		
Tenthredinidae	2828		

Table 5.2 Invertebrate individual totals for the three functional groups in organic and conventional system sampled over the rotation period.

5.5 Data analysis

5.5.1 Effects of current year's crop on invertebrate abundance in different taxa and functional groups

Linear mixed-effects models (LME) were used to determine the relative importance of the current and previous year's crop type on invertebrate abundance, having corrected for variability associated with temperature, rainfall, field boundary type and year of survey. Analyses were done both for individual taxa (family, tribe or subfamily as appropriate) as well as life-history functional groups (epigeal predators, foliar predators/parasitoids and herbivores/pollinators). Separate analyses were undertaken for the organic and conventional datasets, as the large differences between the two management systems (e.g. rotation system, chemical applications) make a single analysis inappropriate.

Invertebrate counts were log-transformed (Crawley, 2007), in a similar procedure used by Eyre and Leifert (2010) prior to analysis with R (Pinheiro *et al.*, 2011a) and the nlme package (Pinheiro and Bates, 2000). Current year's crop was used as a fixed-effect factor, with five levels in organic crops (barley, grass/clover, wheat, potatoes and beans) and three levels in conventional crops (barley, wheat and oilseed rape). Random factors were sampling year (2005-2012) boundary type, and continuous variable temperature and rainfall.

5.5.2 Temporal change in invertebrate assemblage composition across the organic and conventional rotations

Partial canonical correspondence analysis (pCCA) was used to measure changes in invertebrate composition in each functional group over the course of the rotation cycle, as a result of the current year's crop. The current year's crop was used as an active explanatory variable, the previous year's crop was partialled-out (conditional variable) whilst the matrix of invertebrates by sites formed the response variables. Temperature, rainfall and field boundary type were used as partial variables. The contribution of each current crop-type within the rotation was tested via automatic forward selection, determined using Monte Carlo permutation tests (999 permutations). The pCCAs were carried out using the CANOCO software (Ter Braak and Smilauer, 2002); separate analyses were done for each of the three functional groups in both management systems. Separate analyses were undertaken for the organic and conventional datasets, as the large differences between the two management systems (e.g. rotation system, chemical applications) make a single analysis difficult to interpret with taxa (see Figure 5.2).

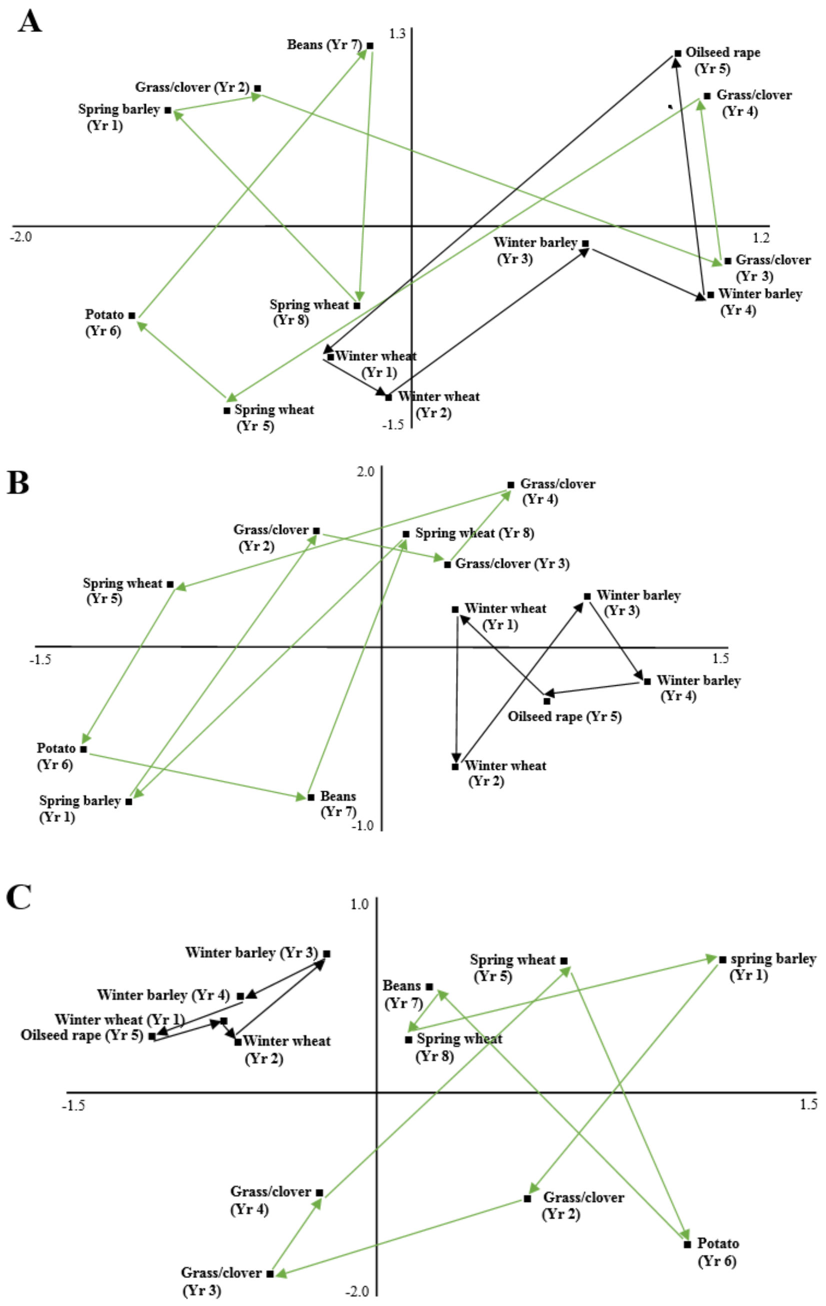


Figure 5.2 pCCA analyses of invertebrates on both the conventional (black) and organic (green) parts of the farm, explained by crop type, in the rotation sequence. A) epigeal predators(axis 1:19.7%, eigenvalue 0.011; axis 2: 12.3%, eigenvalue 0.004); B) foliar predators/parasitoids (axis 1: 22.3%, eigenvalue 0.046; axis 2: 18.5%, eigenvalue 0.007); C) herbivores/pollinators (axis 1: 29.9%, eigenvalue 0.052; axis 2: 21.4%, eigenvalue 0.014). Rainfall and field boundary are partial variables. Points for samples and taxa not shown for clarity.

5.5.3 Relative effect of current and previous- crops on invertebrate assemblages

Variance partitioning was used to quantify individual and / or joint effects of multiple sets of explanatory variables on community composition (see Borcard *et al.* (1992); (Dray *et al.*, 2012). The aim of this analysis was to quantify the effects on the invertebrate community of a) purely the current crop, b) purely the previous crop, c) the joint effect (if any) of both current and previous crops, d) residual unexplained variation. The significance of individual components of purely the current crop and purely the previous crop was tested by Monte Carlo permutation tests (999 permutations); this cannot be done reliably for the joint effect (Buttigieg and Ramette, 2014).

5.6 Results

5.6.1 Organic Management: Effects of current year’s crop on organic invertebrate abundance in different taxa and functional groups

Epigeal predators were more abundant in grass/clover (Yr4), and lowest on potatoes (Yr 6), with a significant difference between the crops ($F_{7, 48}$=3.50, P=0.004). Carabidae was most abundant in the wheat (Yr 5), least in potatoes (Yr 6- $F_{7, 48}$=5.90, P<0.001), whilst most Staphylinidae were found in grass/clover (Yr 4) and least in wheat (Yr 8- $F_{7, 48}$=2.40, P=0.038). At the tribe or subfamily level of epigeal predators, Loricerini was more abundant in those years when grass/clover was cultivated compared to other crops. In contrast, Bembidiini, Platynini and Zabrini were least abundant (reading along rows in Table 5.3). Pterostichini were more abundant in wheat (Yr 5) that immediately followed grass/clover (Wheat 1 in Table 5.3) but their numbers were reduced by approximately 50% in the other wheat crop (Yr 8) that was preceded by beans (Wheat 2 in Table 5.3). Platynini abundance appeared to decline during the three years of grass/clover, and indeed had their lowest abundance in any crop type by the third season of grass/clover (Yr 4). Nine out of the fifteen main epigeal tribes/ subfamilies taxa were more abundant in wheat crop (Yr 5), after 3 years of grass/clover, than in the second wheat (Yr 8) which followed beans in the rotation.

	Barley	**Grass/clover 1**	**Grass/clover 2**	**Grass/clover 3**	**Wheat 1**	**Potatoes**	**Beans**	**Wheat 2**	**F ratio**	**P-value**
Epigeal predators	**1440±113**	**1488±117**	**1378±291**	**2022±286**	**1978±78**	**1093±161**	**1660±168**	**1396±224**	3.5	**0.004**
Carabidae	1010±108	810±80	817±127	1132±178	1415±112	764±141	1239±154	1020±194	5.9	**<0.001**
Bembidiini	292±60	109±14	114±39	143±40	223±45	365±76	362±53	254±69	12.6	**<0.001**
Harpalini	5±1.1	6±1.7	6±2.1	6±2.6	11±4.0	6±2.3	10±3.5	8±4.3	0.3	0.945
Loricerini	55±19.8	112±21	109±24	125±34	27±4.8	11±3.0	62±15.4	37±5.4	13.1	**<0.001**
Nebriini	54±15.1	47±6.1	87±15.5	141±46	104±25	28±8.0	102±26	72±32.1	3.1	**0.009**
Notiophilini	6±1.1	14±3.6	15±3.1	13±3.3	4±0.8	5±1.8	10±2.0	6±1.3	4.1	**<0.001**
Platynini	46±13.9	20±3.8	10±2.1	9±2.6	42±7.6	28±10.5	47±17.6	27±8.8	5.3	**<0.001**
Pterostichini	428±72	405±65	388±39	536±109	901±95	215±52	531±97	462±74.4	5.9	**<0.001**
Sphodrini	1±0.4	1±0.2	1±0.7	9±4.2	18±9.0	7±2.8	5±2.8	8±4.7	3.7	**0.003**
Trechini	99±23.1	74±24.2	80±24.8	142±40	70±23.0	77±48.5	59±26.5	97±30.6	2.9	**0.012**
Zabrini	23±4.9	20±4.3	6±1.3	6±1.2	14±2.3	22±5.5	48±7.2	45±13.2	8.5	**<0.001**
Staphylinidae	179±31	176±41	110±15	261±75	212±18	185±45	137±19	105±14	2.4	**0.038**
Aleocharinae	29±8.2	9±3.4	5±1.7	6±1.8	57±12.9	113±41	24±6.4	27±3.4	15.2	**<0.001**
Paederinae	9±3.6	9±1.2	8±1.7	6±1.7	7±2.0	18±5.5	6±1.7	3±1.4	2.7	**0.021**
Staphylininae	122±29	119±37	74±7.5	201±68	114±16	42±6.0	75±12.8	61±11.1	6	**<0.001**
Steninae	2±0.8	4±1.0	4±1.1	5±1.1	2±1.0	1±0.5	1±0.5	2±0.4	1.8	0.109
Tachyporinae	16±2.9	34±9.6	19±6.1	43±10.1	30±6.5	10±2.6	29±12.3	12±2.9	2.3	**0.039**
Foliar predators/parasitoids	**1453±779**	**158±25**	**110±16**	**299±55**	**385±49**	**238±56**	**876±439**	**153±35**	5.1	**<0.001**
Cantharidae	3±1.1	1±0.6	3±0.6	12±5.0	9±2.4	5±1.0	8±2.7	6±1.5	3.3	**0.006**
Coccinellidae	34±12.5	3±1.3	2±1.2	10±4.5	36±10.6	63±13.4	16±6.6	6±2.8	10.6	**<0.001**
Anthocoridae	4±1.7	-	-	-	-	4±1.5	6±2.7	2±0.9	7.2	**<0.001**
Syrphidae	22±7.6	10±3.8	3±0.9	10±3.9	23±5.4	17±4.0	41±20.2	12±4.0	3.3	**0.006**
Braconidae	130±69	17±4.8	16±5.1	35±9.4	67±24.7	38±11.7	96±33.8	17±7.6	2.5	**0.027**
Ichneumonidae	1175±657	99±18.7	62±13.6	196±47	218±28	128±35	620±350	90±22.8	5	**<0.001**
Platygasteridae	10±3.9	4±1.1	2±0.5	3±1.0	3±0.7	6±2.9	3±0.8	1±0.7	4.1	**<0.001**
Proctotrupidae	81±32.1	23±3.6	21±2.6	39±2.4	60±8.9	34±11.7	84±36.1	32±10.6	2.8	**0.016**
Pteromalidae	21±13.3	2±0.4	-	1±0.3	1±0.9	2±1.0	17±9.5	1±0.2	4.9	**<0.001**
Herbivores/pollinators	**317±43**	**147±23**	**216±27**	**362±52**	**542±168**	**229±49**	**795±283**	**281±40**	12.9	**<0.001**
Chrysomelidae	106±19	14±5.1	10±2.1	7±2.4	195±91	64±14.3	185±68	70±26.4	24.1	**<0.001**
Curculionidae	63±14.5	80±16.9	148±24	277±54	88±18.6	74±18.0	452±180	36±7.2	12.7	**<0.001**
Nitidulidae	16±3.1	3±1.0	1±0.3	8±4.0	69±27.3	5±2.1	42±19.6	14±7.6	9.6	**<0.001**
Cercopidae	6±2.4	2±0.5	1±0.4	2±0.8	2±0.5	1±0.9	1±0.6	1±0.6	1.9	0.085
Cicadellidae	16±5.7	14±6.6	3±0.9	9±2.7	23±9.4	46±27.4	6±2.5	9±3.0	2.3	**0.044**
Miridae	16±8.8	1±0.4	-	1±0.6	34±31.3	2±0.7	13±7.6	3±1.6	3.8	**0.002**
Apidae	4±1.1	6±2.0	8±2.7	9±4.5	8±4.2	8±2.6	9±3.2	6±1.1	2.6	**0.022**
Cynipidae	29±17.4	4±1.2	5±1.3	4±0.8	11±2.6	14±4.2	17±8.4	63±40.0	7.5	**<0.001**
Tenthredinidae	49±18.6	3±1.2	2±0.6	8±3.2	98±45.9	12±5.5	63±28.9	67±42.3	6.6	**<0.001**

Table 5.3 Mean number of each taxa, ± SE, recorded from each organic crop, plus F ratio and probability (*P*) derived from the mixed-effects models (df 7, 48)

Foliar predators/parasitoids were most abundant in barley (Yr 1), and lowest on in grass/clover (Yr 3- $F_{7,48}$=5.10, P<0.001) (Table 5.3). At the family-level, the parasitic Ichneumonidae was most abundant in barley (Yr 1), that follow wheat (Yr 8 in Table 5.3), the last year of the rotation, and lowest in grass/clover (Yr 3- $F_{7,48}$=5.0, P<0.001). Braconidae, Coccinellidae, and Syrphidae were least abundant in the three years of grass/clover and in wheat (Yr 8, Table 5.3). Five out of the nine foliar predator/parasitoid families were most abundant in barley (Yr 1) and beans (Yr 7).

Herbivores/pollinators were most abundant in the bean crops (Yr 7), and lowest on in grass/clover (Yr 2- $F_{7,48}$=12.9, P<0.001) (Table 5.3). Four out of the nine herbivorous families were most abundant in wheat crops, barley and beans (Miridae, Tenthredidinae, Nitidulidae, and Chrysomelidae).

5.6.2 Temporal change in invertebrate community composition across the organic rotation

Community composition of epigeal predators Figure 5.3 along Axis 1 showed a trend from grass/clover (low axis 1 scores) to all the other crops (high axis 1 scores) especially potato. Loricini and Notiophilini were the taxa most associated with grass/clover whilst Aleochorinae and Sphodrini were associated with potatoes. Turnover of taxa along axis 2 was limited, with none showing a strong association to any crop. A number of the abundant and ubiquitious taxa, such as Staphylininae, Pterostichini and Bembidiini occurred near the origin of the axes, showing no affiliation solely to any organic crop. All three grass/clover crops affected community composition (Yr 2 - F=4.27, P=0.004; Yr 3 - F=4.53, P=0.002, Yr 4 - F=4.25, P=0.002), as did barley (Yr 1 - F=4.70, P=0.002), beans (Yr 7 - F=2.95, P=0.012) and potatoes (Yr 6 - F=3.06, P=0.002).

Foliar predator/parasitoid assemblages also showed a trend from those dominated by grass/clover leys to the other crops (Figure 5.3 B). Anthocoridae was strongly associated with beans (Yr 7), whilst Hymenopteran- Platygasteridae predominant in the grass/clover. Spring beans (Yr 7 - F=2.95, P=0.024) had significant effects on the foliar predators/parasitoids taxa composition. This pattern was repeated for the herbivores/pollinators (Figure 5.3 C): Curculionidae being associated with the grass/clover crops, whilst Nitidulidae beans (Yr 7) and wheat (Yr 5 & Yr 8). Whilst there is a broadly anti-clockwise change in community composition across the rotation in Figure 5.3 A, and clockwise in Figure 5.3 B and Figure 5.3 C, this merely reflects the output configuration. No particular conclusions from one being clockwise and the other anti-clockwise should be inferred: it is the relative positions in ordination space that matter. All three grass/clover crops affected community composition (Yr 2 - F=6.42, P=0.002; Yr 3 - F=5.98, P=0.002, Yr 4 - F=6.08, P=0.002), as did barley (Yr 1 - F=2.76, P=0.010), beans (Yr 7 - F=2.23, P=0.018) and potatoes (Yr 6 - F=2.38, P=0.018).

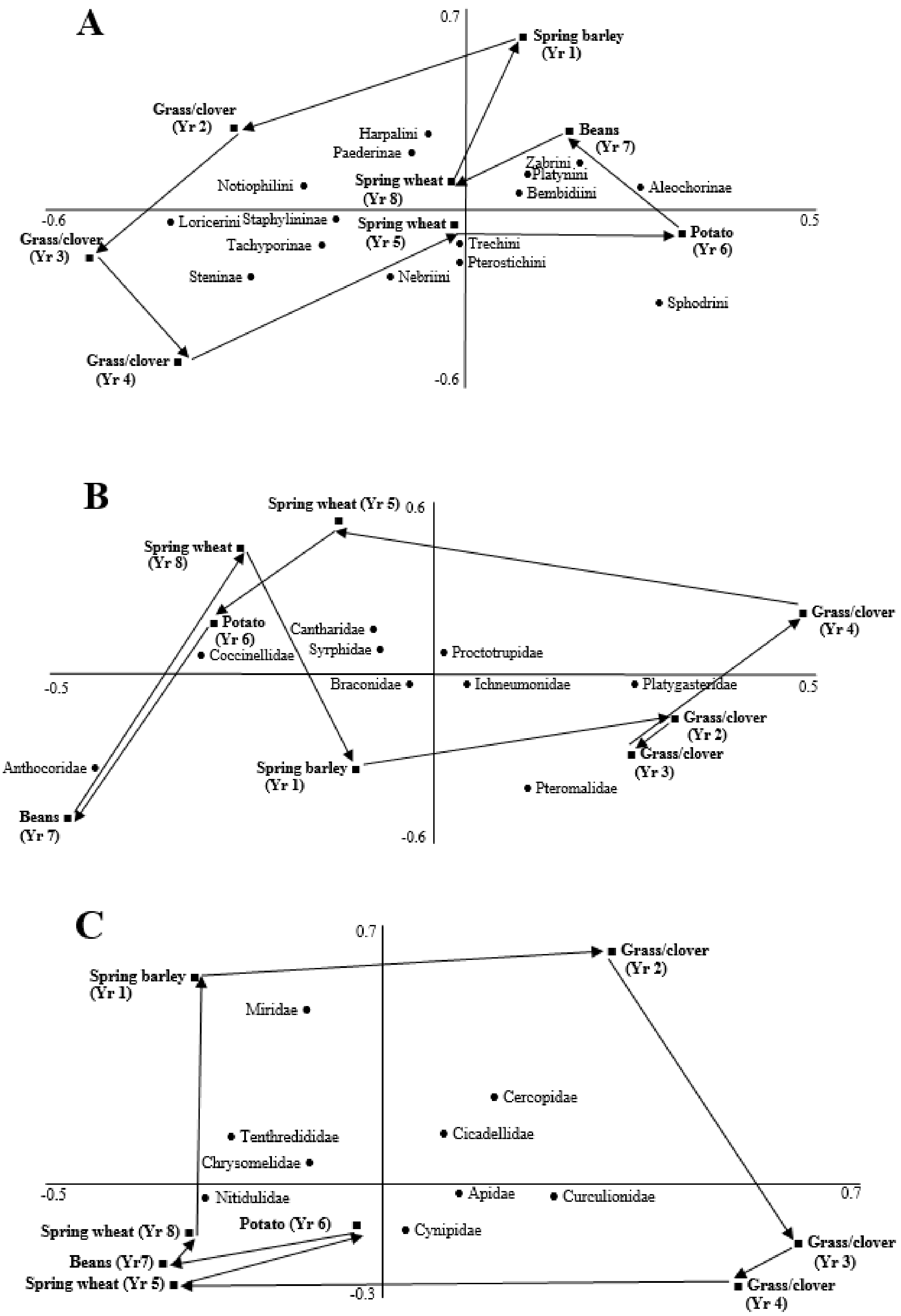


Figure 5.3 pCCA plots of organic taxa; square symbols are centroids of the active explanatory variable, crop type, connected according to rotation sequence, whilst circles are invertebrate taxa. A) epigeal predators (axis 1: 15.6%, eigenvalue 0.013; axis 2: 8.9%, eigenvalue 0.008), B) foliar predators/parasitoids (axis 1: 10.6%, eigenvalue 0.021; axis 2), C) herbivores/pollinators (axis 1: 19.1%, eigenvalue 0.034; axis 2: 5.2%, eigenvalue 0.009). Rainfall and field boundary are partial variables.

5.6.3 Relative effect of current- and previous-crops on organic invertebrate communities

Overall, the current and previous crop types explained between 21% and 25% of the total variation in the organic invertebrate community composition for the three major functional groups Table 5.4. There was relatively little difference in the overall pattern between the functional groups, with most of the variation (6.6 to 11.9%) being explained by the current year's crop, and 6.0% to 12.6% jointly between the previous and current year's crop. Only a small amount of the variation (3.7% to 5.5%) could be uniquely allocated to the previous year's crop. However, irrespective of the crop effects, 75.3% of the variation in epigeal and foliar predators, assemblages was unexplained, slightly more for herbivores/pollinators (79.0%) by either previous or current year's crop influence.

Functional group	Current year's crop	Previous year's crop	Joint effect of current & previous year's crop	Residual
Epigeal predators	10.5	3.7	10.5	75.3
Foliar predators / parasitoids	6.6	5.5	12.6	75.3
Herbivores / pollinators	11.9	3.1	6.0	79.0

Table 5.4 Variation partitioning of unique and joint effects (percentage explained) of the current and previous year's crop on the invertebrate community composition in the organic system.

In the epigeal predators, of the 10.5% purely explained by the current crop (Table 5.4, the two most important were grass/clover (F=5.82, P=0.002) and barley (F=3.07, P=0.006), whilst of the 3.7% purely explained by the previous year's crop this was primarily from grass/clover (F=2.05, P=0.036). In foliar predators/parasitoids (Table 5.4), both barley (F=2.93, P=0.006) and grass/clover (F=2.81, P=0.014) had significant effects on the 6.6% of variation uniquely explained by the current crop, whilst of the 5.5% uniquely explained by the previous crop this was mainly associated with beans (F=2.73, P=0.008) and barley (F=1.99, P=0.038). In the herbivores/pollinators (Table 5.4), 11.9% was uniquely associated with the current crop, especially grass/clover (F=8.18, P=0.002). No crop types were identified as significant with the previous year's crop.

5.6.4 Conventional Management: Effects of current year's crop on conventional invertebrate abundance in different taxa and functional groups

There was no significant difference in the overall numbers of epigeal predators between crops ($F_{4,29}$=0.30, P=0.869 - Table 5.5). Carabidae were most abundant in wheat (Yr 1) and, least in barley (Yr 3 - $F_{4,29}$=3.20, P=0.028) whilst Staphylinidae were most abundant in the oilseed rape (Yr 5) and least in wheat (Yr 2 - $F_{4,29}$=8.70, P<0.001). Six of the most abundant foliar taxa (Nebriini, Notiophilini, Zabrini, Aleocharinae, Tachyporinae and Staphylininae) were most abundant in oilseed rape (Yr 5). Ten taxa, with mean greater than 10, were more abundant in the first year of wheat (Yr 1) than second wheat (Yr 2), whilst 10 taxa, were more abundant in the second year of barley (Yr 4) than first barley (Yr 3).

Foliar predators/parasitoids were most abundant in oilseed rape (Yr 5), and least abundant in the first barley crop (Yr 3 - $F_{4,29}$=18.9, P<0.001 - Table 5.5). Three foliar parasitoids: Braconidae ($F_{4,29}$=21.3, P<0.001), Ichneumonidae ($F_{4,29}$=24.3, P<0.001), and Pteromalidae ($F_{4,29}$=24.4, P<0.001) were most abundant in oilseed rape (Yr 5). Six out of the eight foliar predators/parasitoids were significantly different in their abundance across the rotation. Herbivores/pollinators were most abundant in oilseed rape (Yr 5) and least in the first year of barley (Yr 3 - $F_{4,29}$=40.0, P<0.001). Abundance of Chrysomelidae ($F_{4,29}$=18.4, P<0.001), Curculionidae ($F_{4,29}$=17.9, P<0.001), Cynipidae ($F_{4,29}$=14.3, P<0.001), and Nitidulidae ($F_{4,29}$=17.5, P<0.001) differed over the rotation and were most common in oilseed rape (Yr 5).

	Wheat 1	Wheat 2	Barley 1	Barley 2	Oilseed rape	F ratio	P-value
Epigeal predators	**2669±423**	**2218±217**	**1828±435**	**2302±363**	**2342±275**	0.3	0.869
Carabidae	2425±319	1640±207	1366±420	1613±299	1658±239	3.2	**0.028**
Bembidiini	84±24.1	69±24.4	44±13.5	177±64	115±17	0.8	0.536
Loricerini	116±23	96±18.8	194±67	91±20.5	173±36	5.8	**0.002**
Nebriini	244±77	185±27	113±35	254±66	379±121	1.7	**0.002**
Notiophilini	23±2.5	17±2.0	18±2.9	20±2.7	44±5.7	3.5	**0.018**
Platynini	85±32.0	55±13.8	42±16.4	54±24.3	47±6.6	1.7	**0.016**
Pterostichini	1756±357	1058±184	857±336	806±230	599±78	4.9	**0.004**
Sphodrini	6±3.9	4±1.5	2±0.4	5±1.2	2±0.6	1.5	0.226
Trechini	66±19.9	145±49.7	81±29.7	108±29.4	66±13.4	4.6	**0.009**
Zabrini	33±6.5	9±1.8	14±4.6	96±51.8	232±80.2	7.6	**<0.001**
Staphylinidae	137±22	107±21	203±58	322±44	422±73	8.7	**<0.001**
Aleocharinae	9±3.4	11±3.3	14±5.3	23±6.9	30±7.6	3.2	**0.028**
Omalinae	1±0.3	1±0.4	1±0.2	4±2.1	5±2.5	2.4	0.071
Paederinae	4±1.3	4±1.1	8±2.5	9±2.9	16±4.9	2.2	0.094
Staphylininae	89±16.1	58±14.3	94±33.4	154±26	254±66	6.3	**<0.001**
Steninae	1±0.4	1±0.5	3±0.6	3±1.0	5±1.1	4.3	**0.008**
Tachyporinae	34±6.2	33±10.4	82±21.4	128±38	112±23	9.7	**<0.001**
Foliar predators/parasitoids	**383±66**	**256±39**	**102±19**	**233±47**	**1111±301**	18.9	**<0.001**
Cantharidae	2±0.7	2±0.5	2±0.4	4±1.0	9±3.3	3.8	**0.012**
Coccinellidae	4±1.6	7±2.0	2±0.6	8±3.4	3±0.8	2.4	0.076
Syrphidae	11±2.4	10±2.6	2±0.6	6±1.4	8±2.5	3.9	**0.012**
Braconidae	22±5.4	19±5.6	7±3.3	9±2.3	147±27	21.3	**<0.001**
Ichneumonidae	241±42	101±25	22±5.2	41±10.2	726±280	24.3	**<0.001**
Platygasteridae	2±0.8	41±25.7	9±4.6	18±9.8	70±41	4.8	**0.004**
Proctotrupidae	101±32	54±13.7	38±13.3	131±54	103±27	1.9	0.130
Pteromalidae	1±0.4	25±15.5	21±13.8	22±14.9	44±11.1	24.4	**<0.001**
Herbivores/pollinators	**72±20.6**	**93±23.4**	**54±9.7**	**99±16.9**	**581±93**	40	**<0.001**
Chrysomelidae	10±4.8	18±5.4	10±3.2	14±2.9	114±34	18.4	**<0.001**
Curculionidae	19±6.3	10±3.6	11±2.0	30±7.2	117±46	17.9	**<0.001**
Nitidulidae	3±0.9	5±3.3	1±0.5	3±1.7	177±60	17.5	**<0.001**
Cercopidae	2±0.5	6±2.6	1±0.4	2±0.7	6±1.5	3.2	**0.028**
Cicadellidae	8±3.0	6±2.7	4±1.6	11±2.8	8±3.6	0.5	0.770
Apidae	9±4.3	17±7.0	2±0.8	3±0.9	6±1.9	0.7	0.614
Cynipidae	8±2.3	15±6.5	16±8.9	16±6.5	135±50	14.3	**<0.001**
Tenthredinidae	3±1.3	3±1.2	2±1.1	2±0.5	5±1.1	3.6	**0.017**

Table 5.5 Mean number of each taxa, ± SE, recorded from each conventional crop, plus F ratio and probability (*P*) derived from the mixed-effects models (df 4, 29).

5.6.5 Temporal change in invertebrate community composition across the conventional rotation

Variation in epigeal predator was along a trend from samples in wheat (Yr 1 & Yr 2) through to those from barley (Yr 3 & Yr 4 - Figure 5.4 A) with Harpalini associated with wheat (Yr 1), and Steninae and Omalinae barley (Yr 3 & Yr 4). Monte Carlo permutation tests indicated that oilseed rape (Yr 5 - F=3.92, P=0.004) and both wheat crops (Yr 1 - F=2.90, P=0.004; Yr 2 - F = 2.61, P=0.012) significantly affected the taxonomic composition of epigeal predator assemblages. Axis 1 for foliar predators/parasitoids (Figure 5.4 B) indicated a trend from first year of wheat (Yr 1) through to the second wheat crop (Yr 2), whilst axis 2 separated oilseed rape (Yr 5) from the other crops, but there were no strong associations between crops and any taxa and none of the crops were significant in the permutation tests. In herbivores/pollinators (Figure 5.4 C) the main trend was from oilseed rape (Yr 5) compared to the other crops, especially the second wheat crop. Nitidulidae (pollen beetles) were strongly associated with oilseed rape, with Cicadellidae and Cercopidae characteristic of the cereals. Oilseed rape (Yr 5 - F = 7.69, P=0.002) and the second wheat crop (Yr 2 - F = 2.67, P=0.006) had significant effects on the herbivore taxa composition.

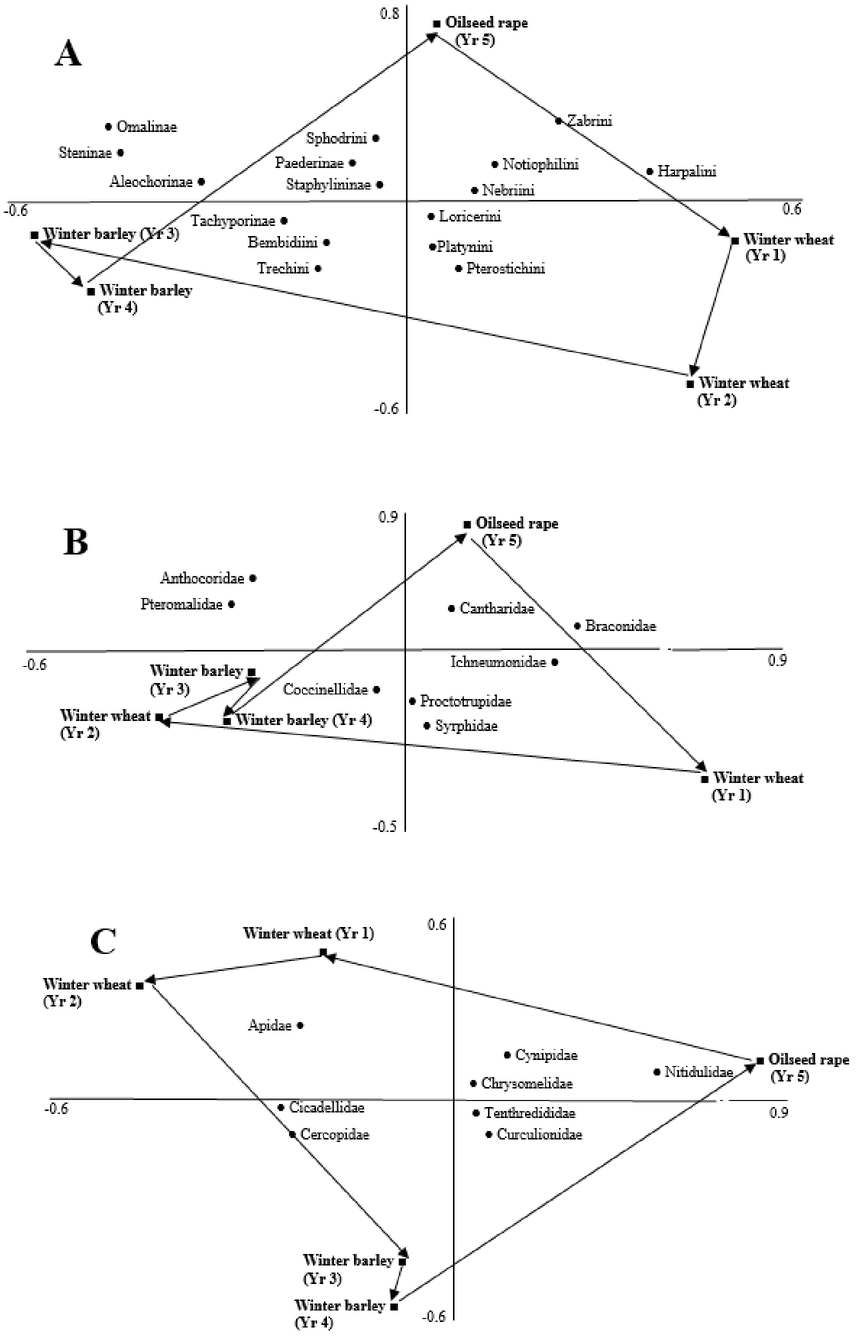


Figure 5.4 pCCA plots of conventional taxa; square symbols are centroids of the active explanatory variable, crop type, connected according to rotation sequence, whilst circles are invertebrate taxa. A) epigeal predators (axis 1: 10.3%, eigenvalue 0.006, axis 2: 7.8%, eigenvalue 0.004), B) foliar predators/parasitoids (axis 1: 5.6%, eigenvalue 0.014, axis 2: 3.9%, eigenvalue 0.010), C) herbivores/pollinators (axis 1: 16.3%, eigenvalue 0.034, axis 2: 6.5%, eigenvalue 0.014). Rainfall and field boundary are partial variables.

5.6.6 Relative effect of current- and previous-crops on conventional invertebrate communities

The current and previous crop types explained between 14% and 19% of the total variation in the invertebrate community composition for the three major functional groups Table 5.6. Differences were apparent between the epigeal predators and herbivores/pollinators compared with foliar predators/parasitoids; most of the variation was explained by the current year's crop for epigeal predators and herbivores/pollinators (10.6 and 6.3% respectively), in contrast most variation (8.3%) was explained by previous year's crop for foliar predators/parasitoids. Only 1.2% to 3.9% of the total variation was explained jointly by the previous and current year's crop and all three functional groups had a large amount of unexplained variation.

In epigeal predators, of the 10.6% purely explained by the current crop, the most important was barley (F=4.21, P=0.002), whilst of the 6.8% purely explained by the previous year's crop this was primarily from wheat (F=2.91, P=0.002). In foliar predators/parasitoids wheat had significant effects on the 8.3% of variation uniquely explained by the previous year's wheat crop (F=3.77, P=0.026). For the herbivores/pollinators, 6.3% was uniquely associated with the current crop, as a result of wheat (F=3.24, P=0.008); no crops from the previous year significantly affected herbivores/pollinators.

Functional group	**Current year's crop**	**Previous year's crop**	**Joint effect of current & previous year's crop**	**Residual**
Epigeal predators	10.6	6.8	2.2	80.4
Foliar predators / parasitoids	4.8	8.3	1.2	85.7
Herbivores / pollinators	6.3	4.0	3.9	85.8

Table 5.6 Variation partitioning of unique and joint effects (percentage explained) of the current and previous year's crop on the invertebrate community composition in the conventional system.

5.7 Discussion

This study has demonstrated that long-term rotation, current and previous crops, and soil-tillage, all affect both the abundance and taxonomic composition of invertebrates in agricultural landscape. Annual soil cultivation was similar within each conventional crop and differences between invertebrate abundance on the conventional crops were more likely to be related to crop type and associated microclimate (Doblas-Miranda *et al.*, 2009; Ewald *et al.*, 2015). In contrast, the amount of soil cultivation was variable in the organic system, with several years of no tillage (grass/clover leys), compared with crops with considerable disturbance (potatoes). In both systems the current year's crop type had, as might be expected, a much larger effect on the invertebrates than that of the previous year's crop, but the latter was, nevertheless, significant.

The application of chemical fertilisers, herbicides and fungicides in the conventional system produced far denser cereal crops than similar crops under organic management, whilst within the conventional system the oilseed rape produced the greatest density of foliage. After petal fall detritivores such as Collembola are attracted in the oilseed rape fields due to its abundant flowers, which provide food for pollinators and pollen-feeders. The numbers of invertebrates per sample was approximately 45% higher from the conventionally managed field compared with the organically managed Eyre *et al.* (2013b) suggested that invertebrate abundance is reduced with soil disturbance, but increases with crop biomass. Given that conventional management imposes greater soil disturbance than organic management, yet nevertheless had higher mean invertebrate abundance, suggests that crop biomass is particularly important.

Epigeal predator abundance in the organic management systems was significantly influenced by crop type. Their abundance however was not constant across all crops, nor within the same crop in different years of the rotation. Epigeal predators are a broad group, with a wide range of life history traits and habitat preferences (Grez *et al.*; Rusch *et al.*, 2015). In the organic rotation, greater epigeal predator abundance in grass/clover (Yr 4) and first year wheat (Yr 5), may have been a result of population increase after a period of low soil disturbance (Kladivko, 2001). In contrast, the crop with the largest amount of soil disturbance, potatoes (Yr 6), with repeated ridging to limit weed growth and protect tubers from light, had the lowest numbers of epigeal predators. Soil tillage is known to have deleterious effect on some invertebrates (Sharley *et al.*, 2008), especially large-bodied invertebrates (Kladivko, 2001), and result in a relative increase in species with small body size and good dispersal abilities

(Ribera *et al.*, 2001). However, invertebrate response to the impacts of soil tillage often varied between different species (Shearin *et al.*, 2007; Lalonde *et al.*, 2012), and body size (Hatten *et al.*, 2007).

Invertebrate taxonomic diversity was greater on the half of the farm under organic management compared with the conventional, in accord with previous studies (Bengtsson *et al.*, 2005; Holzschuh *et al.*, 2007b). This may partially reflect the greater in-field plant diversity, associated with the large number of arable weeds in the organic fields, which are known to be positively associated with increased invertebrate species richness (O'Sullivan and Gormally, 2002).

There were similarities in collembolan-feeding epigeal predators in both management systems, even though they were associated with different crops. In the conventional system, collembolan-feeders such as Loricini and Notiophilini were most abundant in oilseed rape (Yr 5), whilst in the organic systems they were most abundant in grass/clover leys. This may have been a result of similarities in both microclimate and the amount of detritus/organic matter available in the two crops. After the oilseed rape had flowered there was considerable petal-fall, combined with the dense crop and presumably humid microclimate at ground level, which may have increased Collembola density and hence specialist predators. (Birkhofer *et al.*, 2008b). Collembola are also associated with the use of organic manures (Birkhofer *et al.*, 2008a) but as these were only applied to the arable crops in the organic system the greater activity density of collembolan-feeding predators on the grass/clover was unexpected. However, a more humid soil microclimate in the grass/clover leys (Pfiffner and Luka, 2003) plus lack of soil tillage (Petersen, 2000) may also have increased Collembola numbers, although abundance of Collembola was not use in community analyses, they were used to identify detritivores trends. Collembola (springtails) data were only available for 2015, but total numbers were much higher in oilseed rape than winter wheat or winter barley (4239, 2359, and 1972 respectively).

In both management systems the abundance of foliar predators/parasitoids and herbivores/pollinators was significantly influenced by crop type. Within the conventional rotation, there was greater foliar predator/parasitoid and herbivore/pollinator abundance in oilseed rape (Yr 5) than cereals. This may be partly a result of the relatively constant phenology across the growing system of cereals, in contrast to the dramatic phenological changes associated with mass-flowering, petal fall, pod-formation etc. in oilseed rape (Zaller *et al.*, 2008). Eyre and Leifert (2011a) found management and crop type had significant effects on invertebrate activity density, and it is likely that the greater diversity of taxa in the organic crop is a result of the increased plant biodiversity within the crop (Hulugalle *et al.*, 1997; Nkem *et al.*, 2002; Gallandt *et al.*, 2005), due to lack of herbicides (Geiger *et al.*, 2010) and more weed infestations (Navntoft *et al.*, 2006).

The pCCA emphasised changes in assemblage composition over time in each management system and functional group. In the conventional system, there was an obvious circular pattern Figure 5.4 between the crops that closely matched the temporal sequence within which they were cultivated in the rotation. Note that whether or not these rotations in the partial pCCA plot are clockwise or anticlockwise is not relevant. In contrast, on the organic system, such circular patterns were only observed in the herbivores/pollinators group Figure 5.3, with more irregular patterns for epigeal predators and foliar predators/parasitoids, particularly for wheat (Yr 5 & Yr 8), barley (Yr 1), beans (Yr 7) and potatoes (Yr 6). The irregularities might therefore reflect the very different cultivation methods and microclimate of cereals, beans and potatoes compared to grass/clover leys in the organic system. In addition weed cover was high in the two cereal crops, but low on the beans and potatoes, which will have also affected the invertebrate assemblages. This compares to the conventional system, in which herbicides resulted in a similar level of weed cover in crops each year (Moreby *et al.*, 1994). The positions of individual taxa within the pCCA plots were similar to the individual studies described earlier; for example the Nitidulidae (pollen feeders) were closely aligned with oilseed rape (Yr 5) (Gladbach *et al.*, 2011).

The variation partitioning indicated the importance of both the current and previous year's crop on the taxa composition of the invertebrate assemblages. Three broad patterns were observed. First, the amount of variation explained by the current and/or previous crop was lower for the conventional system (at about 14 to 19%) than the organic (21 to 25%). This is a relatively small difference, given the lower overall crop/weed 'complexity' in the conventional system compared to the much weedier organic crops. Second, there was evidence of a 'lag-effect'. It is perhaps not unsurprising that the major determinant of the invertebrate ecology is the current crop, but there was nevertheless a small, but significant, effect from the previous year's crop on the following year's invertebrates. Third, the variation jointly explained by current and previous crop was higher in the organic (6 to 13%) than the conventional (1 to 4%). Whilst the exact mechanisms underlying this differences remain unclear, they may reflect the build-up of seedbanks from weeds, from the preceding and current year, to produce a more diverse vegetation (Honek and Jarosik, 2000; Roschewitz *et al.*, 2005a). This increased weed and floral diversity provide alternative resources for foliar predator/parasitoids (Gabriel *et al.*, 2010a) and weed seeds provide food for some adult, such as Pterostichus (Jonason *et al.*, 2013).

This study indicates the importance of preceding crops on invertebrate community composition and abundance. This is in contrast to Lalonde *et al.* (2012) who report no effect of crop sequence on ground beetle activity. Their study however was only based on a single year of invertebrate sampling from a four year crop rotation in conventional crops, whereas this research was based on annual sampling over 8 years organic and 5 years conventional, and is therefore likely to be more representative of changes in invertebrate ecology. Our study also highlights the importance deleterious effects of soil disturbance on epigeal predators, and suggests that ‘no-till’ methods of agriculture, under either organic or conventional agriculture, may be an important aid to increase the abundance of beneficial invertebrates.

Chapter 6. **Effects of plant cover, structure and traits on the invertebrates at a split organic/conventional farm**

6.1 Abstract

This research investigated the response of three invertebrate groups (epigeal predators, foliar predators/parasitoids and herbivores/pollinators) in relation to plant species cover, plant structure and plant traits on a split organic/conventional farm. Invertebrates were sampled from eighty-six sampling in crops, field boundaries and field edge in 2015.

Canonical correspondence analysis (CCA) was used to determine the effects of all three factors on the invertebrate communities, restricting plant traits to the three primary ones of competitor (C), stress-tolerator (S) and ruderal (R) plus annual/perennial. CCA's suggested that firstly, CSR plant traits affected invertebrates in both management systems, and secondly that plant cover and CSR plant traits were more important in the organic than conventional system, especially for epigeal predators and herbivores/pollinators. However, when all possible plant traits were incorporated into a variation partitioning (VP) analysis of plant cover, structure and traits, the relative importance of plant cover was reduced. The exact causes of this reduced effect of plant cover, especially in the organic system, when all plant traits were included were unclear, but may have been influenced by collinearities with structure and traits. Further studies is required to understand the mechanisms by which these plant attributes affect invertebrate communities.

6.2 Introduction

Conventionally managed arable crops have a lower weed cover (particularly due to use of herbicides), which makes them less suitable for many beneficial invertebrates, especially carabids (Nick *et al.*, 2001). In contrast, herbicides and inorganic fertilizers are prohibited in organic systems, with farmyard manure, animal slurry, and under-sowing with grass/clover used to provide nutrients, leading to greater plant diversity in both crops and field margins (Norton *et al.*, 2009a). This greater diversity of plants provide more potential food sources for herbivorous invertebrates (Haddad *et al.*, 2009; Borer *et al.*, 2012), which in turn will support more predatory invertebrates at higher trophic levels. For example, inter-sowing cabbage fields with cornflower increases abundance of Araneae and Carabidae (Ditner *et al.*, 2013), whilst organic fields with a greater proportion of weed species can increase bee abundance at landscape scales, delivering ecosystem services to nearby crops (Holzschuh *et al.*, 2008).

Different functional groups of invertebrates may have diverse requirements in terms of plant community composition and vegetative structure (Harvey *et al.*, 2008). For example, predatory invertebrates are affected by both plant species composition and structure (Schaffers *et al.*, 2008) being more abundant in species-rich and structurally complex habitats (Langellotto and Denno, 2004; Lassau *et al.*, 2005). In contrast, other groups such as some monophagous herbivores, are favoured by the abundant food resources of intensively-managed agricultural monocultures (Balmer *et al.*, 2013). In addition, the requirements of different groups of invertebrates changes seasonally. For example, Carabids often overwinter in dense tussock vegetation, typically found in the field margins (Collins *et al.*, 2003), whereas in spring and summer they may forage in more open vegetation within the crop (Pywell *et al.*, 2005; Harvey *et al.*, 2008).

The effects of vegetation architecture and plant structure on spiders has long been known (Rushton and Eyre, 1992; Topping and Lovei, 1997; Jeanneret *et al.*, 2003) but plant structure also influences butterfly, grasshopper, leaf-hopper, true bug, herbivorous beetles and parasitic wasp species richness and abundance (Kruess and Tscharntke, 2002; Collinge *et al.*, 2003). The manipulation of vegetation by cutting grass for silage (Haysom *et al.*, 2004) or for roundabouts and roadside edge management (Helden and Leather, 2004; Noordijk *et al.*, 2010) rapidly changes vegetation structure, with concomitant effects on spiders, ground and other beetles. Vegetation height on grazed salt marsh affects Hemiptera assemblages, with more ground dwelling species on shorter vegetation (Ford *et al.*, 2013), whilst livestock grazing modifies the invertebrate abundance (Sjödin *et al.*, 2008). Plant strategies (plant functional types) are described as groups of similar or corresponding adaptive functions amongst plants species with different evolutionary origins but display similarities in their given habitats.(Grime, 1988) suggested that plant life-history strategies that have arisen over evolutionary time can be summarized into a 3-dimensional ordination of competitors, stress-tolerators and ruderal (CSR). Allocation to these strategies can be based on a number of factors (Hodgson *et al.*, 1995), for example: life history (annual, perennial), canopy structure (rosette, semi-rosette, leafy) and canopy height (short, medium, tall) etc.

Grime (1977) triangular plant strategy framework (Competitor, Stress tolerator, Ruderal) has potential to provide useful insights into processes affecting the species composition of invertebrate communities in the vegetation. Other framework and databases have also been utilised in ecology. For example, Kleyer *et al.* (2008) created a database of life-history traits of European flora which has the potential to measure how community trait composition changes as a result of environmental change. Storkey *et al.* (2013) investigated the relationship between a number of simplified plant traits and invertebrate abundance, and concluded that more ruderal communities positively correlate with increased invertebrate abundance. Invertebrate herbivores can have indirect effects on the predominant plant traits in semi-natural vegetation (see review Takayuki, 2005) which resulted in cascading effects on other invertebrates within the community. Kessler and Halitschke (2007) found that herbivore-induced defense chemicals in plants affect other invertebrates e.g. by attracting insect parasitoids and predators. Similarly, Megías and Müller (2010) found root herbivores and detritivores affect other herbivores and parasitoids associated with the host plant.

It is clear from the literature that vegetation may affect the invertebrates through three processes: the species composition, the structural complexity, and the plant traits. Species composition is affected by both the cover-abundance and species identity of the plants, which changes the host plants, other food resources and microclimate in which the invertebrates live. Likewise, vegetation structure affects the microclimate and the availability of resources for invertebrates. The role of plant traits on invertebrates has been little studied in agroecosystems, other than pollinators, but may also affect the invertebrate community composition. In order to determine the response of invertebrates to the plant community composition, vegetation structure and plant species traits, we sampled 86 sites on a split organic/conventional farm. Data for three invertebrate functional groups were collected via pitfall and pan traps in crops and adjacent field boundaries in both management systems. The aims of this study were to:

1) Invertebrate community composition is determined by the vegetative cover composition (i.e. plant species composition) in both the organic and conventional farming systems
2) Vegetation vertical structure will affect invertebrate assemblages in both management systems
3) Plant strategies, as described by Grime (1988) CSR framework of Competitor- Stress tolerator- Ruderal, will affect invertebrate abundance and composition
4) Quantify the relative importance of plant composition, plant structure and plant traits on invertebrate assemblages

6.3 Methods

6.3.1 Survey Area and Management

Samples were collected at Nafferton Farm, a typical mixed commercial conventional farm in northern England, Northumberland, UK (54°59', 09"N; 1°43', 56"W). Full details of the farm are provided in Chapter 2, with information on invertebrate sampling methods in Chapter 2, section 2.2.1.

6.4 Sampling and Data Generation

6.4.1 Invertebrates

Invertebrates were identified to family, sub-family and tribe, according to Chinery (1993); Roberts (2001); Luff (2007) and confirmed by expert entomologist Dr M.D. Eyre, depending on functional group, and counted, see Table 2.3. Invertebrates were sampled in 16 organic and 14 conventional crop fields, and within each field, samples were collected at two sites approximately 20 m apart (Chapter 2, Figure 2.3 and Figure 2.4). At each site, invertebrates were pooled at three points: one in the non-crop field boundary (0 m), field edge (5 m) and in the crop itself (40 m). Invertebrates were sampled monthly from May to September 2015 with 28 samples from the conventional half of the farm: 12 in wheat fields, 4 barley, and 12 in oilseed rape. See Chapter 2 for full details

6.4.2 Vegetation sampling

Plant cover and structure were measured in the field at the same locations used to sample invertebrates. Plant cover was assessed in late July 2015 with 1-m^2 quadrats: the percent cover of all vascular plants and bryophytes were estimated to the nearest 5%, with single individual or rarer species in the quadrat scored at 0.5, 1 or 2% (Woodcock *et al.*, 2007). Plant cover percentage of each species was estimated independently by two people, in order to minimize bias. All plants in the quadrat were identified to species (Hubbard, 1954; Rose, 1981; Stace, 1991). For a detailed list of plant species, see Table 6.1. Full details of vegetation sampling are given in Chapter 2.

Plant species	**Abbreviations**
Agrostis stolonifera	Agrostol
Arrhenatherum elaticus	Arrhelat
Brassica napus	Brasnapu
Bromus mollis	Brommoll
Bromus sterilis	Bromster
Chenopodium album	Chenoalbu
Cirsium vulgare	Cirsvulg
Cirsium arvense	Cirsarve
Cynosurus cristatus	Cynocris
Dactylis glomerata	Dactglom
Festuca pratensis	Festprat
Festuca rubra	Festrubr
Galium aparine	Galiapar
Holcus lanatus	Holclana
Hordeum vulgare	Hordvulg
Hypochaeris radicata	Hypocradi
Lactuca serriola	Lactserr
Lolium perenne	Lolipere
Phaseolus vulgaris	Phasvulg
Phleum pratense	Phleprat
Poa annua	Poaannu
Polygonum convolvulus	Polyconv
Polygonum persicaria	Polypers
Rumex crispus	Rumecris
Rumex obtusifolius	Rumeobtu
Sinapis arvensis	Sinaarve
Trifolium pratense	Trifprat
Trifolium repens	Trifrepe
Triticum aestivum	Tritaset
Urtica dioica	Urtidioi
Veronica chamaedrys	Verocham

Table 6.1 Complete list of plant species used in CCA analyses.

A list of plant traits (see Table 2.5), for those species in the plant cover database, was generated using plant strategy theory by (Grime, 1977; Grime, 1988) especially the electronic database produced by Hodgson *et al.* (1995), which includes:

- life history (annual, perennial)
- life form (chamaephyte – woody perennial with soil level buds; hemicryptophyte – herbaceous perennial with soil level buds; therophyte – annuals overwintering as seeds)
- canopy structure (rosette, semi-rosette, leafy)
- canopy height (short, medium, tall)
- lateral spread (therophytes (seeds), rhizomes, tussocks)
- leaf phonology (seasonal canopy, evergreen canopy)
- flowering time (March/April, May, June, July)
- regenerative strategies (vegetative, seed bank, wind dispersal)
- seed bank (rapid germination, limited persistence in soil, log-term persistent seed bank in soil). For more information on plant traits see Table 2.5

A pragmatic approach was used to the selection of which plant traits to include, applicable to research aims and objectives, in that plant traits most likely to influence invertebrate community composition were included (Weiher *et al.*, 1999). A total of 10 plant traits were collated which reflected different ecological, morphological and life history categories. Each plant trait was subdivided into two to four levels resulting in a total of 29 traits. Some plant traits were represented exclusively (for example, annual, perennial), others were identified based on a semi-quantitative range of values (short <100m, tall 600 mm or more), whilst a small portion as co-existing entities (March and/or April). Separate weighted averages (based on plant cover) of the separate competitor, stress-tolerator, ruderal, annual and perennial scores were also calculated.

6.5 Data analysis

Separate canonical corresponding analyses (CCA – cover, structure and traits) were used to examine the relationships between the three plant attributes and the invertebrates. The matrix of invertebrate taxa by samples was used as the response, constrained by one of the explanatory variables of plant cover, structure and traits types within either the organic or conventional system. The vegetation cover data were highly skewed by a small number of common species, and were therefore Hellinger-transformed which square root the relative abundance data prior to incorporation within the CCA (Legendre and Gallagher, 2001). The CSR and annual/perennial data were used as explanatories in the CCA. The significance of the plant attributes on the invertebrate community composition was analysed using Monte Carlo permutation tests (999 permutations). Invertebrate species count data were log-transformed log 10(n+1) prior to analyses to stabilize the variance and to reduce the influence of extreme values, and analyses undertaken in the R statistical environment, using the "vegan" package (Oksanen J, 2015) in R (R Development Core Team, 2015). Invertebrate taxa with less than five occurrences in the database were excluded from the analyses.

Variance partitioning was used to quantify the effects on the invertebrate community of a) purely the plant cover, b) purely the plant structure, c) purely the plant traits, c) the joint effect (if any), d) residual unexplained variation. For the variation partitioning all plant traits described by Grime (1988) were used, not simply CSR plus annual/perennial Table 2.5. This was to provide a constraining matrix that best describes all the traits in the observed flora. The significance of individual components a) and b) was tested by Monte Carlo permutation tests (999 permutations); this cannot be done reliably for the joint effect c) (Buttigieg and Ramette, 2014).

6.6 Results

Analyses were carried out on a total of 74284 epigeal predators in 23 taxa, 7796 foliar predators in 16 taxa and 43000 herbivores in 25 taxa. The results of the plant species cover, plant structure, plant traits and of these three together using data generated in the organic half of the farm are given below, followed by the same analyses using data from the conventionally managed half.

6.6.1 Organic management: Relationship with plant cover and invertebrate assemblages in the organic system

Overall, plant species composition did not significantly influence epigeal predators community composition ($F_{18,25}$ =1.12, P= 0.077) within the organic system Figure 6.1. Nevertheless, Monte Carlo permutation tests indicated significant influence of three plant species, *Agrostis stolonifera* ($F_{18,25}$ =2.85, P=0.002), *Phaseolus vulgaris* ($F_{18,25}$ = 2.98, P= 0.004) and *Chenopodium album* ($F_{18,25}$ =2.72, P= 0.004). The major variation within the community composition of epigeal predators was associated with changes along CCA Axis 1 (Figure 6.1 A) from non-crop grasses such as *Agrostis stolonifera* and *Arrhenatherum elatius* (short and tall field boundaries) on the negative half through to wheat (*Triticum aestivum*) and two weed species, *Chenopodium album* and *Polygonum convolvulus* with high CCA Axis 1 scores. Axis 2 indicated variation from beans *Phaseolus vulgaris* and the weed *Polygonum convolvulus through* to the grass *Poa annua* with high axis 2 scores. Invertebrate taxa in low abundance across the farm showed distinct associations with some species of plants. For example, Coleoptera- Licinini and Coleoptera- Elaphrini were associated with spring wheat fields infested with *Chenopodium album* whilst Coleoptera- Sphodrini was associated with *Poa annua* and *Agrostis stolonifera*, in tall herbaceous boundaries. Most of the ubiquitous epigeal predator taxa were clustered around the origin, and therefore not closely associated with the cover of any particular individual plant species. Samples taken from within the crop (40 m) had a large convex polygon (Figure 6.1 B).compared with field edge or boundary, suggesting greater variation in taxa composition.

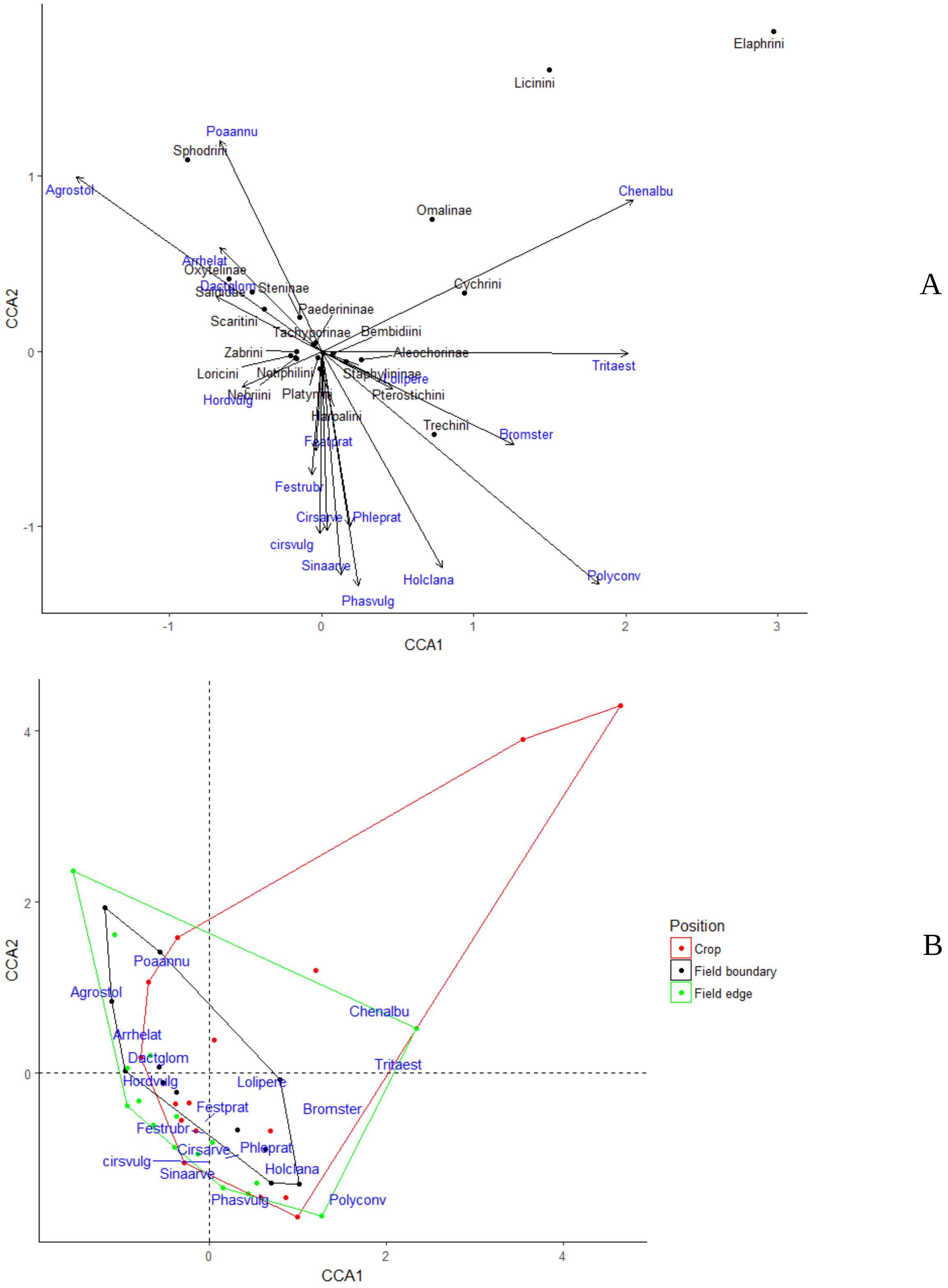


Figure 6.1 Canonical Correspondence Analysis (CCA) ordination diagram of epigeal predator assemblages in the organic system (data from May-September 2015), A) epigeal taxa response to plant species composition (axis1: 15.1%; axis2: 7.4%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant species composition (see Table 6.1 for full species name).

Plant species composition had an overall significant influence on foliar predators/ parasitoids composition within the organic system ($F_{18,25}$ =1.52, P= 0.004 - Figure 6.2). *Festuca pratensis* ($F_{18,25}$ =4.69,$P=0.002$), *Agrostis stolonifera* ($F_{18,25}$ =2.85, P <0.00), *Dactylis glomerata* ($F_{18,25}$ = 2.72, P =0.004), *Poa annua* ($F_{18,25}$ =1.98, P =0.048), *Polygonum convolvulus* ($F_{18,25}$ = 1.93, P= 0.008), *Holcus lanatus* (P= 0.040) and *Bromus sterilis* (P= 0.048) were the most significant plant species. On CCA Axis 1 the main trend of variation in the foliar predators/parasitoids was from areas dominated by weed grass species *Bromus sterilis* and *Holcus lanatus* associated with rarer taxa Hymenoptera-Pteromalidae (mainly in spring beans and grass/clover) through to tall, field boundary grasses *Festuca pratensis* and *Dactylis glomerata* associated with medium size taxa (Figure 6.2 A). Neuroptera- Hemerobiidae and Mecoptera- Panorpidae, Axis 2 varied along boundaries dominated by the grasses *Agrostis stolonifera* and *Poa annua* associated flying Hemiptera- Nabidae, and Neuroptera- Chrysopidae and Dermaptera- Forficulidae through to spring wheat (*Triticum aestivum*) infested with *Polygonum convolvulus* associated with Hymenoptera- Vespidae. Samples taken from within the crop had a small convex polygon in the CCA (Figure 6.2 B) suggesting less variation in taxa than boundaries and field edge.

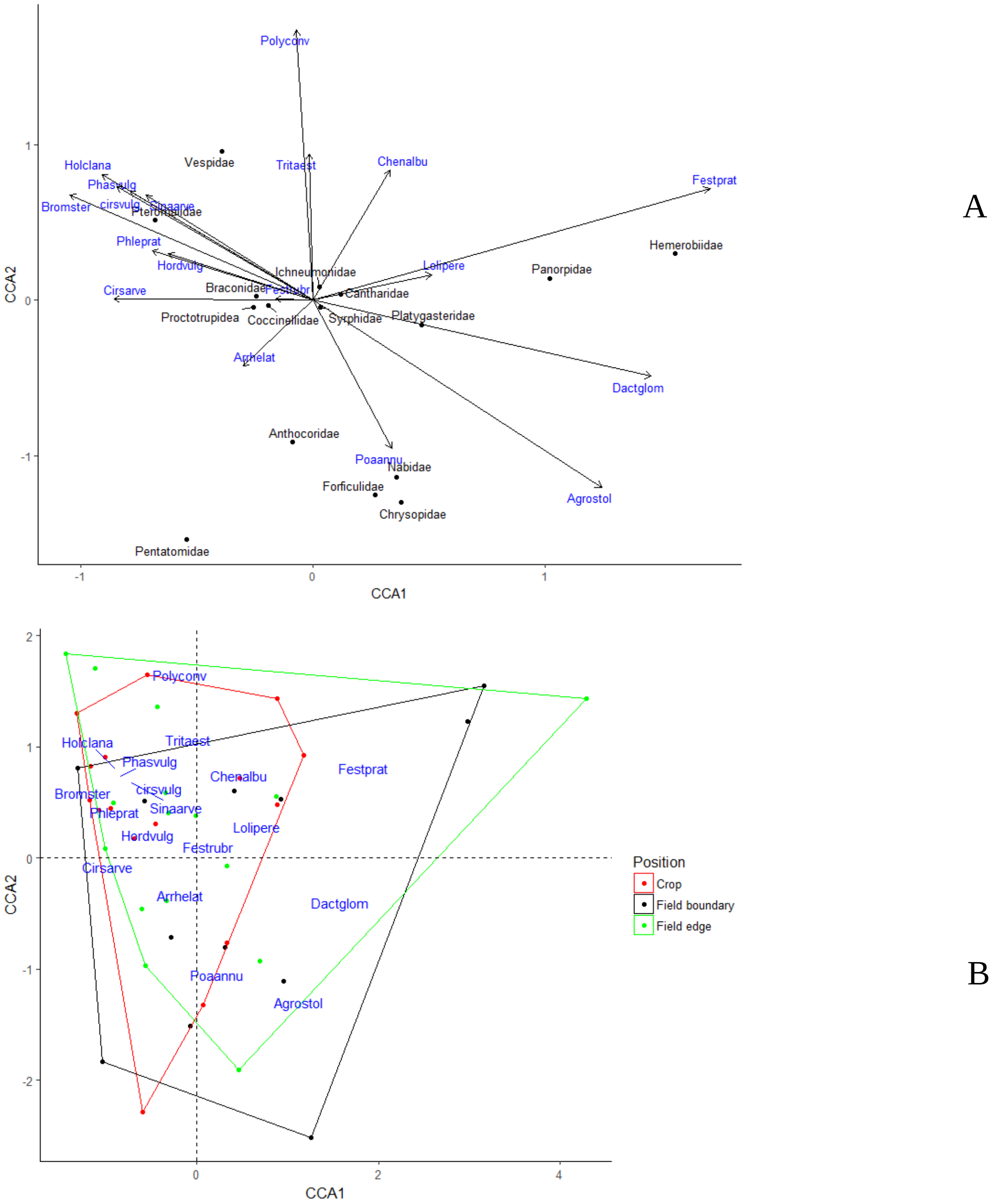


Figure 6.2 Canonical Correspondence Analysis (CCA) ordination diagram of foliar predators/parasitoids assemblages in the organic system (data from May-September 2015), A) foliar predators/parasitoids taxa response to plant species composition (axis1: 14.1%; axis2: 6.2%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant species composition (see Table 6.1 for full species name).

Community composition of herbivores/pollinators was significantly influenced by plant species composition ($F_{18,25}$ = 1.22, P= 0.001 - Figure 6.3). Both organic crop and weed species, especially *Polygonum convolvulus* ($F_{18,25}$ = 5.72, P=0.002), *Triticum aestivum* ($F_{18,25}$ = 2.39, P= 0.008), *Phaseolus vulgaris* ($F_{18,25}$ = 3.35, P= 0.010), *Festuca pratensis* ($F_{18,25}$ = 3.30, P= 0.014) and *Agrostis stolonifera* ($F_{18,25}$ = 2.31, P= 0.044) contributed to the significant effect . The main trends on CCA Axis 1 were from field boundaries dominated by grass species (*Dactylis glomerata*, *Festuca pratensis* and *Agrostis stolonifera)* associated with Coleoptera-Anthicidae and Homoptera-Cercopidae through to spring beans (*Phaseolus vulgaris*), and spring barley (*Hordeum vulgaris*) dominated by the grass weed species (*Bromus sterilis, Phleum pratense* and *Holcus lanatus)* associated with the relatively rare Coleoptera- Galerucellinae (Figure 6.3 A). There were no obvious patterns in the CCA ordination between the three habitats (Figure 6.3 B).

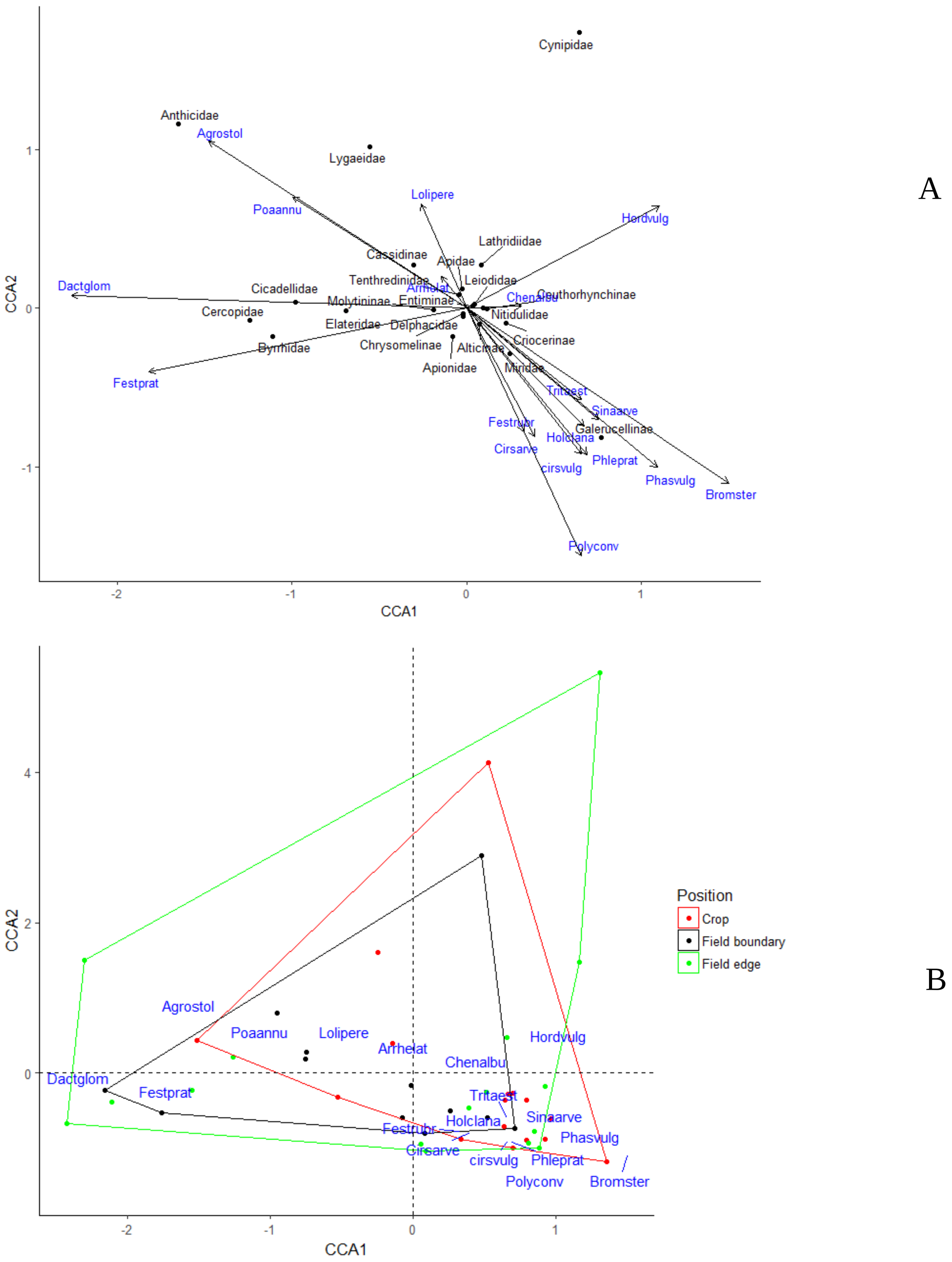


Figure 6.3 Canonical Correspondence Analysis (CCA) ordination diagram of herbivores/pollinators assemblages in the organic system (data from May-September 2015), A) herbivores/pollinators taxa response to plant species composition (axis1: 16.4%; axis2: 6.2%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant species composition (see Table 6.1 for full species name).

6.6.2 Relationship with plant structure and invertebrate assemblages in the organic system

The structural characteristics of the main habitats in the organic system are summarized in Figure 6.4. The tallest habitats were the field beans, spring wheat and tall boundary. The grass/clover ley was relatively “bottom-heavy” with the densest foliage below 25 cm and relatively little above this height. The tall and hedge boundaries were dominated by shorter weed grasses. In the organic system both epigeal predators and foliar predators/parasitoids there was a significant decrease in invertebrate abundance with vegetation density ($F_{1,42}$=7.73, P=0.008; $F_{1,42}$=4.81, P=0.033 respectively; Figure 6.5).

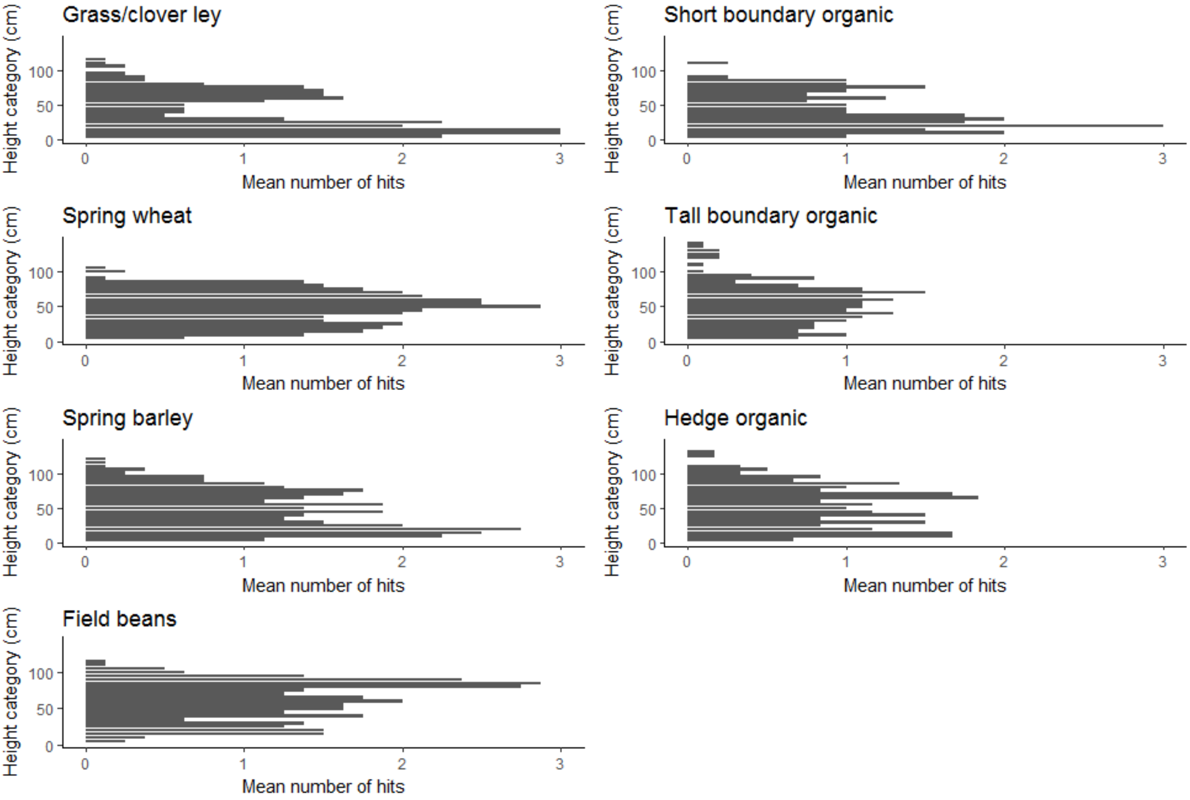


Figure 6.4 Overall structural characteristics of the main habitats in the organic system.

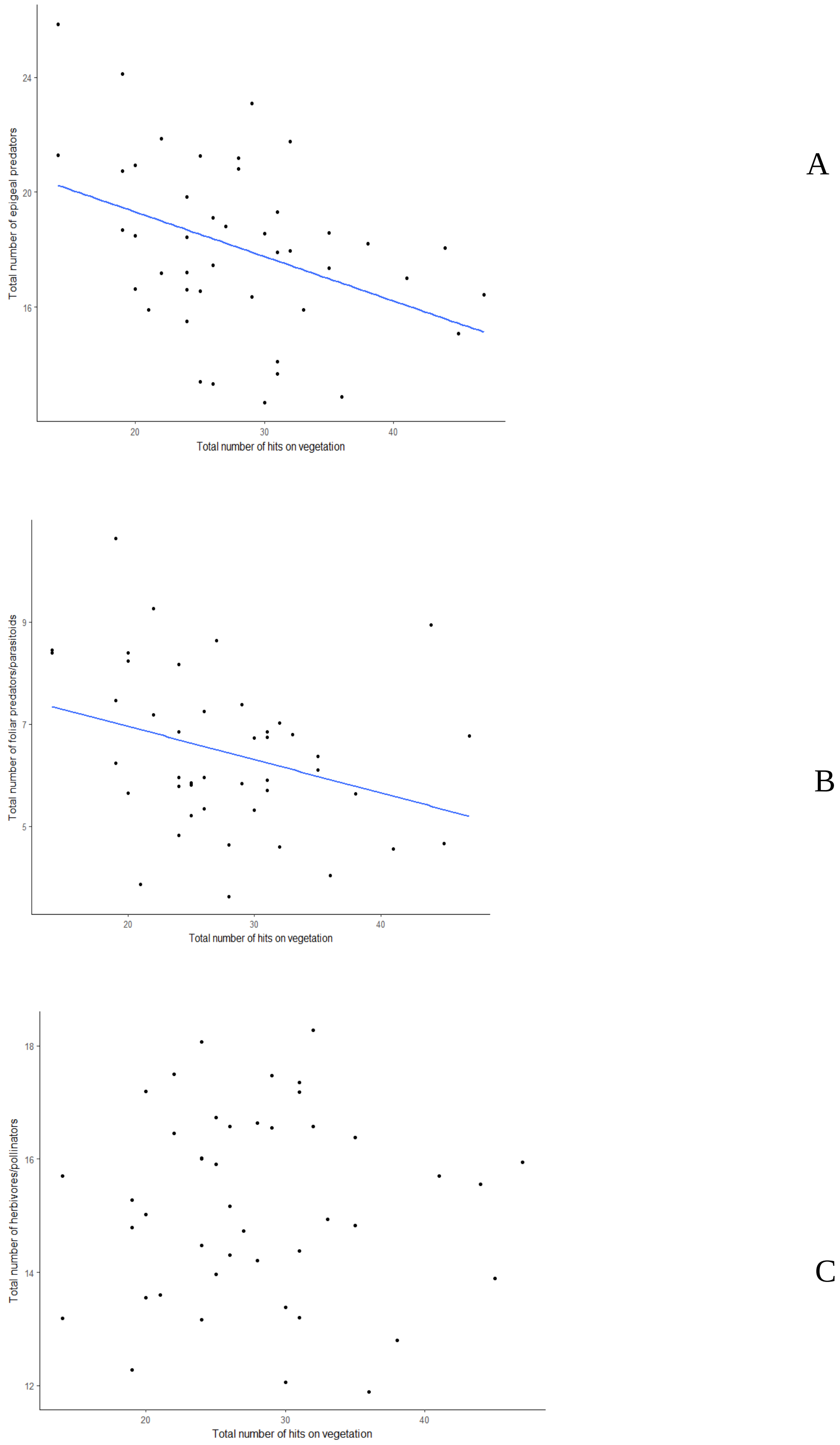


Figure 6.5 Relationship between the overall vegetation density and functional groups total: A) epigeal predators, B) foliar predators/pollinators and C) herbivores/ pollinators totals in the organic system.

The overall response of the organic epigeal predator assemblages to plant structure was not significant ($F_{19,24} = 0.93$, P= 0.492) with the only vegetation height that had a significant relationship with epigeal taxa was at 50 cm ($F_{19,24}=2.85$, P=0.006 - Figure 6.6). In general, shorter and taller vegetation heights had lower Axis 1 score. There was no obvious pattern in vegetation heights along either Axis 1 or Axis 2 of the CCA, again suggesting that vegetation structure was having relatively little effect on the epigeal predators (Figure 6.6 A). Samples in the crops (40 m) had higher variation taxa in taxa composition compared to samples in field boundaries and field edge (Figure 6.6 B). A number of taxa such as Coleoptera- Oxytelinae and Coleoptera- Sphodrini were associated with the shorter and taller field boundaries respectively. Most of the ubiquitous epigeal predator taxa were clustered around the origin, and therefore not closely associated with particular plant structure class, rather combinations of taller and shorter. Other than two outlier samples associated with Elaphrini and Licinini there were no obvious patterns amongst the samples (Figure 6.6 B).

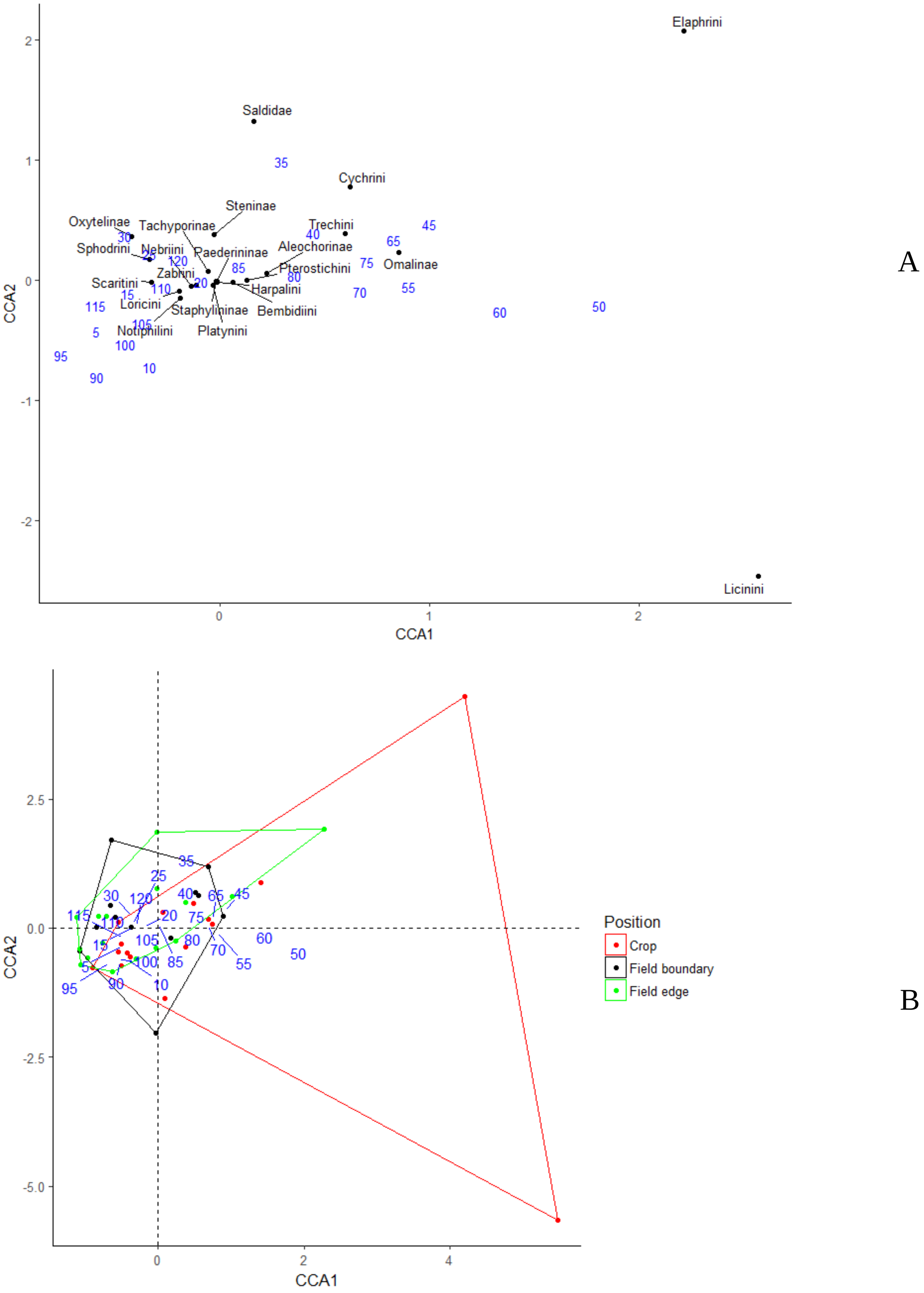


Figure 6.6 Canonical Correspondence Analysis (CCA) ordination diagram of epigeal predator assemblages in the organic system (data from May-September 2015), A) epigeal taxa response to plant structure (axis1: 13.0%; axis2: 4.8%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant structure.

Overall foliar predators/parasitoids were not affected overall by vegetation structure within the organic system ($F_{19,24}$ = 1.17, P= 0.163 - Figure 6.7). Nevertheless, the Monte Carlo Permutation tests indicated significant effects of heights 50 cm ($F_{19,24}$ = 1.72, P= 0.042) and 80 cm ($F_{19,24}$ = 2.91, P=0.002) , on foliar assemblages. The main variation along CCA Axis 1 with the foliar predators was from taller vegetation (75 cm, 80 cm and 85 cm) associated with parasitoid wasp Hymenoptera- Pteromalidae and predatory Hemiptera- Nabidae in spring bean fields to medium vegetative heights (40 cm, 50 cm and 55 cm) associated with Mecoptera- Panorpidae, Neuroptera- Hemerobiidae in tall field boundaries bordering spring wheat. CCA Axis 2 showed taller heights (115cm and 120 cm) associated with Hymenoptera-Platygasteridae, Hemiptera- Anthocoridae and Neuroptera- Chrysopidae in field edge of bean fields. Field boundaries had slightly less variation in taxa composition, indicated by the smaller convex polygon in Figure 6.7 B than crop and field edge.

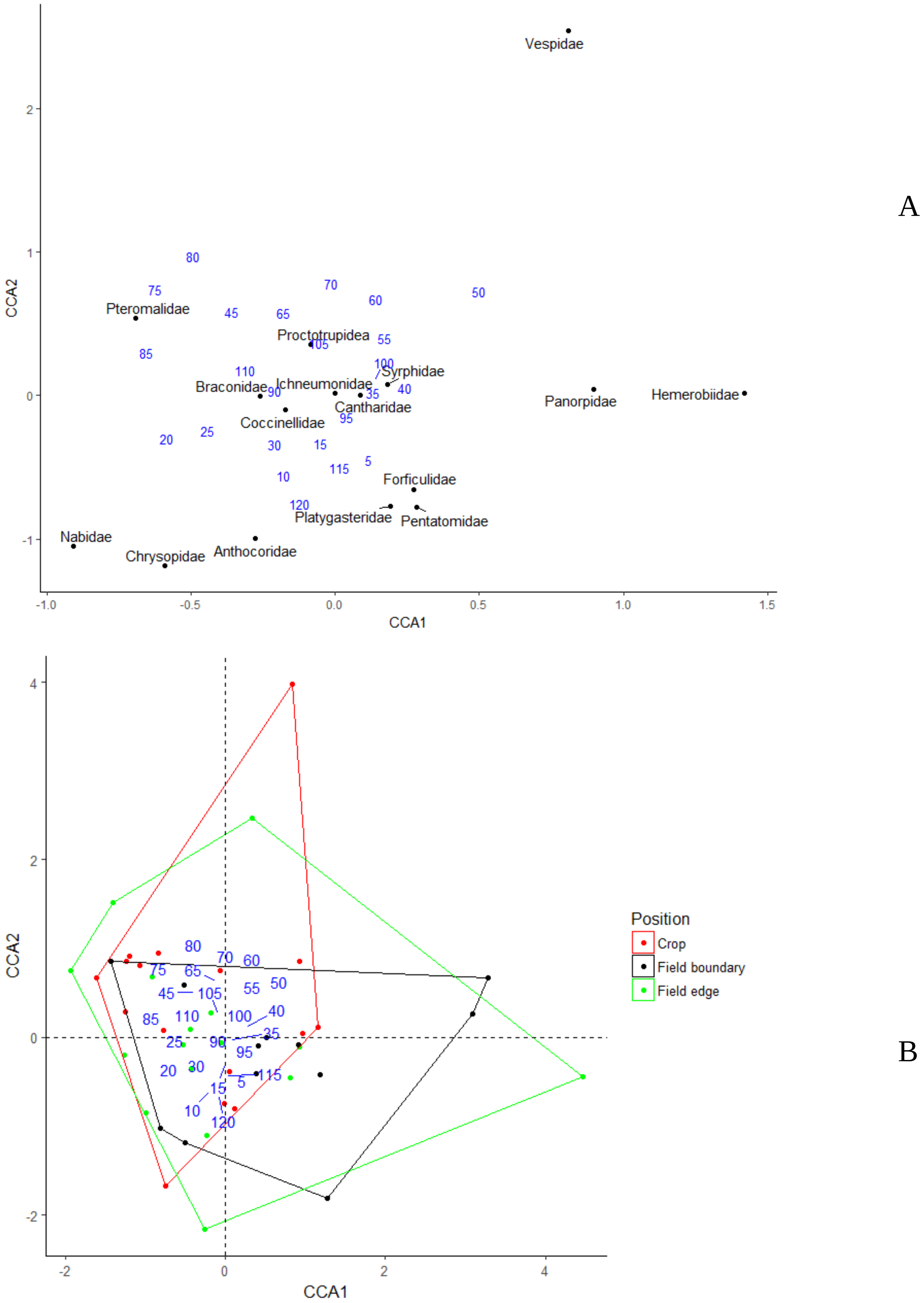


Figure 6.7 Canonical Correspondence Analysis (CCA) ordination diagram of foliar predator/parasitoids assemblages in the organic system (data from May-September 2015), A) foliar predator/parasitoids response to plant structure (axis1: 11.7%; axis2: 1.9%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant structure.

Overall, plant structure did not significantly affect organic herbivore community composition ($F_{19,24}$ = 1.22, P= 0.062 - Figure 6.8), nevertheless the Monte Carlo permutation test identified six plant structure heights with significant influences: 10 cm ($F_{19,24}$ = 1.94, P= 0.038), 20 cm ($F_{19,24}$ = 2.35, P= 0.006), 50 cm ($F_{19,24}$ = 2.70, P <0.002) and 80 cm ($F_{19,24}$ = 2.44, P= 0.008. The main variation in herbivore community composition CCA Axis 1 had relatively tall (80 cm, 85 cm- Figure 6.8 A). Vegetative structures associated with Coleoptera- Galerucellinae in bean fields with low scores, through to taller plant height (120 cm) associated Hymenoptera-Cynipidae within spring barley and wheat fields. Axis 2 had short field boundary plant vegetation (5 cm, 10 cm) associated with Coleoptera- Anthicidae, Hemiptera- Lygaeidae, Coleoptera- Byrrhidae and Homoptera- Cercopidae in grassy boundaries with low axis scores through to a mixture of shorter and taller plants (50 cm, 115 cm, 120 cm) in spring barley and spring wheat crops at the positive end. Samples in field boundaries had less variation in their taxonomical composition Figure 6.8 B than the other two habitats.

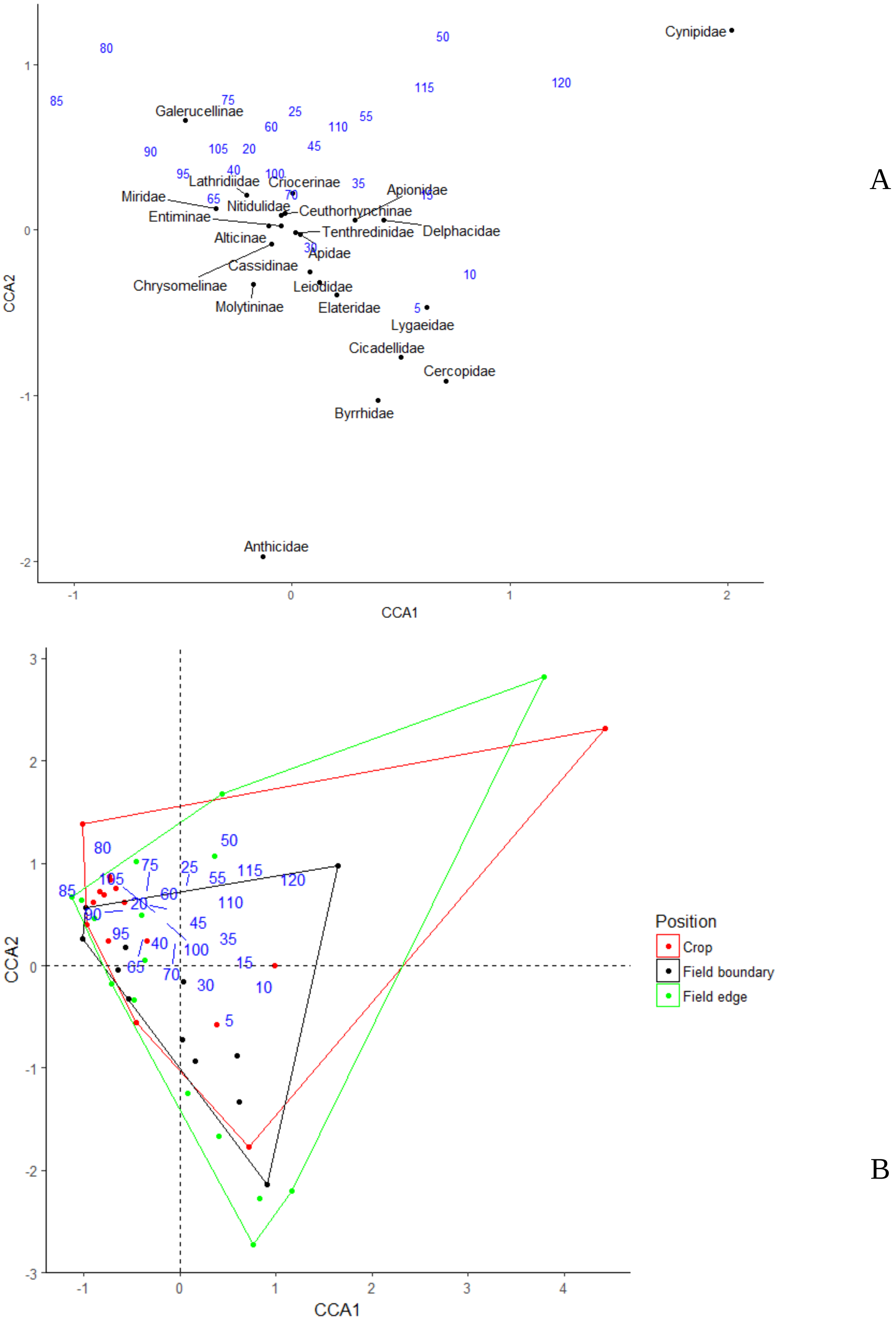


Figure 6.8 Canonical Correspondence Analysis (CCA) ordination diagram of herbivores/pollinators assemblages in the organic system (data from May-September 2015), A) herbivores/pollinators taxa response to plant structure (axis1: 14.8%; axis2: 2.1%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant structure.

6.6.3 Relationship with plant traits and invertebrate assemblages in the organic system

Overall summaries of the positions of the vegetation CSR traits at each site are summarized using standard 3-dimension plots in Figure 6.9, coded according to crop, field boundary or field edge. The CSR traits for the organic samples are relatively similar, dominated by approximately 35 to 45% competitors and ruderals, with fewer stress tolerators at approximately 20% (Table 6.2).

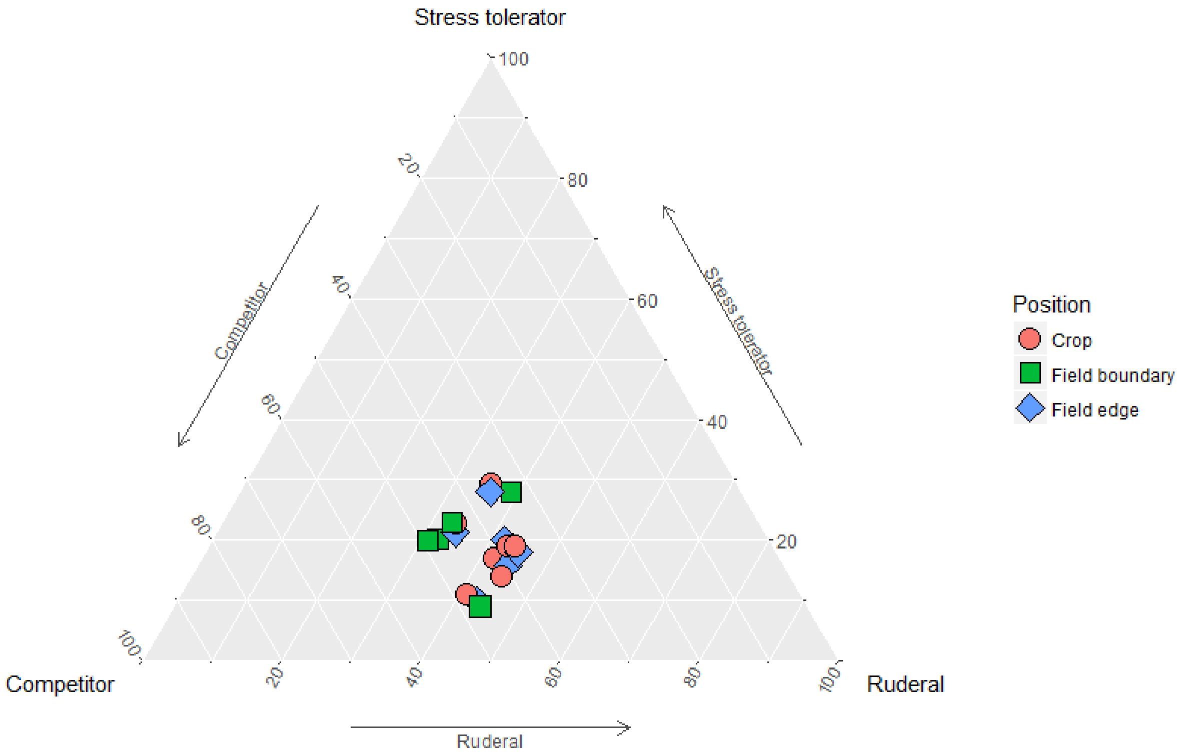


Figure 6.9 Overall summaries of the positions of the vegetation CSR traits at each site in the organic system.

		Crops		Boundaries	
		μ	**σ**	**μ**	**Σ**
Conventional	**Competitors**	47.14	4.6	44.85	4.01
	Stress-tolerators	5.71	9.2	20	5.43
	Ruderals	47.14	4.6	35	3.67
Organic	**Competitors**	39.75	5.79	44.83	5.79
	Stress-tolerators	19.37	5.93	20	5.93
	Ruderals	40.81	5.08	35	5.08

Table 6.2 Mean (μ) and standard deviation (σ) for CSR plant cover in field boundary and crop habitats.

Overall plant traits did not have a significant effect on epigeal predator composition ($F_{1,38}$=1.05, P=0.235 - Figure 6.10) although stepwise selection indicated that the presence of annual plants was important (F1,38=3.48, P=0.010). The main variation on CCA1 showed increased number of stress tolerator plant species associated with Coleoptera-Oxytelinae and Sphodrini associated with perennial species whilst secondary variation CCA2 showed the rarer taxa Elaphrini associated with ruderal plant species (Figure 6.10 A). Foliar predators/parasitoids were significantly affected by plant traits ($F_{5,38}$=1.36, P=0.041 - Figure 6.11) with the weighted cover of annuals and perennials particularly important ($F_{1,38}$=2.93, P=0.009; $F_{1,38}$=2.18, P=0.041 respectively). Increased numbers of perennial plants were associated with Hemipteran- Nabidae and Pentatomidae, whilst there was a greater proportion of Neuropteroid- Chrysopidae associated with competitor plant species (Figure 6.11 A) Herbivores/pollinators were significantly affected overall by all the plant traits ($F_{4,38}$=1.49, P<0.001 - Figure 6.12) with stepwise selection indicating that weighted cover of annual plants was most important (F1,38=2.62, P=0.009). Heteroptera- Miridae, Hemipteran- Delphacidae and Coleoptera- Alticinae were most strongly associated with annual plants whilst Coleopteran- Anthicidae, Hemipteran- Cicadellidae and Lygaeidae were associated with stress tolerator plant species (Figure 6.12 A). In all three plots (Figure 6.10 B, Figure 6.11 B and Figure 6.12 B), there were no obvious consistent patterns in the taxonomic composition of the three habitats, as indicated by the convex polygons.

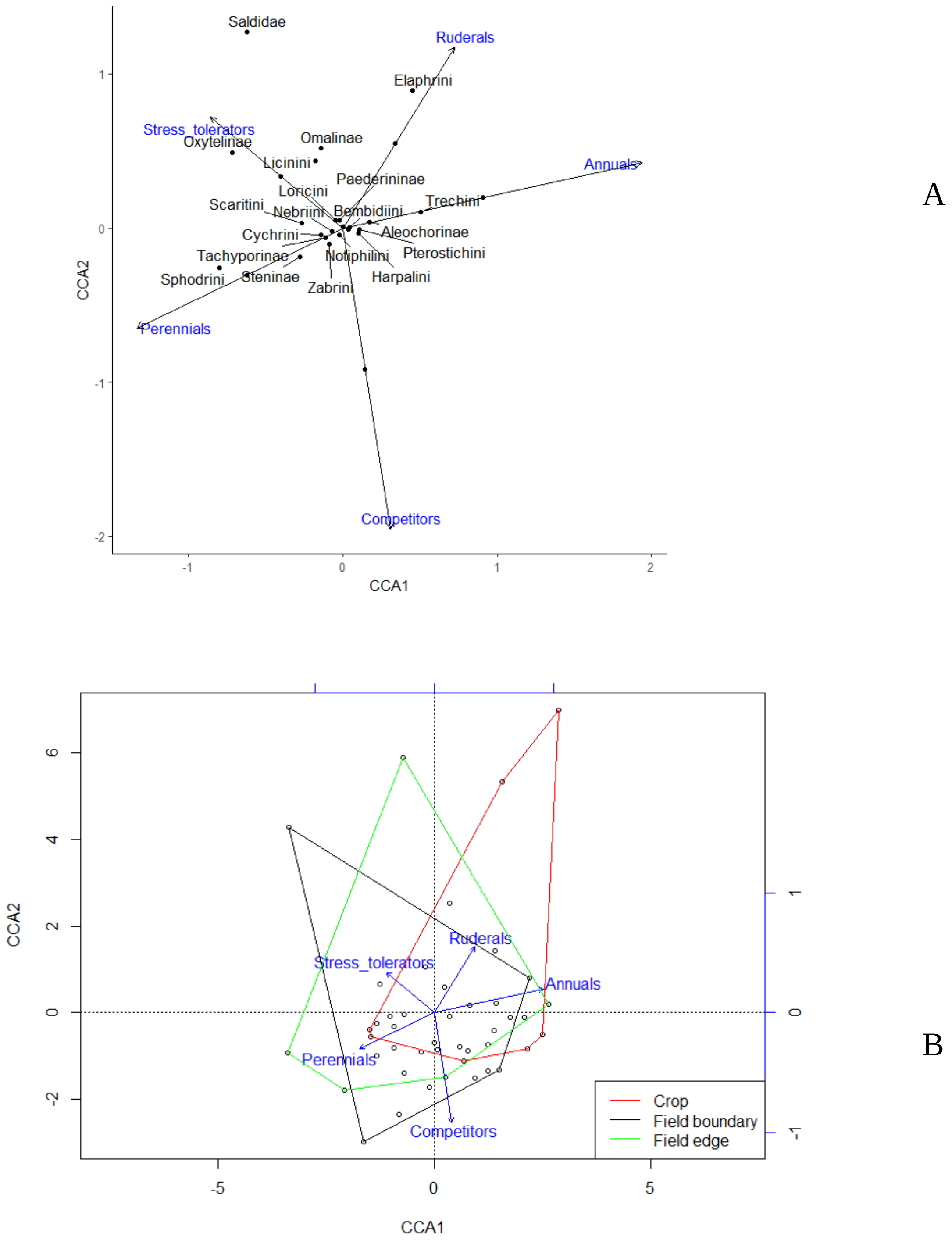


Figure 6.10 Canonical Correspondence Analysis (CCA) ordination diagram of epigeal predators assemblages in the organic system (data from May-September 2015), A) epigeal predators taxa response to CSR plant traits (axis1: 5.7%; axis 2: 2.9%), B) variation in taxa composition in crop, field boundary and field edge habitats response to CSR plant traits.

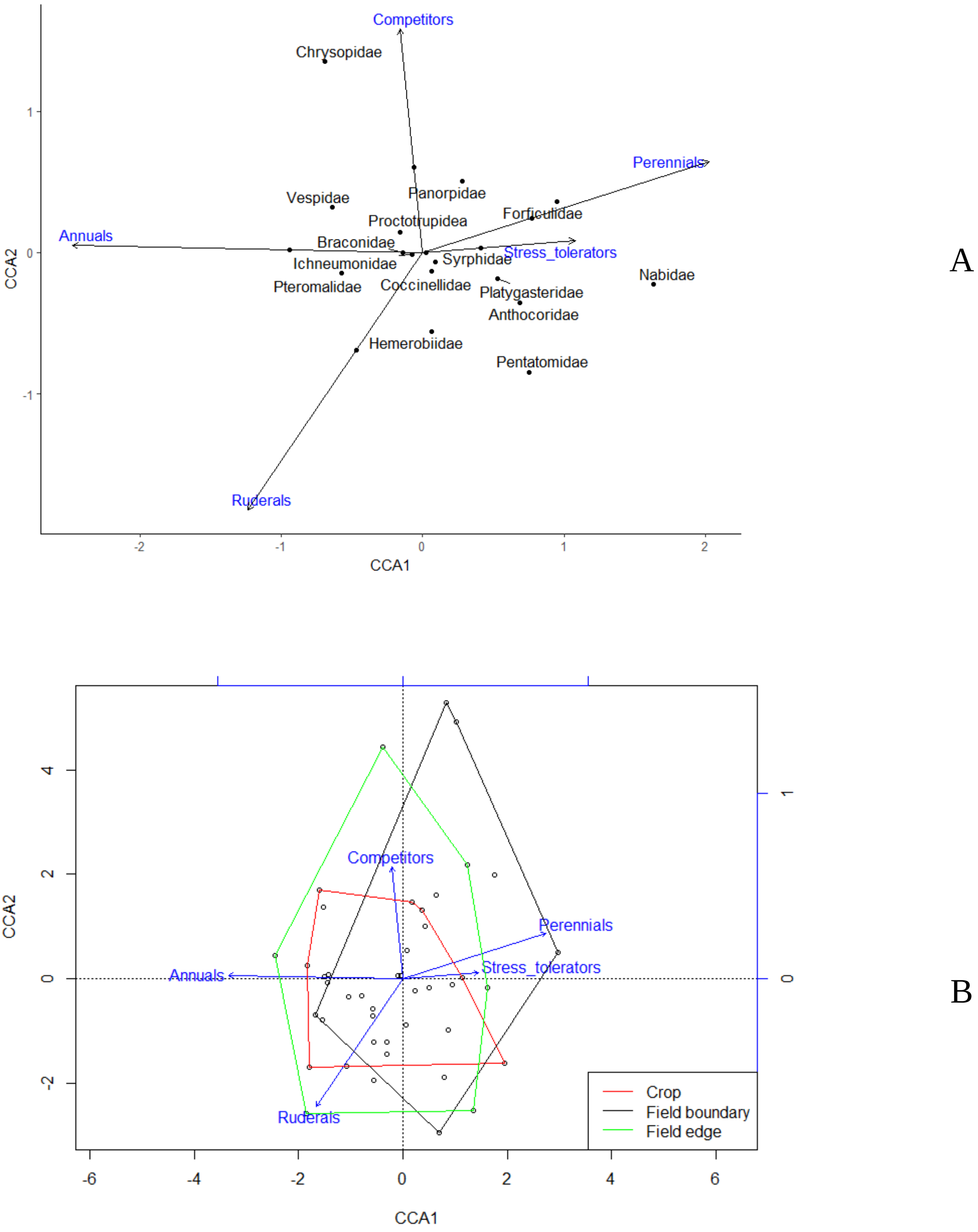


Figure 6.11 Canonical Correspondence Analysis (CCA) ordination diagram of foliar predators/parasitoids assemblages in the organic system (data from May-September 2015), A) foliar predators/parasitoids taxa response to CSR plant traits (axis1: 7.2%; axis2: 3.4%), B) variation in taxa composition in crop, field boundary and field edge habitats response to CSR plant traits.

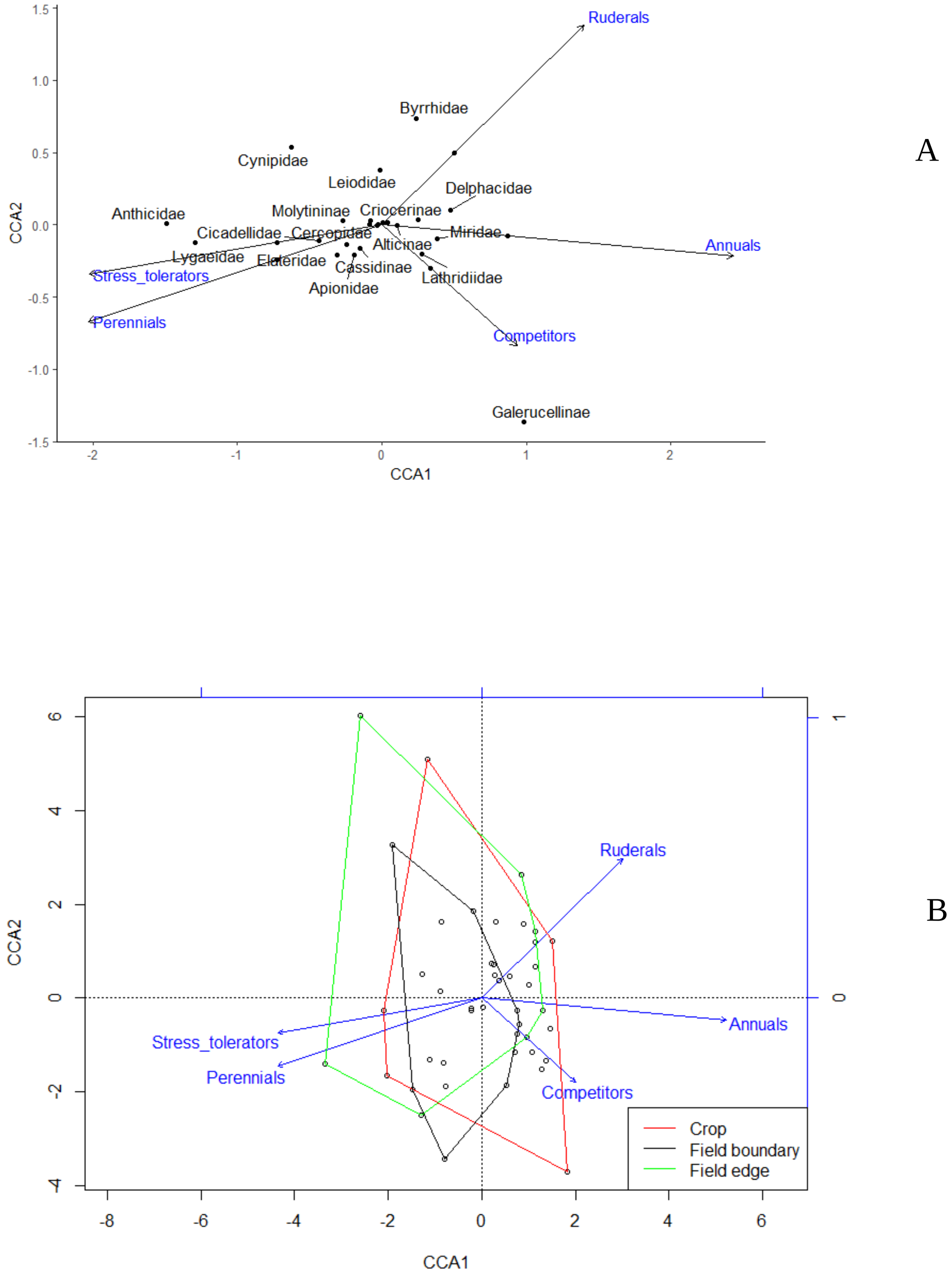


Figure 6.12 Canonical Correspondence Analysis (CCA) ordination diagram of herbivores/pollinators assemblages in the organic system (data from May-September 2015), A) herbivores/pollinators taxa response to CSR plant traits (axis1: 9.8%; axis2: 2.6%), B) variation in taxa composition in crop, field boundary and field edge habitats response to CSR plant traits.

6.6.4 Influence of combined plant cover, structure and traits on invertebrate assemblages in the organic system

Table 6.3 summarizes the results from variation partitioning the effects of plant cover (i.e. plant species composition), structure and traits on all three invertebrate functional groups within the organic system. Overall the plant cover, structure and traits explained between approximately 14% and 22% of the total variation in the invertebrate community composition. There was relatively little difference in the overall pattern between the functional groups, with most of the variation (4.0% to 7.6%) being explained by plant traits and (1.0% to 2.0%) jointly between the plant cover, structure and traits. Only a relatively small amount of variation (4.3% to 5.4%) could be uniquely allocated to plant structure and (up to 1.8%) cover. However, 78.9% and 79.3% of the variation in epigeal predators and herbivores/pollinators respectively was unexplained, with slightly more unexplained for foliar predator/parasitoids (87.9%).

Plant traits and structure affected epigeal predator assemblage composition ($F_{2,37} = 2.89$, P= 0.002; $F_{2,37} = 2.33$, P= 0.005 respectively), explaining 7.6% and 5.4% of the variation respectively (Table 6.3). Plant structure and traits also had significant individual effects (5.0% and 4.0%) on foliar predators/parasitoids ($F_{2,37} = 2.419$, P= 0.023 and $F_{2,37} = 2.02$, P= 0.039 respectively). Similarly, herbivore/pollinator community composition was affected by plant traits (6.3%; $F_{2,37} = 2.90$, P 0.001) and structure (4.3%; $F_{2,37} = 2.06$, P= 0.009).

Functional group	Plant cover	Plant structure	Plant traits	Joint effect of cover & structure	Joint effect of structure & traits	Joint effect of traits & cover	Joint effect of cover, structure & traits	Residual
Epigeal predators	1.8	5.4	7.6	1.4	0.0	3.0	2.0	78.9
Foliar predators / parasitoids	0.0	5.0	4.0	1.0	0.0	1.0	1.1	87.9
Herbivores / pollinators	1.5	4.3	6.3	2.5	3.5	1.6	1.0	79.3

Table 6.3 Variation partitioning showing the unique and joint effects (percentage explained) of the plant cover, structure and traits on the invertebrate community composition in the organic system.

6.6.5 Conventional management: Relationship with plant cover and invertebrate assemblages in the conventional system

Plant cover (i.e. plant species composition) had an overall significant influence on conventional epigeal predator assemblages ($F_{12,29}$ = 2.13, P< 0.001 - Figure 6.13), with significant crop and weed species including *Triticum aestivum* ($F_{12,29}$ = 3.28, P =0.002), *Bromus mollis* ($F_{12,29}$ = 2.98, P= 0.006), *Festuca rubra* ($F_{12,29}$ = 2.62, P= 0.012), H*olcus lanatus* ($F_{12,29}$ = 2.55, P= 0.032) and *Arrhenatherum elatius* ($F_{12,29}$ = 1.89, P= 0.038). CCA Axis 1 Figure 6.13 A showed variation from samples associated with dense oilseed rape (*Brassica napus*) through to winter wheat (*Triticum aestivum*) with high axis scores. Axis 2 varied from winter barley (*Hordeum vulgare*) with low axis score through to field boundaries dominated by grasses (especially *Phleum pratense* and *Holcus lanatus*). Most of the ubiquitous invertebrate taxa were grouped around the origin of the axes. Coleoptera- Lebiini was associated with field hedge boundaries infested with the grass weed *Phleum pratense* whilst Coleoptera- Licinini was associated with tall grassy field boundaries bordering oilseed rape fields. Hemiptera- Saldidae was generally associated with *Arrhenatherum elaticus* grass species with high Axis 1 scores.

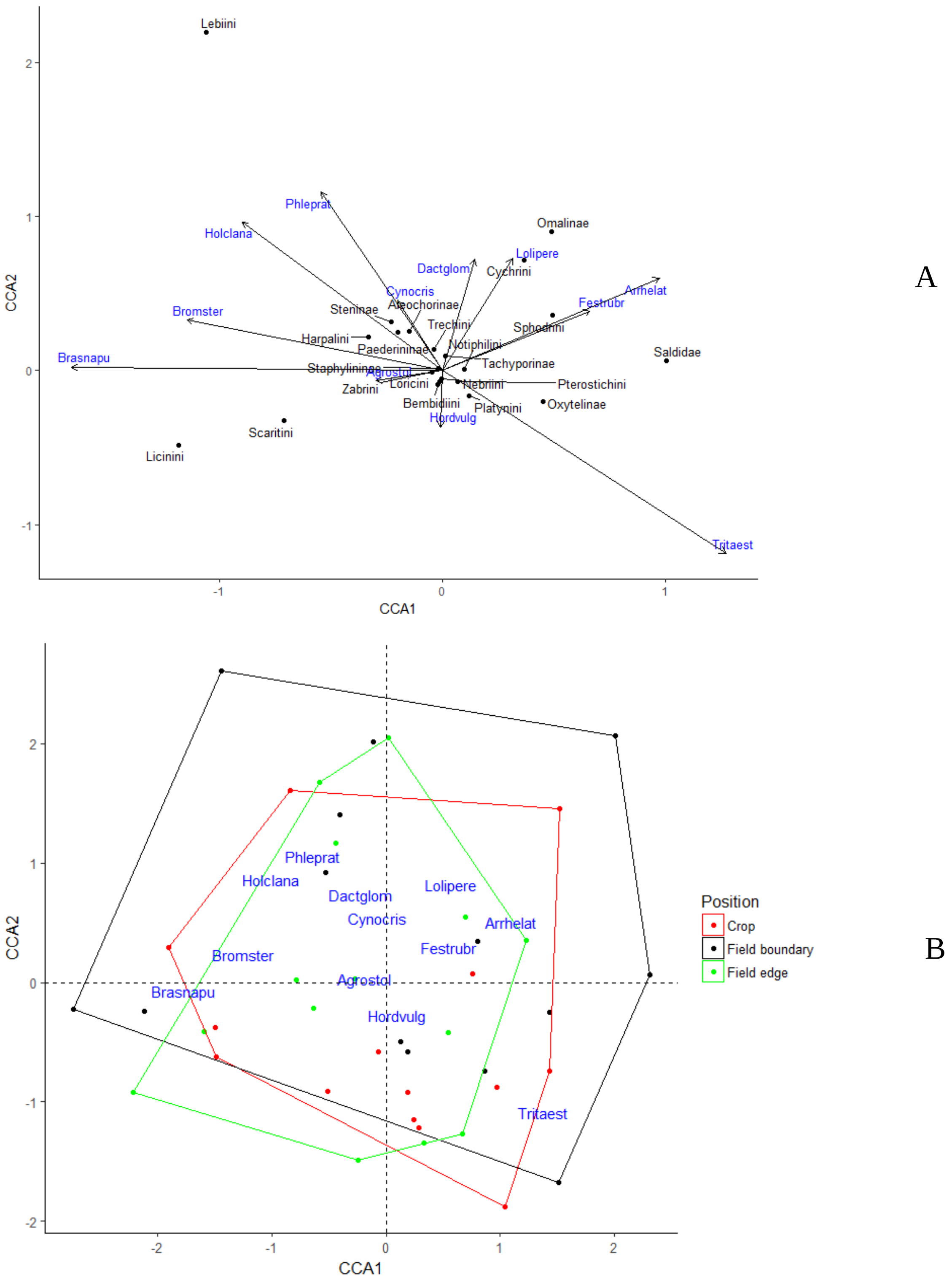


Figure 6.13 Canonical Correspondence Analysis (CCA) ordination diagram of epigeal predators assemblages in the conventional system (data from May-September 2015), A) epigeal predators taxa response to plant species composition (axis1: 10.9%; axis2: 1.0%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant species composition (see Table 6.1 for a complete list of plant species).

Plant species composition did not have an overall effect on foliar predator/parasitoid community composition within the conventional system ($F_{12,29}$ = 1.48, P= 0.098 - Figure 6.14) although two plant species found in the field boundaries had significant individual influences *Arrhenatherum elatius* ($F_{12,29}$ = 3.22, P =0.002) and *Dactylis glomerata* ($F_{12,29}$ = 2.98, P= 0.032). Axis 1 Figure 6.14 A showed variation from field boundaries bordering oilseed rape containing *Cynosurus cristatus* associated with Hemipteran- Nabidae, through to woodland edge habitats dominated by *Arrhenatherum elatius* and *Festuca rubra* associated with Neuropteran- Chrysopidae and Dermapteran- Forficulidae. Axis 2 varied from tall herbaceous boundaries containing *Dactylis glomerata* and *Bromus sterilis,* through to winter wheat crops infested with *Phleum pratense*. Mecoptera- Panorpidae was associated with tall grassy boundaries, whilst Hymenoptera- Platygasteridae was associated with *Phleum pratense* in winter wheat.

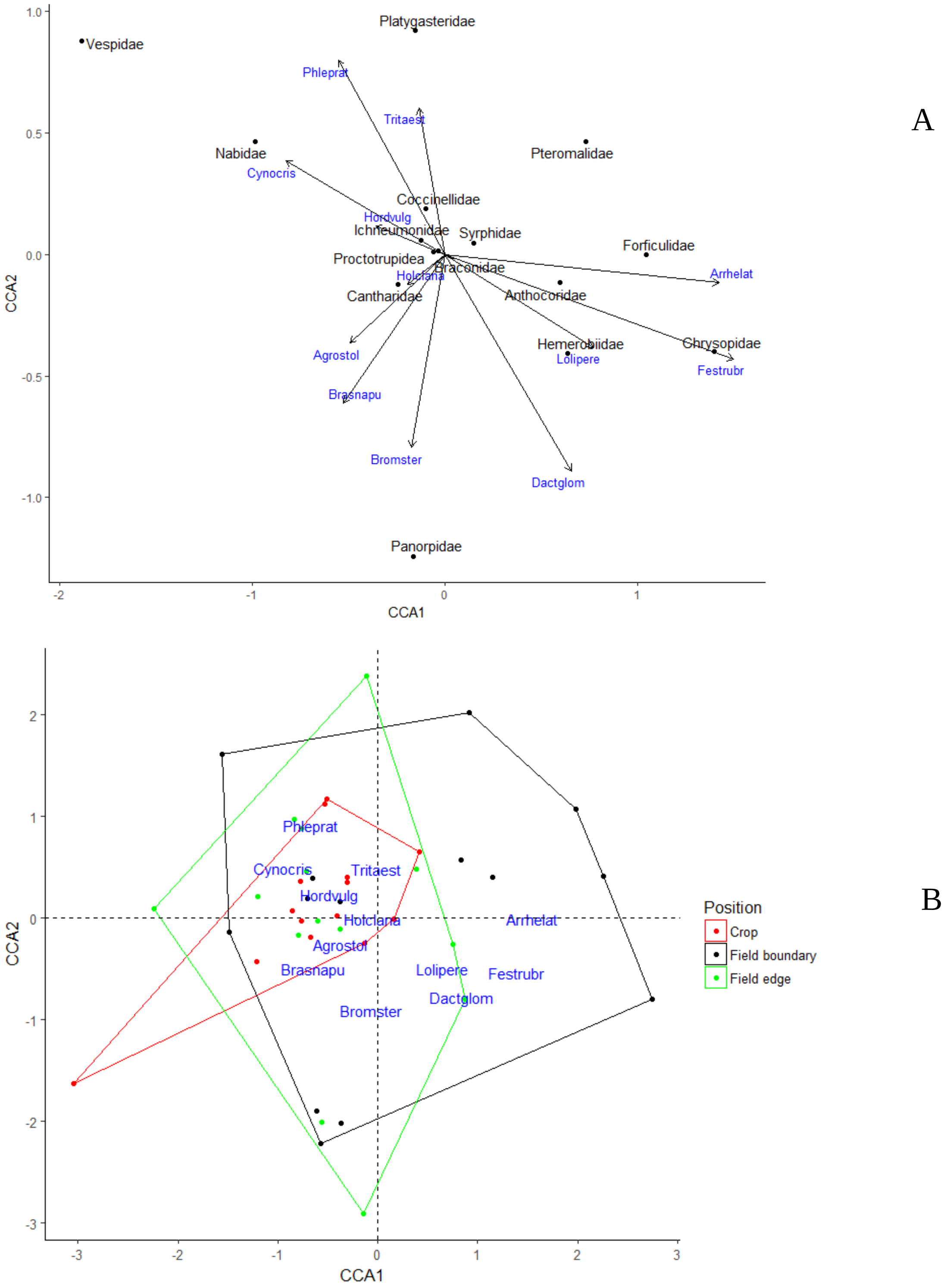


Figure 6.14 Canonical Correspondence Analysis (CCA) ordination diagram of foliar predators/parasitoids assemblages in the conventional system (data from May-September 2015), A) foliar predators/parasitoids taxa response to plant species composition (axis1: 10.3%; axis2: 3.1%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant species composition (see Table 6.1 for a complete list of plant species).

Overall, in the conventional system herbivores/pollinators were significantly influenced by plant species composition ($F_{12,29} = 2.65$, P< 0.001 - Figure 6.15), with four weed species in the field boundaries *Phleum pratense* ($F_{12,29} = 5.73$, P =0.002), *H. lanatus* ($F_{12,29} = 3.96$, P=0.004), *Triticum aestivum* ($F_{12,29} = 2.37$, P= 0.016) and *Lolium perenne* ($F_{12,29} = 1.94$, P= 0.032) and the very dense oilseed rape *Brassica napus* ($F_{12,29} = 4.17$, P =0.002) having significant influence. Major variation on CCA Axis 1(Figure 6.15 A) was between the grass species *Phleum pratense* generally associated with Homoptera- Cercopidae in tall boundaries through to oilseed rape *Brassica napus* associated with Hymenoptera- Cynipidae in the field edge (5 cm). Secondary variation CCA Axis 2 was between oilseed rape (*Brassica napus)* associated with the rare seed weevils Coleoptera- Apionidae through to flower beetles Coleoptera- Melyridae sampled in winter wheat with high axis scores.

In epigeal predators, foliar predators/parasitoids, and herbivores/pollinators, in general there was least taxonomic variation in the crop samples, and greatest in the field boundaries, as indicated by the convex polygons in the CCA ordination plots (Figure 6.15 B, Figure 6.15 B and Figure 6.15 B).

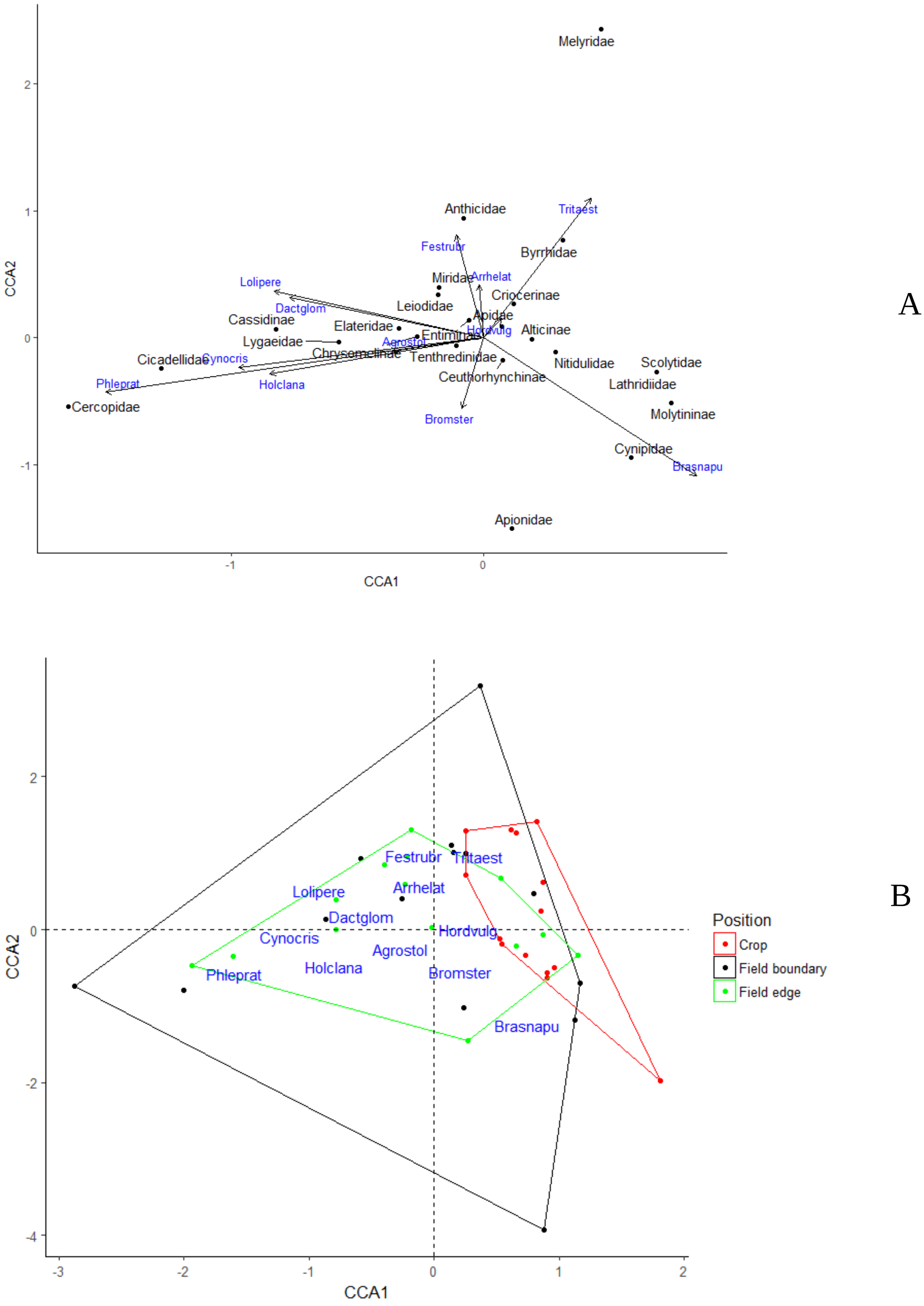


Figure 6.15 Canonical Correspondence Analysis (CCA) ordination diagram of herbivores/pollinators assemblages in the conventional system (data from May-September 2015), A) herbivores/pollinators taxa response to plant species composition (axis1: 15.4%; axis2: 6.8%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant species composition (see Table 6.1 for a complete list of plant species).

6.6.6 Relationship with plant structure and invertebrate assemblages in the conventional system

The structural characteristics of the main habitats in the conventional system are summarized in Figure 6.16. The tallest habitats were the tall grassy boundaries, woodland boundaries and oilseed rape. The OSR was relatively 'top-heavy' with the densest foliage above 75 cm, and relatively little cover below 50 cm in height. The winter wheat and barley were both shorter, but like the OSR, were most dense at the top. In the conventional system the total vegetation density was unrelated to the total number of epigeal predators, but the abundance of both foliar predators/parasitoids and herbivores/pollinators was positively correlated with vegetation density ($F_{1,25}$=14.41, P<0.001; $F_{1,40}$=17.75, P<0.001 respectively; Figure 6.17).

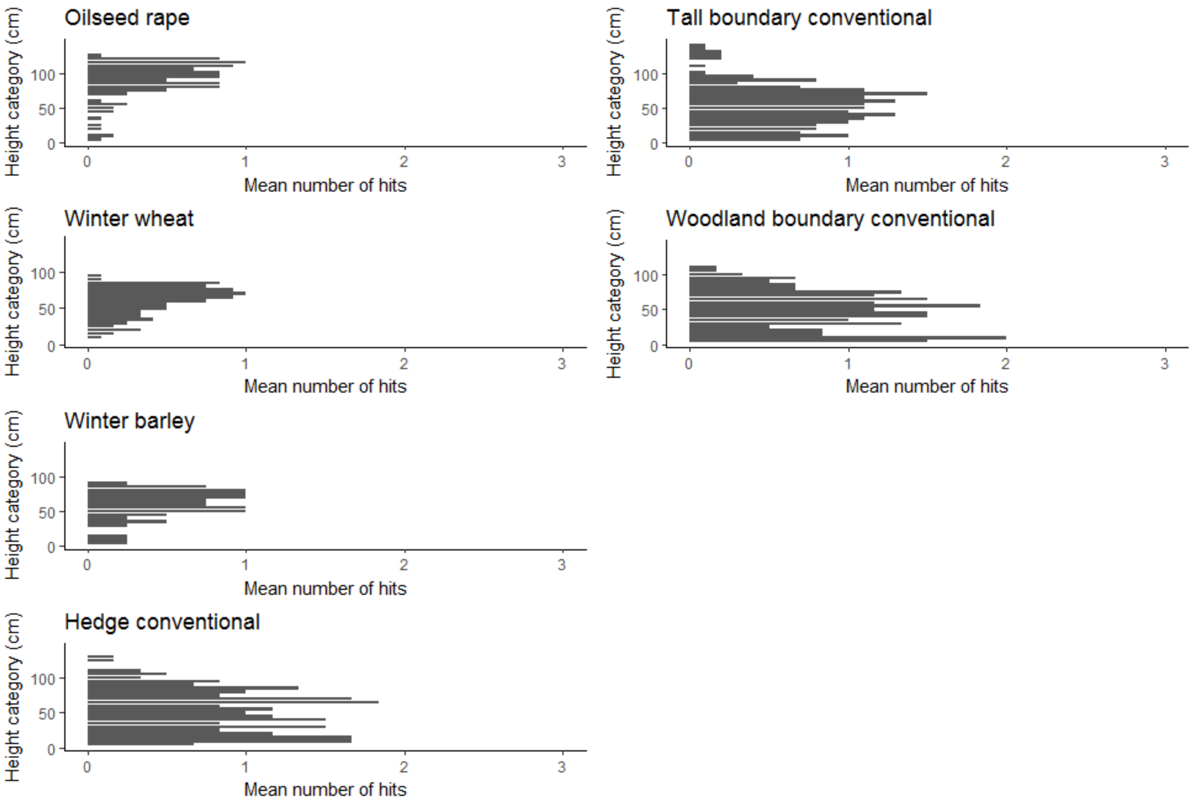


Figure 6.16 Overall structural characteristics of the main habitats in the organic system.

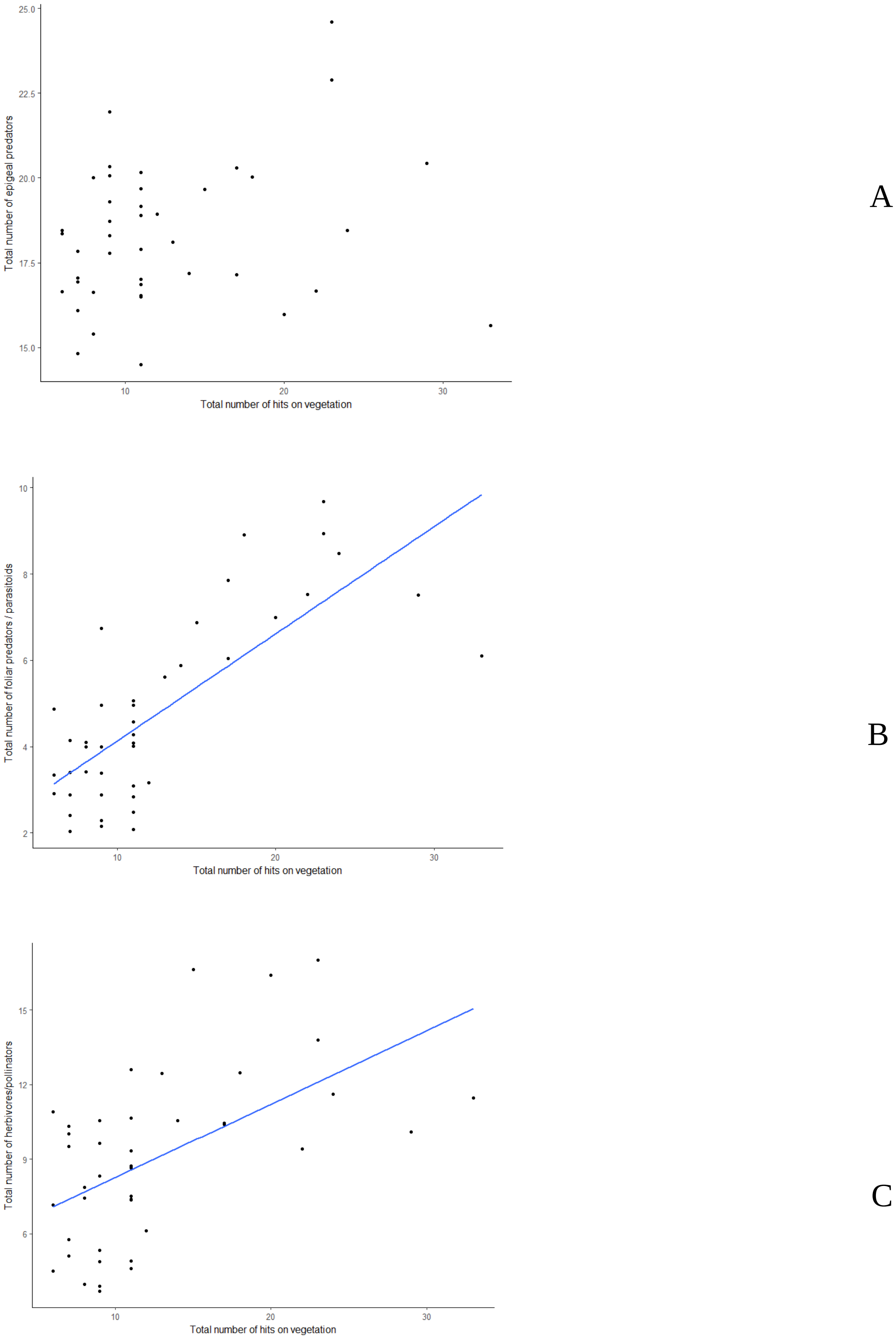


Figure 6.17 Relationship between the overall vegetation density and functional groups total: A) epigeal predators, B) foliar predators/pollinators and C) herbivores/ pollinators totals in the conventional system.

Plant structure had an overall significant influence on epigeal predator community composition within the conventional system ($F_{14,27} = 1.79$, $P < 0.001$ - Figure 6.18). Stepwise tests indicated plant structure heights 10 cm ($F_{14,27} = 2.43$, $P = 0.008$), 60 cm ($F_{14,27} = 2.62$, $P = 0.008$), 110 cm ($F_{14,27} = 2.19$, $P = 0.010$), 70 cm ($F_{14,27} = 2.17$, $P = 0.012$), 20 cm ($F_{14,27} = 2.11$, $P = 0.044$) and 40 cm ($F_{14,27} = 1.81$, $P = 0.044$) contributed to the significant influence. The major variation (Figure 6.18 A) on CCA Axis 1A was between tall vegetation heights (90 cm, 110 cm, 115 cm) associated with three rarer Coleoptera tribes Licinini, Scaritini and Harpalini in taller oilseed rape fields through to shorter plants heights (20 cm, 75 cm, 60 cm) associated with Coleoptera- Saldidae in winter wheat and oilseed rape. CCA Axis 2 varied from moderately tall vegetation heights (80 cm, 85 cm) closely associated with the very abundant Coleoptera- Pterostichini, Coleoptera- Loricini, and Coleoptera- Platynini in winter wheat through to very tall vegetation heights (130 cm) associated with Coleoptera- Cychrini with high scores in tall field boundaries. Most of the ubiquitous invertebrate taxa were grouped around the origin of the axes, with particular association to specific plant heights.

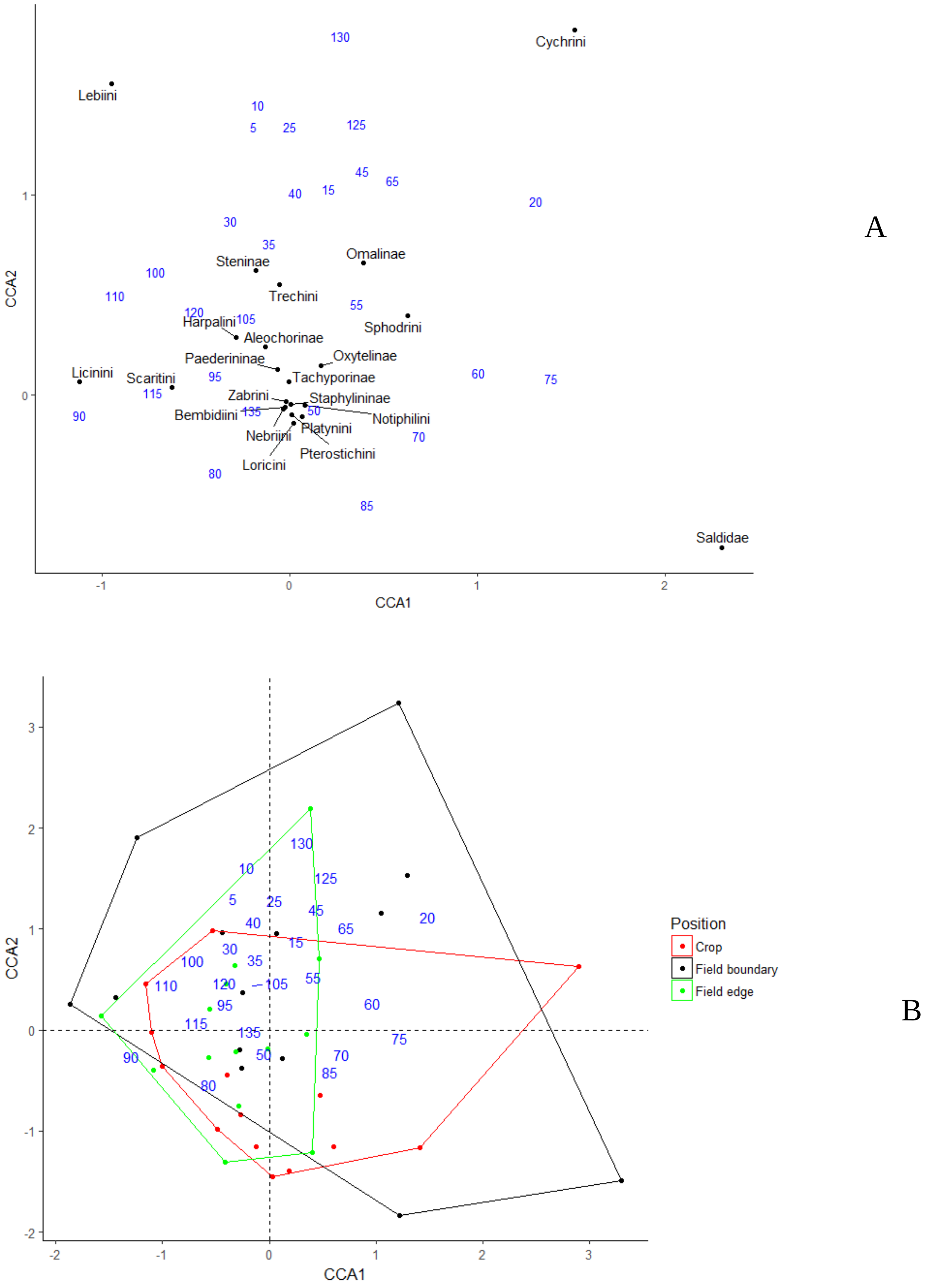


Figure 6.18 Canonical Correspondence Analysis (CCA) ordination diagram of epigeal predators assemblages in the conventional system (data from May-September 2015), A) epigeal predators taxa response to plant structure (axis1: 18.4%; axis2: 2.4%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant structure.

Overall, foliar predators/parasitoids was not significantly influenced by plant structure in the conventional farming system ($F_{14,27} = 1.45$, P= 0.174 - Figure 6.19). Nevertheless, plant structure heights of 130 cm ($F_{14,27} = 3.11$, P= 0.034), 90 cm ($F_{14,27} = 1.97$, P= 0.048) and 134 cm ($F_{14,27} = 3.49$, P= 0.046) had significant individual effects on foliar predator/parasitoid community composition. The major variation on CCA Axis 1 (Figure 6.19 A) was between taller vegetation heights (80 cm, 125 cm, and 130 cm) associated with Hemiptera- Nabidae and Hymenoptera- Platygasteridae found mainly in hedge boundaries, through to medium vegetation heights (55 cm, 65 cm) associated with Neuroptera- Chrysopidae in woodland boundaries. CCA Axis 2 was less consistent, varying from combinations of short and tall vegetation (15 cm, 60 cm, and 130 cm) associated with Hemiptera- Nabidae in winter wheat through to tall vegetation heights (135 cm, 115 cm) associated with Hymenoptera- Vespidae in tall herbaceous boundaries. Most of the ubiquitous taxa were around the origin without any specific association to particular vegetation heights.

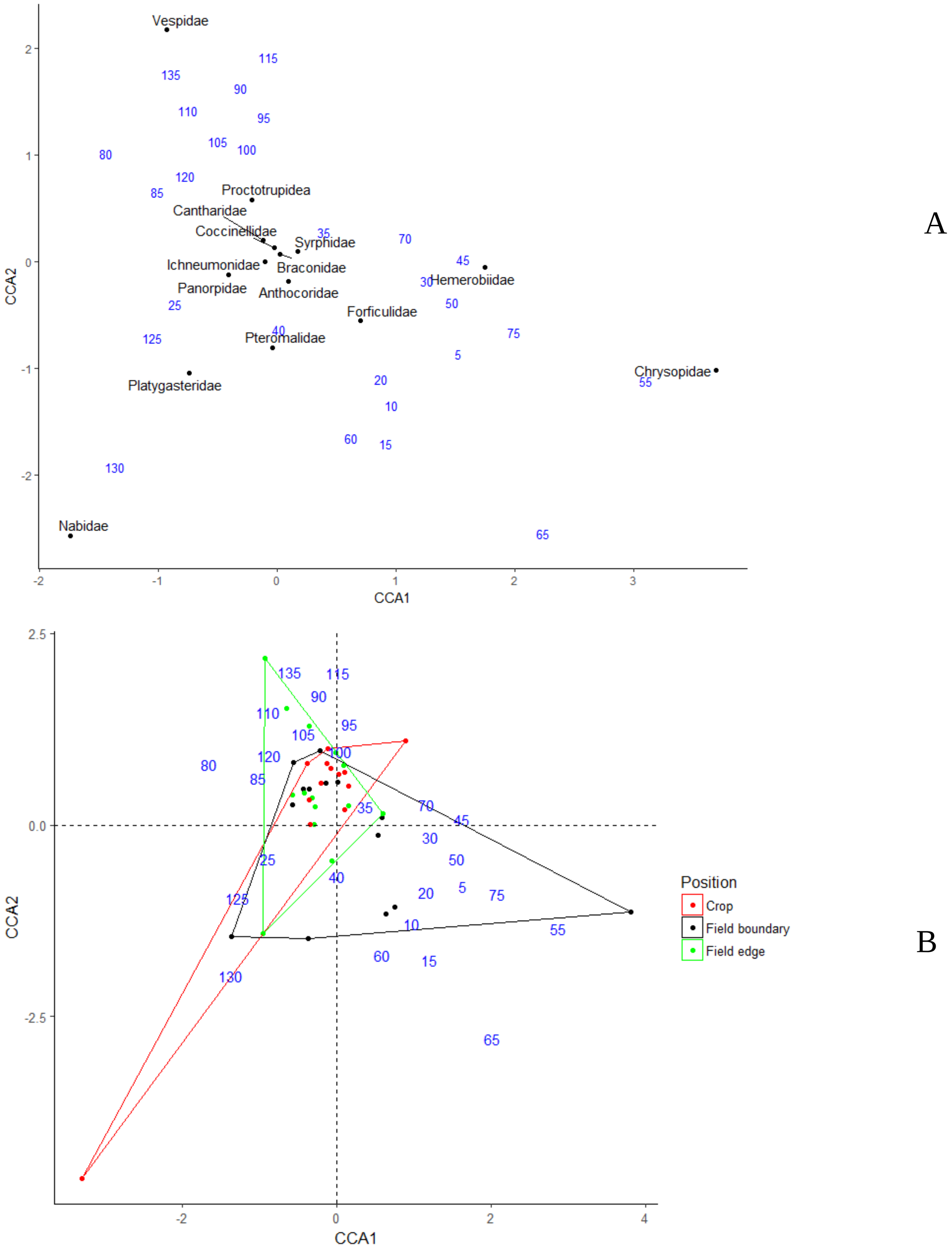


Figure 6.19 Canonical Correspondence Analysis (CCA) ordination diagram of foliar predators/parasitoids assemblages in the conventional system (data from May-September 2015), A) foliar predators/parasitoids taxa response to plant structure (axis1: 15.0%; axis2: 3.0%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant structure.

Overall, plant structure had a significant influence on herbivores/pollinators community composition within the conventional system ($F_{14,27} = 1.42$, $P = 0.037$ - Figure 6.20), with plant heights of 20 cm ($F_{14,27} = 3.51$, $P = 0.002$) and 120 cm ($F_{14,27} = 2.74$, $P = 0.002$) and 10 cm ($F_{14,27} = 1.75$, $P = 0.024$) having significant effects. The main variation along CCA Axis 1 (Figure 6.20 A) was between a mixture of taller and shorter vegetation heights (25 cm, 30 cm, 130 cm) generally associated with two Homoptera taxa Cercopidae and Cicadellidae sampled in tall grassy field boundaries and hedges through to taller vegetation heights (100 cm, 115 cm, 120 cm) associated with Coleoptera- Scolytidae in oilseed rape fields. CCA Axis 2 had height of 120 cm was associated with Coleoptera- Lathridiidae with low axis scores, in oilseed rape fields, through to medium heights (50 cm, 60 cm) associated with Coleoptera- Melyridae and Anthicidae in winter wheat fields.

In all three CCA plots (Figure 6.18 B, Figure 6.19 B, Figure 6.20 B), especially the epigeal predators, and herbivores/pollinators, there appeared to be greater variability in the taxonomic composition of the invertebrates within the boundaries than the crops or field edge.

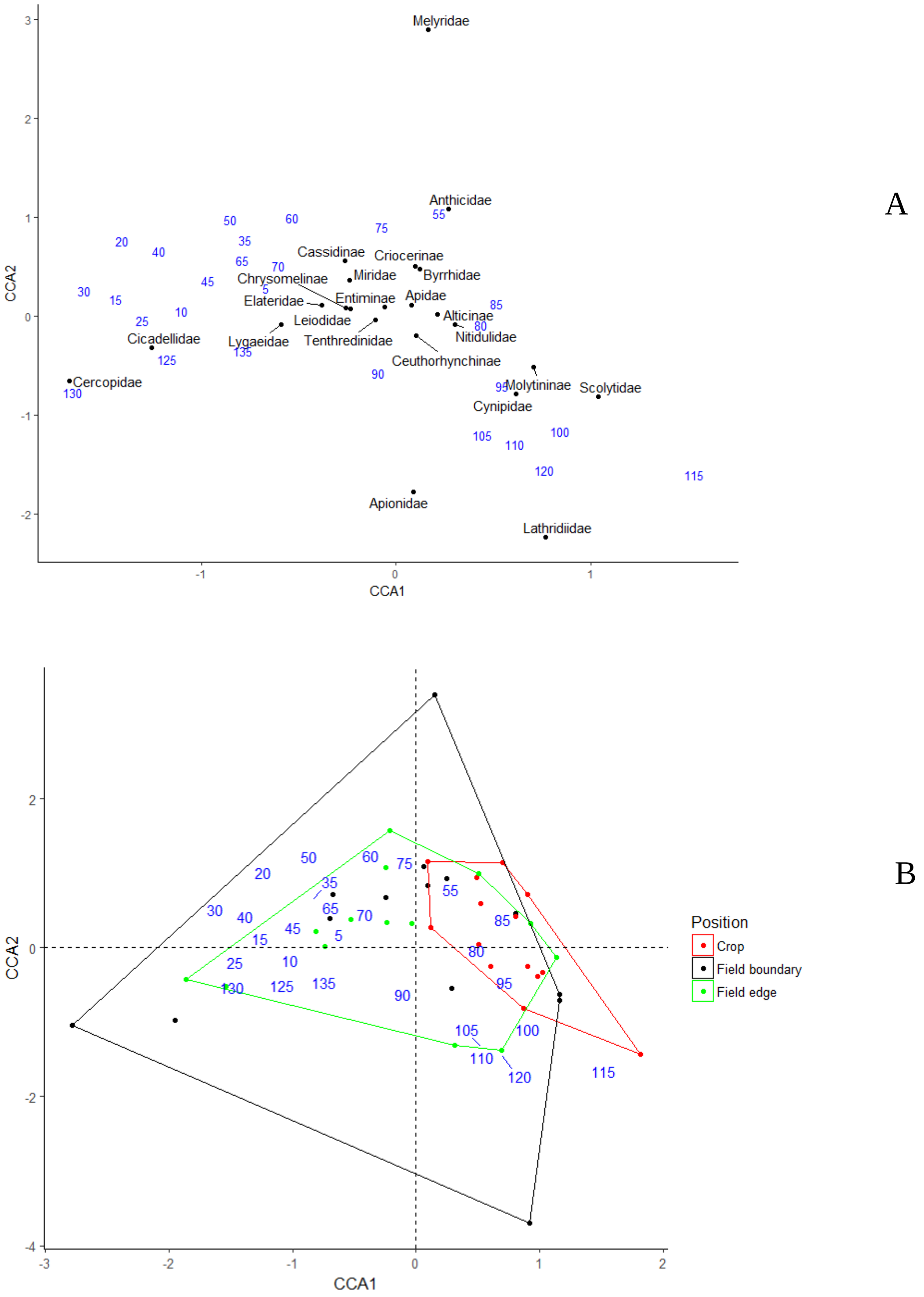


Figure 6.20 Canonical Correspondence Analysis (CCA) ordination diagram of herbivores/ pollinators assemblages in the conventional system (data from May-September 2015), A) herbivores/pollinators taxa response to plant structure (axis1: 16.0%; axis2: 6.8%), B) variation in taxa composition in crop, field boundary and field edge habitats response to plant structure.

6.6.7 Relationship with plant traits and invertebrate assemblages in the conventional system

Figure 6.21 provides an overview of the CSR weighted vegetation patterns in the conventional crops, field boundary and field edge. Crop samples were dominated by competitors and ruderals (on average over 45% each), whilst the stress-tolerators comprised only approximately 5% of the vegetation. In contrast, in the field boundaries, stress-tolerators plant species comprised on average 20% of the cover, whilst the ruderals were only 35% (see Table 6.2).

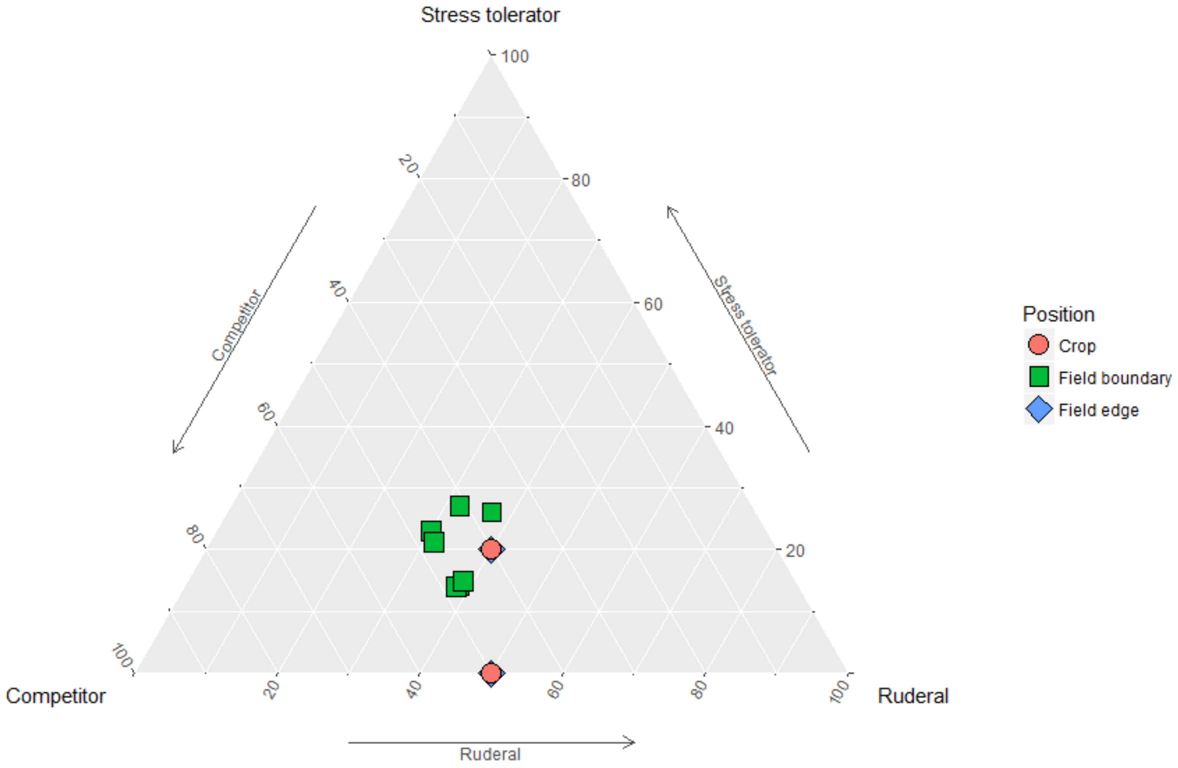


Figure 6.21 Overall summaries of the positions of the vegetation CSR traits at each site in the conventional system, summarized using standard 3-dimension plots.

Epigeal predator community composition was significantly affected by plant traits ($F_{5,36}$=1.90, P<0.001 - Figure 6.22), with perennials, ruderals and stress-tolerator covers most important ($F_{1,38}$=6.27, P<0.001; $F_{1,38}$=4.04, P<0.001; $F_{1,38}$=3.00, P=0.006 respectively). Coleoptera- *Cychrini* and Coleoptera- Omalinae were particularly associated with stress-tolerator plant species whilst Coleoptera- Licinini and Coleoptera- Lebiini were associated with perennial plant species (Figure 6.22 A). There was not a significant effect of plant traits overall on foliar predators/parasitoids ($F_{5,36}$=1.55, P=0.071- Figure 6.23), although stepwise selection suggested that ruderals had an effect ($F_{1,40}$=3.33, P=0.010), with fewer Hymenoptera- Vespidae whilst three parasitoids Hymenopteran- Platygasteridae, Pteromalidae, and Hemipteran- Nabidae were all associated with stress tolerators (Figure 6.23 A). Plant traits had a significant effect overall on conventional herbivores/pollinators ($F_{5,36}$=1.45, P=0.038- Figure 6.24) with perennials and ruderals particularly important ($F_{1,39}$=4.93, P=0.001; $F_{1,39}$=2.19, P=0.042 respectively). Coleoptera- Cassidinae and Coleoptera- Apionidae were associated with increased cover of perennials and ruderals whilst an increase in annuals and competitor cover was associated with Coleopteran- Anthicidae (Figure 6.24 A).

The variation in invertebrate taxonomic composition was considerably greater in the field boundaries than the crop or field edge (Figure 6.22 B, Figure 6.23 B and Figure 6.24 B).

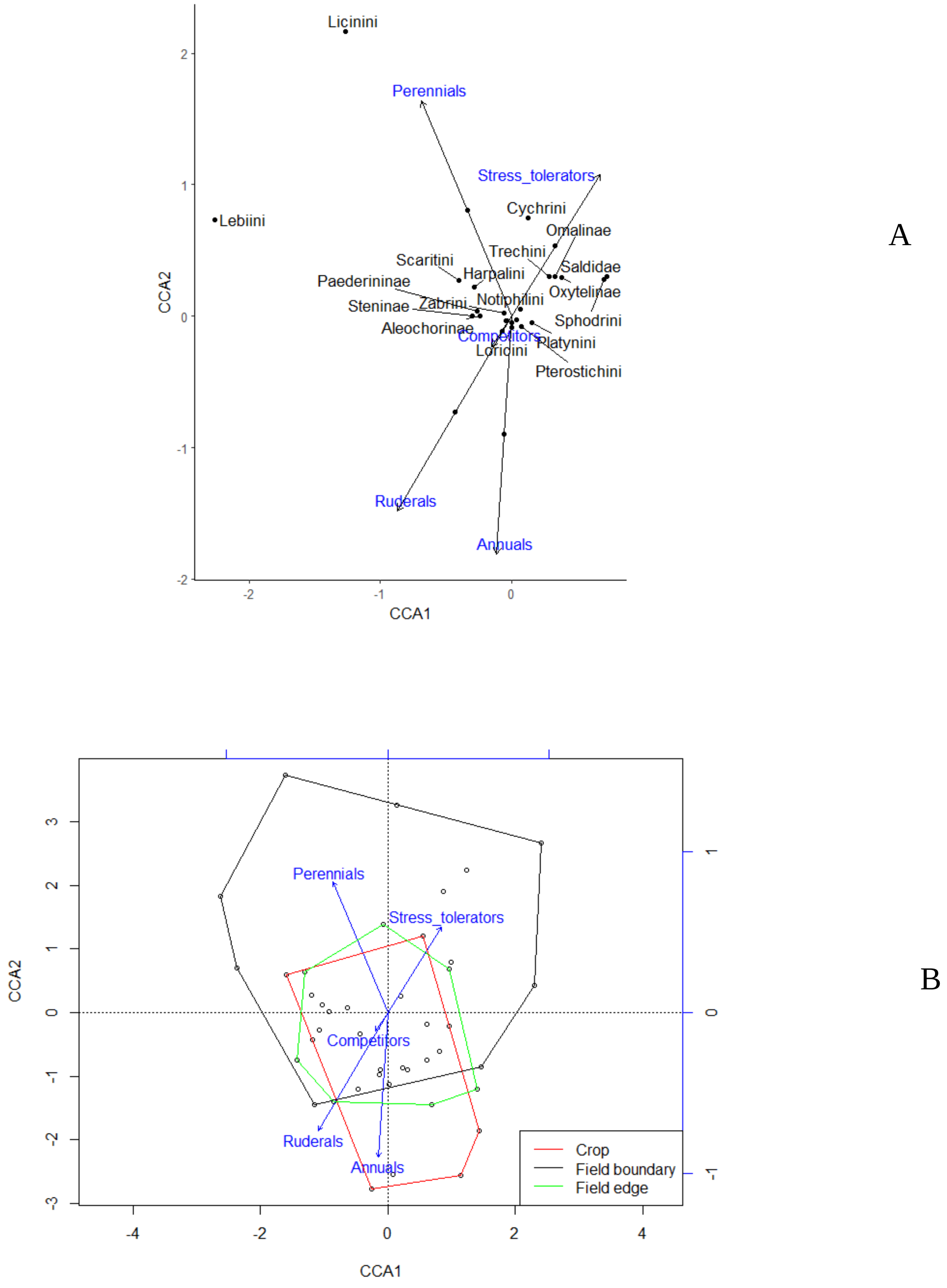


Figure 6.22 Canonical Correspondence Analysis (CCA) ordination diagram of epigeal predators assemblages in the conventional system (data from May-September 2015), A) taxa response to CSR plant traits (axis1: 10.4%; axis2: 5.9%), B) variation in taxa composition in crop, field boundary and field edge habitats response to CSR plant traits.

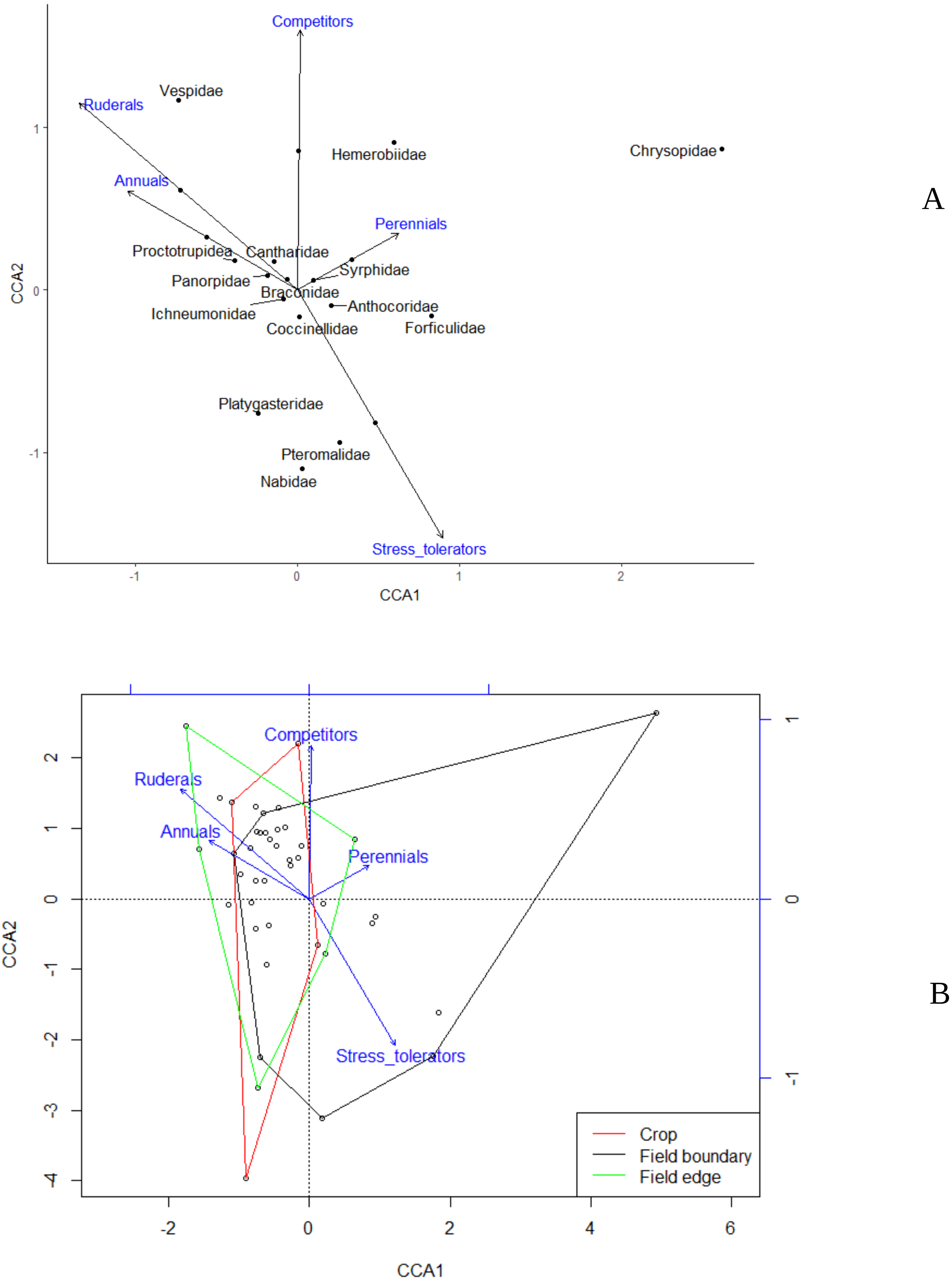


Figure 6.23 Canonical Correspondence Analysis (CCA) ordination diagram of foliar predators/parasitoids assemblages in the conventional system (data from May-September 2015), A) taxa response to CSR plant traits (axis1: 8.0%; axis2: 2.6%), B) variation in taxa composition in crop, field boundary and field edge habitats response to CSR plant traits.

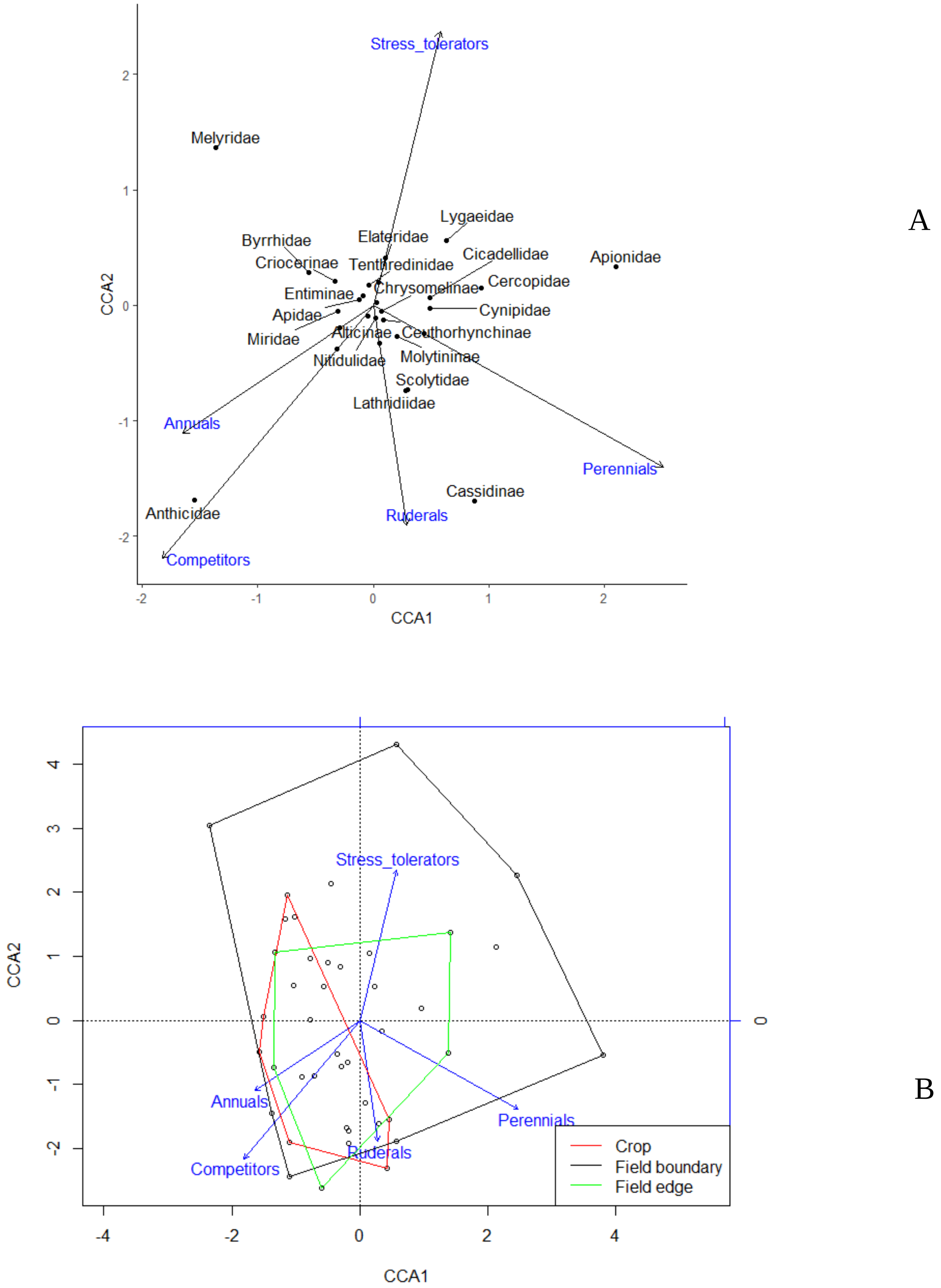


Figure 6.24 Canonical Correspondence Analysis (CCA) ordination diagram of herbivores/pollinators assemblages in the conventional system (data from May-September 2015), A) taxa response to CSR plant traits (axis1: 7.7%; axis2: 4.3%), B) variation in taxa composition in crop, field boundary and field edge habitats response to CSR plant traits.

6.6.8 Influence of combined plant cover, structure and traits on invertebrate assemblages in the conventional system

Overall the three plant attributes explained between approximately 23% and 42% of the total variation in the conventional invertebrate community composition for the three functional groups Table 6.4. There was relatively little difference in the overall pattern between epigeal predators and foliar predators/parasitoids, with plant cover, structure and traits showing similar proportional effect, but greater in herbivores/pollinators assemblages. Irrespective of the plant attributes for epigeal predators and foliar predators/parasitoids approximately 77% of the total variation was unexplained, less for herbivores/pollinators.

Plant traits and structure had similar influence on epigeal predators, with slightly lesser amount for cover. All three plant attributes had significant effects on the epigeal predators community composition: traits ($F_{2,37} = 2.77$, $P < 0.001$), cover ($F_{2,35} = 2.29$, $P < 0.001$) and structure ($F_{2,35} = 2.48$, $P < 0.001$). There was a very small joint cover: structure: traits effect (1%). Similar plant attributes pattern was seen in foliar predators/parasitoids assemblages as epigeal predators. None of the three attributes had significant effects on the foliar predator assemblages, plant traits ($F_{2,35} = 1.51$, $P = 0.116$) plant structure ($F_{2,35} = 1.46$, $P = 0.143$) plant cover ($F_{2,35} = 1.15$, $P = 0.271$) with little variation explained by any of the three attributes (Figure 8b). However, by far the greatest effect on foliar predators was jointly plant: cover: structure: traits combinational effect (15.1%). Herbivore / pollinators assemblages were significantly influenced by plant cover ($F_{2,35} = 6.12$, $P = 0.001$), traits ($F_{2,35} = 3.63$, $P = 001$), structure ($F_{2,35} = 2.27$ $P = 0.008$). As with foliar predators there was a large jointly plant cover: structure: traits effects on the community composition (13.0%).

Functional group	Plant cover	Plant structure	Plant traits	Joint effect of cover & structure	Joint effect of structure & traits.	Joint effect of traits & cover	Joint effect of cover, structure & traits	Residual
Epigeal predators	5.4	5.6	6.5	4.1	0.0	0.0	1.0	77.4
Foliar predators / parasitoids	1.8	2.0	2.0	2.0	0.0	0.0	15.1	77.1
Herbivores / pollinators	16	3.7	8.1	0.0	0.0	1.0	13.0	57.4

Table 6.4 Variation partitioning showing the unique and joint effects (percentage explained) of the plant cover, structure and traits on the invertebrate community composition in the conventional system.

6.7 Discussion

This research has undertaken a detailed investigation of the role of vegetation cover, vertical structure and plant traits on the invertebrate community composition on two farming systems. It is clear that all three factors have major effects on the invertebrates, but the exact patterns depend both on the farming system, and the invertebrate functional group. In general, plant traits appeared to be more important than cover or structure in determining the invertebrate community composition in both systems, and the three plant-related variables had bigger effects in the conventional than organic system.

6.7.1 Plant traits and invertebrate community composition

In both farming systems the invertebrate response to plant life history traits was on a broad trend from vegetation communities dominated by predominantly competitor plant species in the boundaries through to those with ruderal species in the crops (CSR scheme of Grime, 1988). The overall variation in invertebrate taxa composition in response to plant traits, as measured by the scatter of points in the relevant CCA plots (Figure 6.22 B, Figure 6.23B, Figure 6.24 B) was relatively similar in the crops and field edges but considerable greater variation within field boundaries for the conventional system. In contrast, in the organic system, there was considerably greater variation in invertebrate species composition within the crops and field edge (40 m and 5 m) than boundaries (Figure 6.10 B, Figure 6.11 B, Figure 6.12 B), especially epigeal predators and herbivores/pollinators. Whilst the underlying cause is difficult to ascertain, there appears to be a management effect. In the organic system, there was a greater diversity of weeds which provided food sources for seed eating predators and biological weed control, alternative to herbicide in the conventional system (Westerman *et al.*, 2005). In contrast, conventional fields are devoid of flowering plants and crop weeds (Bianchi *et al.*, 2006; Winkler *et al.*, 2009), which provides variation in traits diversity which affected invertebrate groups differently.

In the conventional system the use of herbicides will have resulted in greater homogeneity in arable weeds which may account for the relative similarities observed in the two habitats in the conventional system (Figure 6.22 B, Figure 6.23 B Figure 6.24 B). In contrast, the organic system did not have herbicide drift from crop to field boundaries, this can produce more plant species in the organic hedgerows (Aude *et al.*, 2004). Field boundaries are important for crop pollination, wildflowers, and spillover of other ecosystem services into nearby cropland (Blitzer *et al.*, 2012), and therefore their conversion for cropping should be avoided (Verburg *et al.*, 2006). In the conventional system however, field boundaries have been negatively affected by pesticide drifts, with negative effects on canopy structure resulting in a "knock on effect" on pollinators and natural pest control (Potts *et al.*, 2010; Oliver *et al.*, 2015). In contrast, the lack of herbicides usage in the organic crops enhanced a greater heterogeneity of arable weeds (Hole *et al.*, 2005; Tscharntke *et al.*, 2005c) which includes endangered plant species (van Elsen, 2000) and to a lesser extent the surrounding field boundaries. This may explain the bigger differences in overall variation in the invertebrates in response to plant traits in the two habitats in the organic system (Figure 6.10 B, Figure 6.11 B Figure 6.12 B). Nevertheless, the plant traits in the field boundaries are relatively similar in both parts of the farm, consisting of both annual and perennial plants and predominantly competitors.

Nick *et al.* (2001) suggested that highly diverse plant habitats may provide a greater range of food types for phytophagous carabids (herbivores of flowers and seeds). For example, CCA results showed seed-eating weevils Apionidae were associated with annual wheat crop (i.e. plant traits that result in production of large amount of seeds). The increased Apionidae will in turn attract their associated enemy with increased assemblages of predators (Crowder *et al.*, 2010). At a broader scale, agricultural land use patterns partly determine observed plant traits (Garnier *et al.*, 2007), as plants respond to differences in productivity and disturbance (Grime, 2006) in the agroecosystem.

6.7.2 Plant cover and invertebrate community composition

Plant community composition appeared to be a slightly more important factor affecting the invertebrate community composition in the conventional than organic system (especially epigeal predators and herbivores/pollinators), but nevertheless was important for both (Figure 6.1 A, Figure 6.2 A, Figure 6.3 A, Figure 6.13 A, Figure 6.14 A and Figure 6.15 A). In the organic systems, many weed species grow in both the crop and field boundaries, resulting in fewer differences in plant species composition between both habitats (Zaller *et al.*, 2008). Organic farms incorporate the use of organic manure or slurry to enhance soil nutrients which in turn encourage weeds species in both field edge and crop (Romero *et al.*, 2008; Sharma *et al.*, 2017). Invertebrates can often migrate between crop fields to non-crop boundaries in response to the quality of habitat particularly when there is a large contrast in available food in crop fields compared to boundaries (Dong *et al.*, 2015). Such contrasts are likely to be accentuated in the conventional system due to agronomic practice where there is a smaller seed bank due to winter sown crops. Marshall *et al.* (2003) and the use of herbicides.

O'Sullivan and Gormally (2002) reported that carabid species richness between sites were strongly related to weed cover whilst weed cover increased activity of some species of ground beetles in organic potatoes and cabbage (Armstrong and McKinlay, 1997). In general, plant cover influences invertebrate abundance e.g. ground beetles and rove beetles and wasps: (Varchola and Dunn, 1999; Lassau and Hochuli, 2005; Harvey *et al.*, 2008) and species composition of Auchenorrhyncha- Hemiptera (Sanderson *et al.*, 1995) partly through its effects on local microclimate within the plant canopy (Norris and Kogan, 2017). In addition, dense cover in planted field boundaries (Woodcock *et al.*, 2005a) and cultivated fields (Eyre *et al.*, 2013b) can increase beetle activity with potential beneficial control of pests in the crop.

6.7.3 Plant structure and invertebrate community composition

Vegetation density had variable effects on invertebrate abundance in both management systems, with some functional groups showing positive, negative or no correlation with density (

Figure 6.5 and Figure 6.17). Interpretation of these data is difficult, as sampled the invertebrate abundance is affected by the true invertebrate abundance in the field, as well as the sampling efficiency. The latter, especially for pitfall traps, is itself affected by vegetation density (Thomas *et al.*, 2006).

Overall plant structure had relatively little effects on invertebrate species composition in the organic system, but in the conventional system it affected epigeal predators and herbivores/pollinators community structure. Plant density however had great effects on invertebrate abundance in both management system, especially conventional system. In the organic system, vegetation vertical structure was relatively similar across most crop types and field boundaries with the greatest density of vegetation at lower heights. In contrast in the conventional system the structure was more varied, with taller and 'top-heavy' crops (especially oilseed rape and cereals) compared to 'bottom-heavy' field margins. The tallest vegetation was oilseed rape (conventional) and shortest the grass\clover ley (organic). Tall vegetation can serve as a temperature barrier (Dennis *et al.*, 1994) or provide invertebrates with protection from vertebrate predators such as birds. Whilst numbers of some invertebrate predators, especially Araneae (spiders) will be higher in structurally complex vegetation

(Gibson *et al.*, 1992), the hunting efficiencies of other invertebrate predators such as Carabidae is greater in short vegetation (Eyre *et al.*, 2013b).

In the organic system, the lack of importance for structure probably reflects the relative similarity in the overall structure in the different habitats. Note, however, that vegetation structure was only measured once, and that some crops (particularly grass\clover ley) will have experienced abrupt changes in structure during the course of the growing season due to silage cutting. The rapid removal of existing plant structure due to vegetation cutting, e.g. grass\clover ley and hay, (Cattin *et al.*, 2003; Gardiner and Hassall, 2009) can result in massive migration of invertebrates to nearby field boundaries (Ribera *et al.*, 2001; Thorbek and Bilde, 2004). This may account for some of the observed differences between crops and boundaries reported in Chapter 4.

Vegetation structure affects ground beetles, with larger and fewer species in the densest vegetation (Brose, 2003). Zaller *et al.* (2008) suggested that within-field structure can influence pollen beetle and weevil activity in oilseed rape whilst invertebrate herbivore (butterfly) abundance was shown to increase in taller vegetation (Pöyry *et al.*, 2006). Nevertheless, McCracken and Tallowin (2004) suggested that a mixture of grasses and broad-leaved plants with varied vegetation heights and structures is needed to encourage invertebrate communities. Spiders respond to vegetation structure (Schmidt and Tscharntke, 2005), but they were not included in these analyses.

6.7.4 Relative effect of plant species composition, structure and traits on invertebrate communities

Interpretation of the relative effects of plant cover (i.e. plant species composition), structure and traits on the invertebrate communities is not straightforward compared to the individual analyses described earlier in this chapter. For example, some predictors that appeared to have little or no effect when considered in isolation earlier (e.g. plant structure in the organic system) nevertheless have significant effects when analysed jointly with the other two predictors. The other reason for caution in interpretation is that in all the variation partitioning analyses the most variation unexplained was between 57.4 to 87.9%; Table 6.3.

The overall amount of explained variation from the three factors, unique or joint, was higher for conventional than organic (mean 29.4% and 18.0% respectively). This probably reflects the bigger contrasts in the vegetation in terms of its cover (i.e. plant species composition), structure and traits between the boundaries, edge and crop in the conventional compared to organic. In the conventional system, plant cover had the greatest effects on herbivores/pollinators communities. Schaffers *et al.* (2008) suggested plant species composition tends to affect primary consumer groups (herbivores) that depend on them for food first, which in turn produce a cascading effect on higher trophic groups (predators, parasitoids and parasites).

The three predictor variables (plant cover, plant structure, plant traits) did not have significant unique effects on the foliar predators/parasitoids in the conventional, although there was large joint effect (15.1% Table 6.4) of the three predictors on this functional group. In contrast, the joint effect in the organic system for this group was only 1.1%. The exact mechanisms that give rise to these differences are unclear.

6.7.5 Conclusions

The results presented in this chapter clearly indicate that plant cover (i.e. plant species composition), vegetation structure and plant traits all have important roles in their effects on invertebrates. They can affect both the absolute abundance of some groups of invertebrates but in particular the community composition of the invertebrates. Their effects are however not simple, as the three predictors are inter-related, and different groups of invertebrates respond to them in different ways depending on the farm management. Most studies have typically only looked at one or two of the three components (usually vegetation cover and/or structure), but this chapter demonstrates that plant traits are an important determinant of the invertebrate community. Irrespective of which particular plant trait system is used (CSR being the most common one for the UK), it is evident that it should be considered, along with vegetation cover and structure, to gain more insights into the invertebrate community.

Chapter 7. **General Conclusion**

7.1 The rationale of studying invertebrate abundance and composition on a split organic/conventional farm

The overall objective of this research was to assess the main drivers of invertebrate abundance and composition that could be incorporated into new decision-making practices and used by ecologists. This study required investigations at the whole-farm level, and across several sampling years, to encompass the whole cycle of agricultural management. As a result, a holistic approach was needed because invertebrate abundance and composition are influenced by both crop and non-crop habitats (Gonthier *et al.*, 2014). Patterns change in both time and space, therefore samples from field boundaries, edge and crop have been analysed, in addition to those across rotation cycles. The unique split management system at Nafferton has allowed comparison of organic and conventional farming on invertebrate communities.

A preliminary question was to test the hypothesis that invertebrate biodiversity was greater under organic than conventional management (Hole *et al.*, 2005; Letourneau Deborah and Bothwell Sara, 2008). Biodiversity is influenced by processes operating at different spatio-temporal scales (Belfrage *et al.*, 2005) and differs between management systems (Gabriel *et al.*, 2010b). Nafferton Farm is unique in that both management systems are on adjacent areas. This means that both halves of the farm experienced relatively similar weather, and soil type, in contrast to comparable research where farms are located at different geographical sites, which risk confusion of management with environment (Fuller *et al.*, 2005). A greater number of types of arable crops was cultivated in the organic than conventional system at Nafferton, which is a common practice (Norton *et al.*, 2009a).

Long-term studies are important to determine the possible effects of management on invertebrate abundance and community composition, the entire cycle of agricultural management, specifically crop-rotation. Numerous prior investigations into different aspects of invertebrate biodiversity have been undertaken at Nafferton (Eyre *et al.*, 2009; Eyre and Leifert, 2011b; Eyre and Leifert, 2012; Eyre *et al.*, 2013a; Sanderson *et al.*, 2015) which has provided a solid foundation on which to build the research described in this thesis.

7.2 Summary of key findings

7.2.1 Overall biodiversity: organic vs conventional

At Nafferton farm, both invertebrate biodiversity and abundance were greater in organic compared to conventional management, in accordance with previous research (Bengtsson *et al.*, 2005; Burgio *et al.*, 2015). The lack of artificial fertilizers and herbicides in the organic system, in addition to greater weed cover may have contributed to a more hospitable micro-climate, which had positive effects on invertebrate abundance. In contrast, cutting, spraying, ploughing etc. in conventional crops may result in arthropods seeking refuge in nearby field boundaries (Kleijn *et al.*, 2001; Meek *et al.*, 2002). Our results indicated the greatest invertebrate biodiversity was along conventional woodland boundaries, whilst invertebrates were most abundant in organic short-grass field boundaries. However, note that there were no woodland boundaries on the organic part of the farm. The large number of taxa along woodland boundaries may have been related to the greater habitat diversity, with a complex mixture of grasses of different heights, scrub and trees. This provides a variety of different habitats for different invertebrate groups. In addition to management and field boundary type, crop type had major effects on invertebrate abundance, being especially abundant in organic spring beans, and conventional winter barley and oilseed rape.

7.2.2 Temporal process: rotation patterns overtime

Major differences in community composition over time were observed in both the five-year conventional rotation and eight-year organic rotation. Invertebrate communities were, as might be expected, mainly affected by the current year's crop. Nevertheless, there was evidence of a significant "lag effect" from the previous year's crop, but only in the organic system. The organic rotation had less soil disturbance, as a result of the three years' of unploughed grass/clover leys, which allowed invertebrates to recover from the harmful effects of soil tillage. Furthermore, arable crops in the conventional system had fewer weeds and may have responded differently as a result of tillage compared to the organic (Marshall *et al.*, 2003). Therefore farmers should consider including crops such as grass/clover that do not require regular ploughing that leave the land bare after annual crop harvest, or wider adoption of 'no-till' agriculture.

7.2.3 Vegetation structure, composition, traits and invertebrate composition and traits in relation to spatial scale

Multivariate analyses showed vegetation structure, cover and traits all had major effects on invertebrate community composition. CSR patterns were particularly important, especially the abundance of competitors and ruderals, which were abundant in the field boundaries and crops respectively. Plant cover and CSR plant traits were more important in the organic system where there was a greater abundance of weeds and lack of chemical usage. These positive organic benefits were further observed in Chapter 3, where we looked at the relationship of field boundaries and their most abundant associated invertebrates to the same invertebrate taxa in field edge and crop. As might expected, more of the invertebrate taxa in the field boundary were found in the field edge than crop in both systems, given the spatial scale of the study. Furthermore, relationships between boundary and field edge/crop invertebrates were generally greater in the organic than conventional. This may have been because of less contrast between boundary, field edge and crop microhabitats, especially for diurnally foraging invertebrates. There was also clear evidence that relationships between the invertebrates in the boundaries and the same taxa in the field edge or crop were strongly affected by the invertebrate life-history characteristics, especially dispersal ability and body size.

7.3 Future research

7.3.1 Temporal changes

The results of this study suggested that all three invertebrate functional groups in the organic system (8 year rotation) showed a cyclical change in their community composition that closely matched the crop rotation sequence. In contrast in the conventional system (5 year rotation) this pattern was disrupted by regular soil cultivation and was only seen in herbivores/pollinators. Future research on invertebrate communities in agro-ecosystems must be undertaken across multiple years to encompass the entire crop rotation in the system under study, see (Eyre *et al.*, 2016a). Samples were collected via two methods from May to September each year to capture the majority of the invertebrate breeding season. Some studies have only undertaken surveys over short periods, e.g. 2 weeks (van Heezik *et al.*, 2016) or one month, using a single sampling method, which would appear to be too short to characterize the community. Sampling over short time periods is also at greater risk of biased samples due to temporary variation in weather conditions. We therefore recommend that future research takes place over longer time periods (both within and across years) using multiple sampling methods, whilst acknowledging the increased financial and time costs involved.

7.3.2 Spatial scale

Invertebrate foraging and dispersal occurs at different spatial scales, and is strongly affected life history. Some taxa are able to travel considerable distances across landscapes, for example *Bombus* to at over 1km from their nesting sites (Knight M *et al.*, 2005; Osborne Juliet *et al.*, 2008). Therefore the spatial scales at which samples are collected are important to capture these differences. In this research, we sampled at 0m, 5m and 40m into the crops using two samples at each distance in order to be compatible with previous invertebrate sampling at Nafferton by Eyre *et al.* (2013b). Future research should ideally incorporate samples at greater distances, e.g. 0, 5, 50 and 100 m into the crop. It could be extended to the landscape scale by including samples from neighbouring fields and even farms. Whilst landscape-scale studies have been undertaken (Tscharntke *et al.*, 2005a) to our knowledge relatively few studies have been undertaken at both small-scales (i.e. 50 m or less) and landscape scales (fields and farms). Integration of both approaches in a single research program is necessary to fully understand the effects of spatial scale. If resources allowed, ideally three samples would be taken per distance (rather than two as in our study) to provide greater statistical power.

7.3.3 Species level

The main limitation on the use of a broad range of invertebrate species is not sampling *per se* but the time, taxonomical expertise and cost required to identify the considerable number of species sampled. Parasitic Hymenoptera, which are particularly important in crop pest control, present particular taxonomic challenges for identification. This has led to the advocacy of identification to higher taxonomic rank, for example, family or subfamily, rather than genus and species in agroecosystem research (Báldi, 2003). In this research, invertebrates were identified to family, sub-family and tribe, depending on functional group. Whilst higher taxa have been used to assess biodiversity in landscapes (Sauberer *et al.*, 2004), it would be better to make interpretation based on species-level observations. Most individual research studies into invertebrates of agroecosystems have focused on a small number of taxonomic groups, for example Rösch *et al.* (2015) studied only three groups of invertebrates (Heteroptera, Auchenorrhyncha, Gastropoda-snails) but these were all identified to species level. Whilst this provides high taxonomic resolution for one family or order, its disadvantage is that it does not provide as good a representation of the wide range of invertebrates present, with contrasting life-histories that interact with each other.

Metabarcoding might potentially provide a rapid, reliable (Ji *et al.*, 2013), and (theoretically) less expensive methods to obtain large amounts of taxonomic species data. The basic premise in metabarcoding is to obtain select barcode genes of interest from genomic DNA (Douglas *et al.*, 2017) from specimens already identified using traditional taxonomic methods. Previous studies have used metabarcoding to compare nematodes diversity (Porazinska *et al.*, 2012). One advantage of metabarcoding is that the results are more "reproducible", in the sense that the DNA sequences from different samples can be more readily compared with each other, in contrast to traditional manual taxonomic identification where human error or lack of expertise may alter results. Nevertheless, there remain a number of major hurdles before such methods can be adopted to identify invertebrates in the type of study described for Nafferton. First, the majority of invertebrate taxa have currently not been barcoded, and are limited to a narrow subset of taxa present (Andersen *et al.*, 2012). Second, samples are vulnerable to contamination, both in the field and laboratory, therefore current metabarcoding requires highly trained personnel with excellent field and laboratory skills to undertake the DNA sequencing. Third, metabarcoding do not produce quantitative representation of species found in a sample, rather the particular type of species present. Final, the actual laboratory equipment and chemicals needed for metabarcoding is still expensive, and this needs to fall sharply before the technology can be widely adopted.

7.3.4 Invertebrate life history traits database

One of the hazards of the research described in thesis is that of inferring process from pattern. Large amounts of habitat, vegetation, invertebrate and environmental data were collected, but it was often difficult to determine the exact mechanisms that caused changes in abundance in individual invertebrate taxa across the farm. This problem was exacerbated by the lack of detailed knowledge about the life-history traits of many common invertebrates. Unified life-history trait databases have been developed successfully for plants, such as the CSR framework (Grime, 1988) used in Chapter 6, but no such framework has been developed in the UK or internationally for invertebrates. The invertebrate trait data used in Chapter 3 were collated from numerous peer-reviewed references, but individual authors did not report traits using the same categories, labels or scales. This made it challenging to produce a reliable system to describe the traits invertebrates. Once such a framework is agreed, it could be made available on the internet and entomologists could submit records into such a trait database to provide a solid resource for other scientist. Several international trait databases are being developed, for example SCALETOOL (http://scales.ckff.si/scaletool/) and Encyclopaedia of Life’s Trait Bank (http://eol.org/info/516). New initiatives such are currently being proposed, but it is clear that an internationally agreed framework is urgently needed.

Chapter 8. **Bibliography**

Alignier, A. (2018) 'Two decades of change in a field margin vegetation metacommunity as a result of field margin structure and management practice changes', *Agriculture, Ecosystems & Environment*, 251, pp. 1-10.

Alistair, G.B.P., Megan, J.W., Rocky de, N., James, K.L. and Peter, D.S. (2000) 'Patterns of host use among alga- and sponge-associated amphipods', *Marine Ecology Progress Series*, 208, pp. 183-196.

Amici, V., Rocchini, D., Filibeck, G., Bacaro, G., Santi, E., Geri, F., Landi, S., Scoppola, A. and Chiarucci, A. (2015) 'Landscape structure effects on forest plant diversity at local scale: Exploring the role of spatial extent', *Ecological Complexity*, 21, pp. 44-52.

Andersen, K., Bird Karen, L., Rasmussen, M., Haile, J., Breuning-Madsen, H., KjÆR Kurt, H., Orlando, L., Gilbert M. Thomas, P. and Willerslev, E. (2012) 'Meta-barcoding of ‘dirt’ DNA from soil reflects vertebrate biodiversity', *Molecular Ecology*, 21(8), pp. 1966-1979.

Anjum-Zubair, M., Martin, H.S.E., Pascal, Q. and Thomas, F. (2010) 'Influence of within-field position and adjoining habitat on carabid beetle assemblages in winter wheat', *Agricultural and Forest Entomology*, 12(3), pp. 301-306.

Armstrong, G. and McKinlay, R.G. (1997) 'Vegetation management in organic cabbages and pitfall catches of carabid beetles', *Agriculture, Ecosystems & Environment*, 64(3), pp. 267-276.

Arnett Jr, R.H. and Thomas, M.C. (2001) 'American beetles: Archostemata', *Myxophaga, Adephaga, Polyphaga: Staphyliniformia*, 1.

Aude, E., Tybirk, K. and Bruus Pedersen, M. (2003) 'Vegetation diversity of conventional and organic hedgerows in Denmark', *Agriculture, Ecosystems & Environment*, 99(1–3), pp. 135-147.

Aude, E., Tybirk, K., Michelsen, A., Ejrnæs, R., Hald, A.B. and Mark, S. (2004) 'Conservation value of the herbaceous vegetation in hedgerows – does organic farming make a difference?', *Biological Conservation*, 118(4), pp. 467-478.

Aviron, S., Nitsch, H., Jeanneret, P., Buholzer, S., Luka, H., Pfiffner, L., Pozzi, S., Schüpbach, B., Walter, T. and Herzog, F. (2009) 'Ecological cross compliance promotes farmland biodiversity in Switzerland', *Frontiers in Ecology and the Environment*, 7(5), pp. 247-252.

Báldi, A. (2003) 'Using higher taxa as surrogates of species richness: a study based on 3700 Coleoptera, Diptera, and Acari species in Central-Hungarian reserves', *Basic and Applied Ecology*, 4(6), pp. 589-593.

Balmer, O., Pfiffner, L., Schied, J., Willareth, M., Leimgruber, A., Luka, H. and Traugott, M. (2013) 'Noncrop flowering plants restore top-down herbivore control in agricultural fields', *Ecology and Evolution*, 3(8), pp. 2634-2646.

Balota, E.L., Colozzi-Filho, A., Andrade, D.S. and Dick, R.P. (2003) 'Microbial biomass in soils under different tillage and crop rotation systems', *Biology and Fertility of Soils*, 38(1), pp. 15-20.

Balota, E.L., Kanashiro, M., Colozzi Filho, A., Andrade, D.S. and Dick, R.P. (2004) 'Soil enzyme activities under long-term tillage and crop rotation systems in subtropical agro-ecosystems', *Brazilian Journal of Microbiology*, 35, pp. 300-306.

Batáry, P., Holzschuh, A., Orci, K.M., Samu, F. and Tscharntke, T. (2012) 'Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands', *Agriculture, Ecosystems & Environment*, 146(1), pp. 130-136.

Baudry, J., Burel, F., Thenail, C. and Le Cœur, D. (2000) 'A holistic landscape ecological study of the interactions between farming activities and ecological patterns in Brittany, France', *Landscape and Urban Planning*, 50(1), pp. 119-128.

Belfrage, K., Björklund, J. and Salomonsson, L. (2005) 'The Effects of Farm Size and Organic Farming on Diversity of Birds, Pollinators, and Plants in a Swedish Landscape', *AMBIO: A Journal of the Human Environment*, 34(8), pp. 582-588.

Bengtsson, J., AhnstrÖM, J. and Weibull, A.-C. (2005) 'The effects of organic agriculture on biodiversity and abundance: a meta-analysis', *Journal of Applied Ecology*, 42(2), pp. 261-269.

Biaggini, M., Consorti, R., Dapporto, L., Dellacasa, M., Paggetti, E. and Corti, C. (2007) 'The taxonomic level order as a possible tool for rapid assessment of Arthropod diversity in agricultural landscapes', *Agriculture, Ecosystems & Environment*, 122(2), pp. 183-191.

Bianchi, F.J.J.A., Booij, C.J.H. and Tscharntke, T. (2006) 'Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control', *Proceedings of the Royal Society of London B: Biological Sciences*, 273(1595), pp. 1715-1727.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., Van Wingerden, W.K.R.E., Zobel, M. and Edwards, P.J. (2008) 'Indicators for biodiversity in agricultural landscapes: a pan-European study', *Journal of Applied Ecology*, 45(1), pp. 141-150.

Birkhofer, K., Fließbach, A., Wise, D.H. and Scheu, S. (2008a) 'Generalist predators in organically and conventionally managed grass-clover fields: implications for conservation biological control', *Annals of Applied Biology*, 153(2), pp. 271-280.

Birkhofer, K., Wise, D.H. and Scheu, S. (2008b) 'Subsidy from the detrital food web, but not microhabitat complexity, affects the role of generalist predators in an aboveground herbivore food web', *Oikos*, 117(4), pp. 494-500.

Blaauw, B.R., Isaacs, R. and Clough, Y. (2014) 'Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop', *Journal of Applied Ecology*, 51(4), pp. 890-898.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A. and Tscharntke, T. (2012) 'Spillover of functionally important organisms between managed and natural habitats', *Agriculture, Ecosystems & Environment*, 146(1), pp. 34-43.

Bommarco, R., Kleijn, D. and Potts, S.G. (2013) 'Ecological intensification: harnessing ecosystem services for food security', *Trends in ecology & evolution*, 28(4), pp. 230-238.

Borcard, D., Legendre, P. and Drapeau, P. (1992) 'Partialling out the spatial component of ecological variation', *Ecology*, 73(3), pp. 1045-1055.

Borer, E.T., Seabloom, E.W. and Tilman, D. (2012) 'Plant diversity controls arthropod biomass and temporal stability', *Ecology Letters*, 15(12), pp. 1457-1464.

Bourassa, S., Cárcamo, H.A., Spence, J.R., Blackshaw, R.E. and Floate, K. (2010) 'Effects of crop rotation and genetically modified herbicide-tolerant corn on ground beetle diversity, community structure, and activity density', *The Canadian Entomologist*, 142(2), pp. 143-159.

Boutin, C. and Jobin, B.t. (1998) 'Intensity of Agricultural Practices and Effects on Adjacent Habitats', *Ecological Applications*, 8(2), pp. 544-557.

Breeze, T.D., Bailey, A.P., Balcombe, K.G. and Potts, S.G. (2011) 'Pollination services in the UK: How important are honeybees?', *Agriculture, Ecosystems & Environment*, 142(3), pp. 137-143.

Brereton, T., Roy, D.B., Middlebrook, I., Botham, M. and Warren, M. (2011) 'The development of butterfly indicators in the United Kingdom and assessments in 2010', *Journal of Insect Conservation*, 15(1), pp. 139-151.

Brooks, D.R., Bater, J.E., Clark, S.J., Monteith, D.T., Andrews, C., Corbett, S.J., Beaumont, D.A. and Chapman, J.W. (2012) 'Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity', *Journal of Applied Ecology*, 49(5), pp. 1009-1019.

Brose, U. (2003) 'Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity?', *Oecologia*, 135(3), pp. 407-413.

Burgio, G., Campanelli, G., Leteo, F., Ramilli, F., Depalo, L., Fabbri, R. and Sgolastra, F. (2015) 'Ecological sustainability of an organic four-year vegetable rotation system: Carabids and other soil arthropods as bioindicators', *Agroecology and Sustainable Food Systems*, 39(3), pp. 295-316.

Burgio, G., Ferrari, R., Boriani, L., Pozzati, M. and van Lenteren, J. (2006) 'The role of ecological infrastructures on Coccinellidae (Coleoptera) and other predators in weedy field margins within northern Italy agroecosystems', *Bulletin of Insectology*, 59(1), p. 59.

Buttigieg, P.L. and Ramette, A. (2014) 'A guide to statistical analysis in microbial ecology: a community-focused, living review of multivariate data analyses', *FEMS Microbiology Ecology*, 90(3), pp. 543-550.

Calderone, N.W. (2012) 'Insect Pollinated Crops, Insect Pollinators and US Agriculture: Trend Analysis of Aggregate Data for the Period 1992–2009', *PLOS ONE*, 7(5), p. e37235.

Carola, G.R., Andrea, F. and Andrés, B. (2015) 'Dispersal and ecological traits explain differences in beta diversity patterns of European beetles', *Journal of Biogeography*, 42(8), pp. 1526-1537.

Carvalho, F.P. (2006) 'Agriculture, pesticides, food security and food safety', *Environmental Science & Policy*, 9(7), pp. 685-692.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. and Nowakowski, M. (2007) 'Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins', *Journal of applied ecology*, 44(1), pp. 29-40.

Castella, E. and Speight, M. (1996) 'Knowledge representation using fuzzy coded variables: an example based on the use of Syrphidae (Insecta, Diptera) in the assessment of riverine wetlands', *Ecological Modelling*, 85(1), pp. 13-25.

Cattin, M.-F., Blandenier, G., Banašek-Richter, C. and Bersier, L.-F. (2003) 'The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities', *Biological Conservation*, 113(2), pp. 179-188.

Chamberlain, D.E., Wilson, J.D. and Fuller, R.J. (1999) 'A comparison of bird populations on organic and conventional farm systems in southern Britain', *Biol. Conserv.*, 88, p. 307.

Chinery, M. (1993) *collins Field Guide: Insects of Britain and Nothern Europe*. HarperCollins, London (1993).

Clough, Y., Kruess, A. and Tscharntke, T. (2007) 'Local and landscape factors in differently managed arable fields affect the insect herbivore community of a non-crop plant species', *Journal of Applied Ecology*, 44(1), pp. 22-28.

Cloyd, R. and Bethke, J. (2011) 'Impact of neonicotinoid insecticides on natural enemies in greenhouse and interiorscape environments', *Pest Management Science*, 67(1), pp. 3-9.

Cole, L.J., McCracken, D.I., Dennis, P., Downie, I.S., Griffin, A.L., Foster, G.N., Murphy, K.J. and Waterhouse, T. (2002) 'Relationships between agricultural management and ecological groups of ground beetles (Coleoptera: Carabidae) on Scottish farmland', *Agriculture, Ecosystems & Environment*, 93(1–3), pp. 323-336.

Cole, L.J., McCracken, D.I., Downie, I.S., Dennis, P., Foster, G.N., Waterhouse, T., Murphy, K.J., Griffin, A.L. and Kennedy, M.P. (2005) 'Comparing the effects of farming practices on ground beetle (Coleoptera: Carabidae) and spider (Araneae) assemblages of Scottish farmland', *Biodiversity & Conservation*, 14(2), pp. 441-460.

Collinge, S.K., Prudic, K.L. and Oliver, J.C. (2003) 'Effects of Local Habitat Characteristics and Landscape Context on Grassland Butterfly Diversity

Efectos de las Características del Hábitat Local y el Contexto del Paisaje sobre la Diversidad de Mariposas de Pastizal', *Conservation Biology*, 17(1), pp. 178-187.

Collins, K.L., Boatman, N.D., Wilcox, A. and Holland, J.M. (2003) 'Effects of different grass treatments used to create overwintering habitat for predatory arthropods on arable farmland', *Agriculture, Ecosystems & Environment*, 96(1), pp. 59-67.

Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M. and Chaney, K. (2002) 'Influence of beetle banks on cereal aphid predation in winter wheat', *Agriculture, Ecosystems & Environment*, 93(1–3), pp. 337-350.

Crawley, M.J. (2007) 'Statistical modelling', *The R Book, Second Edition*, pp. 388-448.

Crotty, F.V., Fychan, R., Scullion, J., Sanderson, R. and Marley, C.L. (2015) 'Assessing the impact of agricultural forage crops on soil biodiversity and abundance', *Soil Biology and Biochemistry*, 91, pp. 119-126.

Crowder, D.W., Northfield, T.D., Strand, M.R. and Snyder, W.E. (2010) 'Organic agriculture promotes evenness and natural pest control', *Nature*, 466(7302), pp. 109-112.

Cushman, S.A. and McGarigal, K. (2002) 'Hierarchical, Multi-scale decomposition of species-environment relationships', *Landscape Ecology*, 17(7), pp. 637-646.

Davis, B.N.K., Brown, M.J., Frost, A.J., Yates, T.J. and Plant, R.A. (1994) 'The Effects of Hedges on Spray Deposition and on the Biological Impact of Pesticide Spray Drift', *Ecotoxicology and Environmental Safety*, 27(3), pp. 281-293.

Deeming, D.C., Bennett, S.L. and Morrant, C. (2010) 'Effect of hedge maturity on composition of invertebrate assemblages at a site in Lincolnshire', *Aspects of Applied Biology*, (No.100), pp. 397-403.

den Boer, P.J. (1977) 'Dispersal power and survival. Carabids in a cultivated coutryside', *Miscellaneous papers/Landbouwhogeschool Wageningen*.

Dennis, P. and Fry, G.L.A. (1992) 'Field margins: can they enhance natural enemy population densities and general arthropod diversity on farmland? A2 - Paoletti, M.G', in Pimentel, D. (ed.) *Biotic Diversity in Agroecosystems*. Amsterdam: Elsevier, pp. 95-115.

Dennis, P., Thomas, M.B. and Sotherton, N.W. (1994) 'Structural Features of Field Boundaries Which Influence the Overwintering Densities of Beneficial Arthropod Predators', *Journal of Applied Ecology*, 31(2), pp. 361-370.

Denys, C. and Tscharntke, T. (2002) 'Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows', *Oecologia*, 130(2), pp. 315-324.

Diekötter, T., Wamser, S., Wolters, V. and Birkhofer, K. (2010) 'Landscape and management effects on structure and function of soil arthropod communities in winter wheat', *Agriculture, Ecosystems & Environment*, 137(1–2), pp. 108-112.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. and Collen, B. (2014) 'Defaunation in the Anthropocene', *Science*, 345(6195), pp. 401-406.

Ditner, N., Balmer, O., Beck, J., Blick, T., Nagel, P. and Luka, H. (2013) 'Effects of experimentally planting non-crop flowers into cabbage fields on the abundance and diversity of predators', *Biodiversity & Conservation*, 22(4), pp. 1049-1061.

Doblas-Miranda, E., Sánchez-Piñero, F. and González-Megías, A. (2009) 'Different microhabitats affect soil macroinvertebrate assemblages in a Mediterranean arid ecosystem', *Applied Soil Ecology*, 41(3), pp. 329-335.

Dong, Z., Ouyang, F., Lu, F. and Ge, F. (2015) 'Shelterbelts in agricultural landscapes enhance ladybeetle abundance in spillover from cropland to adjacent habitats', *BioControl*, 60(3), pp. 351-361.

Douglas, Y., Yinqiu, J., Brent, E., Xiaoyang, W., Chengxi, Y., Chunyan, Y. and Zhaoli, D. (2017) 'Biodiversity soup: metabarcoding of arthropods for rapid biodiversity assessment and biomonitoring', *Methods in Ecology and Evolution*, pp. 613-623.

Dray, S., Pélissier, R., Couteron, P., Fortin, M.J., Legendre, P., Peres-Neto, P.R., Bellier, E., Bivand, R., Blanchet, F.G. and De Cáceres, M. (2012) 'Community ecology in the age of multivariate multiscale spatial analysis', *Ecological Monographs*, 82(3), pp. 257-275.

Duelli, P. and Obrist, M.K. (2003) 'Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands', *Basic and Applied Ecology*, 4(2), pp. 129-138.

Duelli, P., Obrist, M.K. and Schmatz, D.R. (1999) 'Biodiversity evaluation in agricultural landscapes: above-ground insects', *Agriculture, Ecosystems & Environment*, 74(1–3), pp. 33-64.

Duffield, S.J. and Aebischer, N.J. (1994) 'The Effect of Spatial Scale of Treatment with Dimethoate on Invertebrate Population Recovery in Winter Wheat', *Journal of Applied Ecology*, 31(2), pp. 263-281.

Egan, J.F., Bohnenblust, E., Goslee, S., Mortensen, D. and Tooker, J. (2014) 'Herbicide drift can affect plant and arthropod communities', *Agriculture, Ecosystems & Environment*, 185, pp. 77-87.

Ekroos, J., Heliölä, J. and Kuussaari, M. (2010a) 'Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes', *Journal of Applied Ecology*, 47(2), pp. 459-467.

Ekroos, J., Hyvönen, T., Tiainen, J. and Tiira, M. (2010b) 'Responses in plant and carabid communities to farming practises in boreal landscapes', *Agriculture, Ecosystems & Environment*, 135(4), pp. 288-293.

Ewald, J.A., Wheatley, C.J., Aebischer, N.J., Moreby, S.J., Duffield, S.J., Crick, H.Q.P. and Morecroft, M.B. (2015) 'Influences of extreme weather, climate and pesticide use on invertebrates in cereal fields over 42 years', *Global change biology*, 21(11), pp. 3931-3950.

Eyre, M.D. (2006) 'A strategic interpretation of beetle (Coleoptera) assemblages, biotopes, habitats and distribution, and the conservation implications', *Journal of Insect Conservation*, 10(2), pp. 151-160.

Eyre, M.D., Labanowska-Bury, D., Avayanos, J.G., White, R. and Leifert, C. (2009) 'Ground beetles (Coleoptera, Carabidae) in an intensively managed vegetable crop landscape in eastern England', *Agriculture Ecosystems & Environment*, 131(3-4), pp. 340-346.

Eyre, M.D. and Leifert, C. (2010) 'Crop and field boundary influences on the activity of a wide range of beneficial invertebrate groups on a split conventional/organic farm in northern England', *Bulletin of Entomological Research*, 101(2), pp. 135-144.

Eyre, M.D. and Leifert, C. (2011a) 'Crop and field boundary influences on the activity of a wide range of beneficial invertebrate groups on a split conventional/organic farm in northern England', *Bulletin of Entomological Research*, 101(2), pp. 135-144.

Eyre, M.D. and Leifert, C. (2011b) 'Crop and field boundary influences on the activity of a wide range of beneficial invertebrate groups on a split conventional/organic farm in northern England', *Bull Entomol Res*, 101(2), pp. 135-44.

Eyre, M.D. and Leifert, C. (2012) 'A pragmatic approach for improving invertebrate biodiversity assessment in the agricultural landscape', *Journal of Insect Conservation*, 16(6), pp. 847-855.

Eyre, M.D., Luff, M.L., Atlihan, R. and Leifert, C. (2012) 'Ground beetle species (Carabidae, Coleoptera) activity and richness in relation to crop type, fertility management and crop protection in a farm management comparison trial', *Annals of Applied Biology*, 161(2), pp. 169-179.

Eyre, M.D., Luff, M.L. and Leifert, C. (2013a) 'Crop, field boundary, productivity and disturbance influences on ground beetles (Coleoptera, Carabidae) in the agroecosystem', *Agriculture, Ecosystems & Environment*, 165, pp. 60-67.

Eyre, M.D., Luff, M.L. and Leifert, C. (2013b) 'Crop, field boundary, productivity and disturbance influences on ground beetles (Coleoptera, Carabidae) in the agroecosystem', *Agriculture, Ecosystems & Environment*, 165(0), pp. 60-67.

Eyre, M.D., McMillan, S.D. and Critchley, C.N.R. (2016a) 'Ground beetles (Coleoptera, Carabidae) as indicators of change and pattern in the agroecosystem: Longer surveys improve understanding', *Ecological Indicators*, 68, pp. 82-88.

Eyre, M.D., Sanderson, R.A., McMillan, S.D. and Critchley, C.N.R. (2016b) 'Crop cover the principal influence on non-crop ground beetle (Coleoptera, Carabidae) activity and assemblages at the farm scale in a long-term assessment', *Bulletin of entomological research*, 106(2), pp. 242-248.

Firbank, L., Bradbury, R.B., McCracken, D.I. and Stoate, C. (2013) 'Delivering multiple ecosystem services from Enclosed Farmland in the UK', *Agriculture, ecosystems & environment*, 166, pp. 65-75.

Ford, H., Garbutt, A., Jones, D.L. and Jones, L. (2012) 'Impacts of grazing abandonment on ecosystem service provision: Coastal grassland as a model system', *Agriculture, Ecosystems & Environment*, 162(Supplement C), pp. 108-115.

Ford, H., Garbutt, A., Jones, L. and Jones, D.L. (2013) 'Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure', *Insect Conservation and Diversity*, 6(2), pp. 189-200.

Forsythe, T.G. (1983) 'Locomotion in ground beetles (Coleoptera carabidae): An interpretation of leg structure in functional terms', *Journal of Zoology*, 200(4), pp. 493-507.

Fox, R. (2013) 'The decline of moths in Great Britain: a review of possible causes', *Insect Conservation and Diversity*, 6(1), pp. 5-19.

Frank, T. and Reichhart, B. (2007) 'Staphylinidae and Carabidae overwintering in wheat and sown wildflower areas of different age', *Bulletin of Entomological Research*, 94(3), pp. 209-217.

Freeman, P.W. (1979) 'Specialized Insectivory: Beetle-Eating and Moth-Eating Molossid Bats', *Journal of Mammalogy*, 60(3), pp. 467-479.

French, D.D. and Cummins, R.P. (2001) 'Classification, composition, richness and diversity of British hedgerows', *Applied Vegetation Science*, 4(2), pp. 213-228.

Fry, G. and Main, A. (1993) 'Restoring seemingly natural communities on agricultural land. ', in *Nature conservation* pp. pp 224–241.

Fuller, R.J., Chamberlain, D.E., Burton, N.H.K. and Gough, S.J. (2001) 'Distributions of birds in lowland agricultural landscapes of England and Wales: How distinctive are bird communities of hedgerows and woodland?', *Agriculture, Ecosystems & Environment*, 84(1), pp. 79-92.

Fuller, R.J., Norton, L.R., Feber, R.E., Johnson, P.J., Chamberlain, D.E., Joys, A.C., Mathews, F., Stuart, R.C., Townsend, M.C., Manley, W.J., Wolfe, M.S., Macdonald, D.W. and Firbank, L.G. (2005) 'Benefits of organic farming to biodiversity vary among taxa', *Biology Letters*, 1(4), pp. 431-434.

Gabriel, D., Roschewitz, I., Tscharntke, T. and Thies, C. (2006) 'Beta diversity at different spatial scales: Plant communities in organic and conventional agriculture', *Ecological Applications*, 16(5), pp. 2011-2021.

Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E. and Benton, T.G. (2010a) 'Scale matters: the impact of organic farming on biodiversity at different spatial scales', *Ecology Letters*, 13(7), pp. 858-869.

Gabriel, D., Sait Steven, M., Hodgson Jenny, A., Schmutz, U., Kunin William, E. and Benton Tim, G. (2010b) 'Scale matters: the impact of organic farming on biodiversity at different spatial scales', *Ecology Letters*, 13(7), pp. 858-869.

Gabriel, D., Thies, C. and Tscharntke, T. (2005) 'Local diversity of arable weeds increases with landscape complexity', *Perspectives in Plant Ecology, Evolution and Systematics*, 7(2), pp. 85-93.

Gallai, N., Salles, J.-M., Settele, J. and Vaissière, B.E. (2009) 'Economic valuation of the vulnerability of world agriculture confronted with pollinator decline', *Ecological Economics*, 68(3), pp. 810-821.

Gallandt, E.R., Molloy, T., Lynch, R.P. and Drummond, F.A. (2005) 'Effect of cover-cropping systems on invertebrate seed predation', *Weed science*, 53(1), pp. 69-76.

Gardiner, T. and Hassall, M. (2009) 'Does microclimate affect grasshopper populations after cutting of hay in improved grassland?', *Journal of Insect Conservation*, 13(1), pp. 97-102.

Gardiner, T., Pye, M., Field, R. and Hill, J. (2002) 'The influence of sward height and vegetation composition in determining the habitat preferences of three Chorthippus species (Orthoptera: Acrididae) in Chelmsford, Essex, UK', *Journal of Orthoptera Research*, 11(2), pp. 207-213.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Lepš, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quested, H., Quétier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.-P., Thébault, A., Vile, D. and Zarovali, M.P. (2007) 'Assessing the Effects of Land-use Change on Plant Traits, Communities and Ecosystem Functioning in Grasslands: A Standardized Methodology and Lessons from an Application to 11 European SitesGarnier et al. — Methodology to Assess Effects of Land-use ChangeGarnier et al. — Methodology to Assess Effects of Land-use Change', *Annals of Botany*, 99(5), pp. 967-985.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W. and Inchausti, P. (2010) 'Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland', *Basic and Applied Ecology*, 11(2), pp. 97-105.

Gibb, H. and Hochuli, D.F. (2002) 'Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages', *Biological Conservation*, 106(1), pp. 91-100.

Gibson, C.W.D., Hambler, C. and Brown, V.K. (1992) 'Changes in Spider (Araneae) Assemblages in Relation to Succession and Grazing Management', *Journal of Applied Ecology*, 29(1), pp. 132-142.

Gibson, R.H., Pearce, S., Morris, R.J., Symondson, W.O.C. and Memmott, J. (2007a) 'Plant diversity and land use under organic and conventional agriculture: a whole-farm approach', *Journal of Applied Ecology*, 44(4), pp. 792-803.

Gibson, R.H., Pearce, S., Morris, R.J., Symondson, W.O.C. and Memmott, J. (2007b) 'Plant diversity and land use under organic and conventional agriculture: a whole-farm approach', *Journal of Applied Ecology*, 44(4), pp. 792-803.

Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.M.N. and Swift, M.J. (1997) 'Agricultural intensification, soil biodiversity and agroecosystem function', *Applied Soil Ecology*, 6(1), pp. 3-16.

Gladbach, D.J., Holzschuh, A., Scherber, C., Thies, C., Dormann, C.F. and Tscharntke, T. (2011) 'Crop–noncrop spillover: arable fields affect trophic interactions on wild plants in surrounding habitats', *Oecologia*, 166(2), pp. 433-441.

Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.-Y., Iverson, A.L., Batáry, P., Rudolphi, J., Tscharntke, T., Cardinale, B.J. and Perfecto, I. (2014) 'Biodiversity conservation in agriculture requires a multi-scale approach', *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1791), p. 20141358.

Goulson, D., Lye, G.C. and Darvill, B. (2008) 'Decline and Conservation of Bumble Bees', *Annual Review of Entomology*, 53(1), pp. 191-208.

Gower, J.C. (1975) 'Generalized procrustes analysis', *Psychometrika*, 40(1), pp. 33-51.

Gower, J.C. (1987) Berlin, Heidelberg. Springer Berlin Heidelberg.

Grez, A.A., Zaviezo, T., Hernández, J., Rodríguez-San Pedro, A. and Acuña, P. 'The heterogeneity and composition of agricultural landscapes influence native and exotic coccinellids in alfalfa fields', *Agricultural and Forest Entomology*, 16(4), pp. 382-390.

Grime, J.P. (1974) 'Vegetation classification by reference to strategies', *Nature*, 250(5461), pp. 26-31.

Grime, J.P. (1977) 'Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory', *The American Naturalist*, 111(982), pp. 1169-1194.

Grime, J.P. (1988) 'The CSR model of primary plant strategies—origins, implications and tests', in *Plant evolutionary biology*. Springer, pp. 371-393.

Grime, J.P. (2006) *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley & Sons.

Groenendijk, D. and Ellis, W.N. (2011) 'The state of the Dutch larger moth fauna', *Journal of Insect Conservation*, 15(1), pp. 95-101.

Habel, J.C., Segerer, A., Ulrich, W., Torchyk, O., Weisser, W.W. and Schmitt, T. (2016) 'Butterfly community shifts over two centuries', *Conserv Biol*, 30(4), pp. 754-62.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H. and Tilman, D. (2009) 'Plant species loss decreases arthropod diversity and shifts trophic structure', *Ecology Letters*, 12(10), pp. 1029-1039.

Haenke, S., Kovács-Hostyánszki, A., Fründ, J., Batáry, P., Jauker, B., Tscharntke, T. and Holzschuh, A. (2014) 'Landscape configuration of crops and hedgerows drives local syrphid fly abundance', *Journal of Applied Ecology*, 51(2), pp. 505-513.

Hallmann, C.A., Foppen, R.P.B., van Turnhout, C.A.M., de Kroon, H. and Jongejans, E. (2014) 'Declines in insectivorous birds are associated with high neonicotinoid concentrations', *Nature*, 511, p. 341.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. and de Kroon, H. (2017) 'More than 75 percent decline over 27 years in total flying insect biomass in protected areas', *PLOS ONE*, 12(10), p. e0185809.

Hansen, J.P., Eriksen, J. and Jensen, L.S. (2005) 'Residual nitrogen effect of a dairy crop rotation as influenced by grass-clover ley management, manure type and age', *Soil use and management,* 21(3), pp. 278-286.

Hanson, H.I., Palmu, E., Birkhofer, K., Smith, H.G. and Hedlund, K. (2016) 'Agricultural Land Use Determines the Trait Composition of Ground Beetle Communities', *PLoS ONE,* 11(1), p. e0146329.

Harvey, J.A., van der Putten, W.H., Turin, H., Wagenaar, R. and Bezemer, T.M. (2008) 'Effects of changes in plant species richness and community traits on carabid assemblages and feeding guilds', *Agriculture, Ecosystems & Environment*, 127(1), pp. 100-106.

Hatten, T.D., Bosque-Pérez, N.A., Labonte, J.R., Guy, S.O. and Eigenbrode, S.D. (2007) 'Effects of tillage on the activity density and biological diversity of carabid beetles in spring and winter crops', *Environmental entomology,* 36(2), pp. 356-368.

Haysom, K.A., McCracken, D.I., Foster, G.N. and Sotherton, N.W. (2004) 'Developing grassland conservation headlands: response of carabid assemblage to different cutting regimes in a silage field edge', *Agriculture, Ecosystems & Environment,* 102(3), pp. 263-277.

Helden, A.J. and Leather, S.R. (2004) 'Biodiversity on urban roundabouts—Hemiptera, management and the species–area relationship', *Basic and Applied Ecology*, 5(4), pp. 367-377.

Herzog, F. (2005) 'Agri-environment schemes as landscape experiments', *Agriculture, Ecosystems & Environment,* 108(3), pp. 175-177.

Hodgson, J., Grime, J. and Hunt, R. (1995) *The electronic comparative plant ecology. Chapman and Hall , London.* Springer, Dordrecht.

Hof, A.R. and Bright, P.W. (2010) 'The impact of grassy field margins on macro-invertebrate abundance in adjacent arable fields', *Agriculture, ecosystems & environment,* 139(1), pp. 280-283.

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V. and Evans, A.D. (2005) 'Does organic farming benefit biodiversity?', *Biological Conservation*, 122(1), pp. 113-130.

Holland, J.M., Hutchison, M.A.S., Smith, B. and Aebischer, N.J. (2006) 'A review of invertebrates and seed-bearing plants as food for farmland birds in Europe', *Annals of Applied Biology,* 148(1), pp. 49-71.

Holland, J.M. and Luff, M.L. (2000) 'The Effects of Agricultural Practices on Carabidae in Temperate Agroecosystems', *Integrated Pest Management Reviews,* 5(2), pp. 109-129.

Holland, J.M., Oaten, H., Southway, S. and Moreby, S. (2008) 'The effectiveness of field margin enhancement for cereal aphid control by different natural enemy guilds', *Biological Control*, 47(1), pp. 71-76.

Holland, J.M., Thomas, C.F.G., Birkett, T., Southway, S. and Oaten, H. (2005) 'Farm-scale spatiotemporal dynamics of predatory beetles in arable crops', *Journal of Applied Ecology,* 42(6), pp. 1140-1152.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. and Tscharntke, T. (2007a) 'Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context', *Journal of Applied Ecology*, 44(1), pp. 41-49.

Holzschuh, A., Steffan-Dewenter, I. and Tscharntke, T. (2008) 'Agricultural landscapes with organic crops support higher pollinator diversity', *Oikos*, 117(3), pp. 354-361.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. and Tscharntke, T. (2007b) 'Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context', *Journal of Applied Ecology*, 44(1), pp. 41-49.

Honek, A. and Jarosik, V. (2000) 'The role of crop density, seed and aphid presence in diversification of field communities of Carabidae (Coleoptera)', *European Journal of Entomology*, 97(4), pp. 517-526.

Hubbard, C.E. (1954) *Grasses. A guide to their structure, identification, uses, and distribution in the British Isles*. Harmondsworth ; Penguin Books Ltd.

Huber, M., Rembiałkowska, E., Średnicka, D., Bügel, S. and van de Vijver, L.P.L. (2011) 'Organic food and impact on human health: Assessing the status quo and prospects of research', *NJAS - Wageningen Journal of Life Sciences*, 58(3), pp. 103-109.

Hulugalle, N.R., Lobry de Bruyn, L.A. and Entwistle, P. (1997) 'Residual effects of tillage and crop rotation on soil properties, soil invertebrate numbers and nutrient uptake in an irrigated Vertisol sown to cotton', *Applied Soil Ecology*, 7(1), pp. 11-30.

Inclán, D.J., Cerretti, P. and Marini, L. (2014) 'Interactive effects of area and connectivity on the diversity of tachinid parasitoids in highly fragmented landscapes', *Landscape Ecology*, 29(5), pp. 879-889.

Inclán, D.J., Cerretti, P. and Marini, L. (2015) 'Landscape composition affects parasitoid spillover', *Agriculture, Ecosystems & Environment*, 208, pp. 48-54.

Ives, A.R. (2015) 'For testing the significance of regression coefficients, go ahead and log-transform count data', *Methods in Ecology and Evolution*, 6(7), pp. 828-835.

Ives, A.R., Cardinale, B.J. and Snyder, W.E. (2004) 'A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning', *Ecology Letters*, 8(1), pp. 102-116.

Jeanneret, P., Schüpbach, B. and Luka, H. (2003) 'Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes', *Agriculture, Ecosystems & Environment*, 98(1), pp. 311-320.

Jenni, A.S., John, B., Simon, J.L., Mark, R.Y., Glenn, R.I., Simon, R.L. and Nick, L. (2014) 'Effects of riparian buffer strips on ground beetles (Coleoptera, Carabidae) within an agricultural landscape', *Insect Conservation and Diversity*, 7(2), pp. 172-184.

Ji, Y., Ashton, L., Pedley Scott, M., Edwards David, P., Tang, Y., Nakamura, A., Kitching, R., Dolman Paul, M., Woodcock, P., Edwards Felicity, A., Larsen Trond, H., Hsu Wayne, W., Benedick, S., Hamer Keith, C., Wilcove David, S., Bruce, C., Wang, X., Levi, T., Lott, M., Emerson Brent, C. and Yu Douglas, W. (2013) 'Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding', *Ecology Letters*, 16(10), pp. 1245-1257.

Jonason, D., Smith, H.G., Bengtsson, J. and Birkhofer, K. (2013) 'Landscape simplification promotes weed seed predation by carabid beetles (Coleoptera: Carabidae)', *Landscape Ecology*, 28(3), pp. 487-494.

Jonsson, M., Straub, C.S., Didham, R.K., Buckley, H.L., Case, B.S., Hale, R.J., Gratton, C., Wratten, S.D. and Clough, Y. (2015) 'Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity', *Journal of Applied Ecology*, 52(5), pp. 1274-1282.

Katharina, H., Nils, H., Florian, S., Andreas, S., Thorsten, A., Calvin, D. and Robert, E. (2014) 'Carabids.org – a dynamic online database of ground beetle species traits (Coleoptera, Carabidae)', *Insect Conservation and Diversity*, 7(3), pp. 195-205.

Kessler, A. and Halitschke, R. (2007) 'Specificity and complexity: the impact of herbivore-induced plant responses on arthropod community structure', *Current Opinion in Plant Biology*, 10(4), pp. 409-414.

Khan, M.S. and Yogi, M.K. (2017) 'Insect Crop Pollinators', in Omkar (ed.) *Industrial Entomology*. Singapore: Springer Singapore, pp. 397-412.

Kladivko, E.J. (2001) 'Tillage systems and soil ecology', *Soil and Tillage Research*, 61(1), pp. 61-76.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M. and Yela, J.L. (2006) 'Mixed biodiversity benefits of agri-environment schemes in five European countries', *Ecology Letters*, 9(3), pp. 243-254.

Kleijn, D., Berendse, F., Smit, R. and Gilissen, N. (2001) 'Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes', *Nature*, 413, p. 723.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. and Peco, B. (2008) 'The LEDA Traitbase: a database of life-history traits of the Northwest European flora', *Journal of Ecology*, 96(6), pp. 1266-1274.

Knight M, E., Martin A, P., Bishop, S., Osborne J, L., Hale R, J., Sanderson R, A. and Goulson, D. (2005) 'An interspecific comparison of foraging range and nest density of four bumblebee (Bombus) species', *Molecular Ecology*, 14(6), pp. 1811-1820.

Kotze, D.J. and O'Hara, R.B. (2003) 'Species decline—but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe', *Oecologia*, 135(1), pp. 138-148.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T.a., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.-M., Regetz, J. and Ricketts, T.H. (2007) 'Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change', *Ecology Letters*, 10(4), pp. 299-314.

Kremen, C., Williams, N.M. and Thorp, R.W. (2002) 'Crop pollination from native bees at risk from agricultural intensification', *Proceedings of the National Academy of Sciences,* 99(26), pp. 16812-16816.

Kruess, A. and Tscharntke, T. (2002) 'Grazing Intensity and the Diversity of Grasshoppers, Butterflies, and Trap-Nesting Bees and Wasps

Intensidad de Pastoreo y la Diversidad de Chapulines, Mariposas y Abejas y Avispas', *Conservation Biology,* 16(6), pp. 1570-1580.

Lacasella, F., Gratton, C., De Felici, S., Isaia, M., Zapparoli, M., Marta, S. and Sbordoni, V. (2015) 'Asymmetrical responses of forest and "beyond edge" arthropod communities across a forest–grassland ecotone', *Biodiversity and Conservation*, 24(3), pp. 447-465.

Lalonde, O., Légère, A., Stevenson, F.C., Roy, M. and Vanasse, A. (2012) 'Carabid beetle communities after 18 years of conservation tillage and crop rotation in a cool humid climate', *The Canadian Entomologist,* 144(05), pp. 645-657.

Landis, D.A., Wratten, S.D. and Gurr, G.M. (2000) 'Habitat management to conserve natural enemies of arthropod pests in agriculture', *Annual review of entomology*, 45(1), pp. 175-201.

Langellotto, G.A. and Denno, R.F. (2004) 'Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis', *Oecologia*, 139(1), pp. 1-10.

Lassau, S.A. and Hochuli, D.F. (2005) 'Wasp community responses to habitat complexity in Sydney sandstone forests', *Austral Ecology*, 30(2), pp. 179-187.

Lassau, S.A., Hochuli, D.F., Cassis, G. and Reid, C.A.M. (2005) 'Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently?', *Diversity and Distributions,* 11(1), pp. 73-82.

Leather, S.R. (2018) '"Ecological Armageddon" – more evidence for the drastic decline in insect numbers', *Annals of Applied Biology,* 172(1), pp. 1-3.

Legendre, P. and Gallagher, E.D. (2001) 'Ecologically meaningful transformations for ordination of species data', *Oecologia*, 129(2), pp. 271-280.

Letourneau Deborah, K. and Bothwell Sara, G. (2008) 'Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional', *Frontiers in Ecology and the Environment*, 6(8), pp. 430-438.

Liu, Y., Rothenwöhrer, C., Scherber, C., Batáry, P., Elek, Z., Steckel, J., Erasmi, S., Tscharntke, T. and Westphal, C. (2014) 'Functional beetle diversity in managed grasslands: effects of region, landscape context and land use intensity', *Landscape Ecology,* 29(3), pp. 529-540.

Longley, M., Čilgi, T., Jepson Paul, C. and Sotherton Nicolas, W. (1997) 'Measurements of pesticide spray drift deposition into field boundaries and hedgerows: 1. Summer applications', *Environmental Toxicology and Chemistry,* 16(2), pp. 165-172.

López-Fando, C. and Bello, A. (1995) 'Variability in soil nematode populations due to tillage and crop rotation in semi-arid Mediterranean agrosystems', *Soil and Tillage Research*, 36(1), pp. 59-72.

Luff, M.L. (2007) *The Carabidae (Ground Beetles) of Britian and Ireland.* . Royal Entomological Society, London.

Luff, M.L. and Turner, J. (2007) *The Carabidae (ground beetles) of Britain and Ireland*. St. Albans [England]: Royal Entomological Society.

Lupwayi, N.Z., Rice, W.A. and Clayton, G.W. (1998) 'Soil microbial diversity and community structure under wheat as influenced by tillage and crop rotation', *Soil Biology and Biochemistry*, 30(13), pp. 1733-1741.

Lüscher, G., Jeanneret, P., Schneider, M.K., Turnbull, L.A., Arndorfer, M., Balázs, K., Báldi, A., Bailey, D., Bernhardt, K.G., Choisis, J.-P., Elek, Z., Frank, T., Friedel, J.K., Kainz, M., Kovács-Hostyánszki, A., Oschatz, M.-L., Paoletti, M.G., Papaja-Hülsbergen, S., Sarthou, J.-P., Siebrecht, N., Wolfrum, S. and Herzog, F. (2014) 'Responses of plants, earthworms, spiders and bees to geographic location, agricultural management and surrounding landscape in European arable fields', *Agriculture, Ecosystems & Environment*, 186, pp. 124-134.

Lys, J.A. (1994) 'The positive influence of strip-management on ground beetles in a cereal field: increase, migration and overwintering', in *Carabid beetles: Ecology and evolution*. Springer, pp. 451-455.

Macfadyen, S., Craze, P.G., Polaszek, A., van Achterberg, K. and Memmott, J. (2011) 'Parasitoid diversity reduces the variability in pest control services across time on farms', *Proceedings of the Royal Society of London B: Biological Sciences*, 278(1723), pp. 3387-3394.

Macfadyen, S. and Muller, W. (2013) 'Edges in Agricultural Landscapes: Species Interactions and Movement of Natural Enemies', *PLOS ONE*, 8(3), p. e59659.

MacLeod, A., Wratten, S.D., Sotherton, N.W. and Thomas, M.B. (2004) '‘Beetle banks’ as refuges for beneficial arthropods in farmland: long-term changes in predator communities and habitat', *Agricultural and Forest Entomology*, 6(2), pp. 147-154.

Mäder, P., Fliessbach, A., Dubois, D., Gunst, L., Fried, P. and Niggli, U. (2002) 'Soil fertility and biodiversity in organic farming', *Science*, 296(5573), pp. 1694-1697.

Mäder, P., Hahn, D., Dubois, D., Gunst, L., Alföldi, T., Bergmann, H., Oehme, M., Amadò, R., Schneider, H., Graf, U., Velimirov, A., Fließbach, A. and Niggli, U. (2007) 'Wheat quality in organic and conventional farming: results of a 21 year field experiment', *Journal of the Science of Food and Agriculture*, 87(10), pp. 1826-1835.

Maeder, P., Fliessbach, A., Dubois, D., Gunst, L., Fried, P. and Niggli, U. (2002) 'Soil Fertility and Biodiversity in Organic Farming', *Science*, 296(5573), pp. 1694-1697.

Magoba, R.N. and Samways, M.J. (2012) 'Comparative footprint of alien, agricultural and restored vegetation on surface-active arthropods', *Biological Invasions*, 14(1), pp. 165-177.

Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R. and Ward, L.K. (2003) 'The role of weeds in supporting biological diversity within crop fields*', *Weed Research*, 43(2), pp. 77-89.

Marshall, E.J.P. and Moonen, A.C. (2002) 'Field margins in northern Europe: their functions and interactions with agriculture', *Agriculture, Ecosystems & Environment*, 89(1-2), pp. 5-21.

Maudsley, M., Seeley, B. and Lewis, O. (2002) 'Spatial distribution patterns of predatory arthropods within an English hedgerow in early winter in relation to habitat variables', *Agriculture, Ecosystems & Environment*, 89(1), pp. 77-89.

Maudsley, M.J. (2000) 'A review of the ecology and conservation of hedgerow invertebrates in Britain', *Journal of Environmental Management*, 60(1), pp. 65-76.

McCracken, D.I. and Tallowin, J.R. (2004) 'Swards and structure: the interactions between farming practices and bird food resources in lowland grasslands', *Ibis*, 146, pp. 108-114.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. and Nowakowski, M. (2002) 'The effect of arable field margin composition on invertebrate biodiversity', *Biological Conservation*, 106(2), pp. 259-271.

Megías, A.G. and Müller, C. (2010) 'Root herbivores and detritivores shape above-ground multitrophic assemblage through plant-mediated effects', *Journal of Animal Ecology*, 79(4), pp. 923-931.

Menalled, F.D., Smith, R.G., Dauer, J.T. and Fox, T.B. (2007) 'Impact of agricultural management on carabid communities and weed seed predation', *Agriculture, Ecosystems & Environment*, 118(1–4), pp. 49-54.

Molina, G.A.R., Poggio, S.L. and Ghersa, C.M. (2014) 'Epigeal arthropod communities in intensively farmed landscapes: Effects of land use mosaics, neighbourhood heterogeneity, and field position', *Agriculture, Ecosystems & Environment*, 192, pp. 135-143.

Moonen, A.C. and Marshall, E.J.P. (2001) 'The influence of sown margin strips, management and boundary structure on herbaceous field margin vegetation in two neighbouring farms in southern England', *Agriculture, Ecosystems & Environment*, 86(2), pp. 187-202.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. and Worm, B. (2011) 'How Many Species Are There on Earth and in the Ocean?', *PLOS Biology*, 9(8), p. e1001127.

Moreby, S.J., Aebischer, N.J., Southway, S.E. and Sotherton, N.W. (1994) 'A comparison of the flora and arthropod fauna of organically and conventionally grown winter wheat in southern England', *Annals of applied Biology*, 125(1), pp. 13-27.

Morris, M.A., Croft, B.A. and Berry, R.E. (1996) 'Overwintering and effects of autumn habitat manipulation and carbofuran on Neoseiulus fallacis and Tetranychus urticae in peppermint', *Experimental & Applied Acarology*, 20(5), pp. 249-257.

Morris, M.G. (2000) 'The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands', *Biological Conservation*, 95(2), pp. 129-142.

Navntoft, S., Esbjerg, P. and Riedel, W. (2006) 'Effects of reduced pesticide dosages on carabids (Coleoptera: Carabidae) in winter wheat', *Agricultural and Forest Entomology*, 8(1), pp. 57-62.

Nick, M.H., David Tilman, John Haarstad, Mark Ritchie and Johannes, M.H.K. (2001) 'Contrasting Effects of Plant Richness and Composition on Insect Communities: A Field Experiment', *The American Naturalist*, 158(1), pp. 17-35.

Nkem, J.N., Lobry de Bruyn, L.A., Hulugalle, N.R. and Grant, C.D. (2002) 'Changes in invertebrate populations over the growing cycle of an N-fertilised and unfertilised wheat crop in rotation with cotton in a grey Vertosol', *Applied Soil Ecology*, 20(1), pp. 69-74.

Noordijk, J., Delille, K., Schaffers, A.P. and Sýkora, K.V. (2009) 'Optimizing grassland management for flower-visiting insects in roadside verges', *Biological Conservation*, 142(10), pp. 2097-2103.

Noordijk, J., Schaffers, A.P., Heijerman, T., Boer, P., Gleichman, M. and Sýkora, K.V. (2010) 'Effects of vegetation management by mowing on ground-dwelling arthropods', *Ecological Engineering*, 36(5), pp. 740-750.

Norris, R.F. and Kogan, M. (2000) 'Interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems', *Weed Science*, 48(1), pp. 94-158.

Norris, R.F. and Kogan, M. (2017) 'Interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems', *Weed Science*, 48(1), pp. 94-158.

Norton, L., Johnson, P., Joys, A., Stuart, R., Chamberlain, D., Feber, R., Firbank, L., Manley, W., Wolfe, M., Hart, B., Mathews, F., Macdonald, D. and Fuller, R.J. (2009a) 'Consequences of organic and non-organic farming practices for field, farm and landscape complexity', *Agriculture, Ecosystems & Environment,* 129(1), pp. 221-227.

Norton, L., Johnson, P., Joys, A., Stuart, R., Chamberlain, D., Feber, R., Firbank, L., Manley, W., Wolfe, M., Hart, B., Mathews, F., Macdonald, D. and Fuller, R.J. (2009b) 'Consequences of organic and non-organic farming practices for field, farm and landscape complexity', *Agriculture, Ecosystems & Environment*, 129(1–3), pp. 221-227.

O'Sullivan, C.M. and Gormally, M.J. (2002) 'A Comparison of Ground Beetle (Carabidae: Coleoptera) Communities in an Organic and Conventional Potato Crop', *Biological Agriculture & Horticulture*, 20(2), pp. 99-110.

O’Rourke, M.E., Liebman, M. and Rice, M.E. (2008) 'Ground Beetle (Coleoptera: Carabidae) Assemblages in Conventional and Diversified Crop Rotation Systems', *Environmental Entomology*, 37(1), pp. 121-130.

Öberg, S. (2007) 'Diversity of spiders after spring sowing – influence of farming system and habitat type', *Journal of Applied Entomology,* 131(8), pp. 524-531.

Öberg, S., Ekbom, B. and Bommarco, R. (2007) 'Influence of habitat type and surrounding landscape on spider diversity in Swedish agroecosystems', *Agriculture, Ecosystems & Environment*, 122(2), pp. 211-219.

Ødegaard, F. (2000) 'How many species of arthropods? Erwin's estimate revised', *Biological Journal of the Linnean Society*, 71(4), pp. 583-597.

Oksanen J, B.F., Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H: vegan (2015) 'Community Ecology Package. R package version 20–5'. Wien: Institute for Statistics and Mathematics. Available at: [http://CRAN.R-project.org/package=vegan], .

Oliver, T.H., Isaac, N.J.B., August, T.A., Woodcock, B.A., Roy, D.B. and Bullock, J.M. (2015) 'Declining resilience of ecosystem functions under biodiversity loss', *Nature Communications*, 6, p. 10122.

Olson, D.M. and Wäckers, F.L. (2007) 'Management of field margins to maximize multiple ecological services', *Journal of Applied Ecology*, 44(1), pp. 13-21.

Osborne Juliet, L., Martin Andrew, P., Carreck Norman, L., Swain Jennifer, L., Knight Mairi, E., Goulson, D., Hale Roddy, J. and Sanderson Roy, A. (2008) 'Bumblebee flight distances in relation to the forage landscape', *Journal of Animal Ecology*, 77(2), pp. 406-415.

Petersen, H. (2000) 'Collembola populations in an organic crop rotation: Population dynamics and metabolism after conversion from clover-grass ley to spring barley', *Pedobiologia*, 44(3), pp. 502-515.

Pfiffner, L. and Luka, H. (2003) 'Effects of low-input farming systems on carabids and epigeal spiders – a paired farm approach', *Basic and Applied Ecology*, 4(2), pp. 117-127.

Pfiffner, L. and Niggli, U. (1996) 'Effects of Bio-dynamic, Organic and Conventional Farming on Ground Beetles (Col. Carabidae) and Other Epigaeic Arthropods in Winter Wheat', *Biological Agriculture & Horticulture*, 12(4), pp. 353-364.

Pinheiro, J., Bates, D., DebRoy, S. and Sarkar, D. (2011a) 'the R Development Core Team (2010)', *Nlme: Linear and nonlinear mixed effects models. R package version*, pp. 3.1-103.

Pinheiro, J., Bates, D., DebRoy, S. and Sarkar, D. (2011b) 'R Development Core Team. 2010. nlme: linear and nonlinear mixed effects models. R package version 3.1-97', *R Foundation for Statistical Computing, Vienna*.

Pinheiro, J.C. and Bates, D.M. (2000) 'Linear mixed-effects models: basic concepts and examples', *Mixed-effects models in S and S-Plus*, pp. 3-56.

Poggio, S.L., Chaneton, E.J. and Ghersa, C.M. (2013) 'The arable plant diversity of intensively managed farmland: Effects of field position and crop type at local and landscape scales', *Agriculture, Ecosystems & Environment*, 166, pp. 55-64.

Porazinska, D.L., Giblin-Davis, R.M., Powers, T.O. and Thomas, W.K. (2012) 'Nematode Spatial and Ecological Patterns from Tropical and Temperate Rainforests', *PLOS ONE*, 7(9), p. e44641.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. and Kunin, W.E. (2010) 'Global pollinator declines: trends, impacts and drivers', *Trends in Ecology & Evolution*, 25(6), pp. 345-353.

Power Eileen, F. and Stout Jane, C. (2011) 'Organic dairy farming: impacts on insect–flower interaction networks and pollination', *Journal of Applied Ecology*, 48(3), pp. 561-569.

Pöyry, J., Luoto, M., Paukkunen, J., Pykälä, J., Raatikainen, K. and Kuussaari, M. (2006) 'Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age', *Oikos*, 115(3), pp. 401-412.

Purvis, G. and Fadl, A. (2002) 'The influence of cropping rotations and soil cultivation practice on the population ecology of carabids (Coleoptera: Carabidae) in arable land', *Pedobiologia*, 46(5), pp. 452-474.

Pywell, R.F., Heard, M.S., Bradbury, R.B., Hinsley, S., Nowakowski, M., Walker, K.J. and Bullock, J.M. (2012) 'Wildlife-friendly farming benefits rare birds, bees and plants', *Biology Letters*, 8(5), pp. 772-775.

Pywell, R.F., James, K.L., Herbert, I., Meek, W.R., Carvell, C., Bell, D. and Sparks, T.H. (2005) 'Determinants of overwintering habitat quality for beetles and spiders on arable farmland', *Biological Conservation*, 123(1), pp. 79-90.

Rand, T.A. and Louda, S.M. (2006) 'Spillover of Agriculturally Subsidized Predators as a Potential Threat to Native Insect Herbivores in Fragmented Landscapes

El Excedente de Depredadores Subsidiados por la Agricultura como una Amenaza Potencial para los Insecto Herbívoros Nativos en Paisajes Fragmentados', *Conservation Biology*, 20(6), pp. 1720-1729.

Rand, T.A., Tylianakis, J.M. and Tscharntke, T. (2006) 'Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats', *Ecology Letters*, 9(5), pp. 603-614.

Rasmussen, J., Gylfadóttir, T., Loges, R., Eriksen, J. and Helgadóttir, Á. (2013) 'Spatial and temporal variation in N transfer in grass–white clover mixtures at three Northern European field sites', *Soil Biology and Biochemistry*, 57, pp. 654-662.

Ribera, I., Dolédec, S., Downie, I.S. and Foster, G.N. (2001) 'Effect of land disturbance and stress on species traits of ground beetle assemblages', *Ecology*, 82(4), pp. 1112-1129.

Rinaldi, M. and Vonella, A.V. (2006) 'The response of autumn and spring sown sugar beet (Beta vulgaris L.) to irrigation in Southern Italy: Water and radiation use efficiency', *Field Crops Research*, 95(2), pp. 103-114.

Roberts, M.J. (2001) *Field Guide to the Spiders of Britain and Northern Europe*. Collins, London (2001).

Robins., N., Roberts., S. and Abbot., J. (2000) *Who Benefits? A Social Assessment of Environmentally Driven Trade*. IIED, London

Robinson, R.A. and Sutherland, W.J. (2002) 'Post-war changes in arable farming and biodiversity in Great Britain', *Journal of Applied Ecology*, 39(1), pp. 157-176.

Romero, A., Chamorro, L. and Sans, F.X. (2008) 'Weed diversity in crop edges and inner fields of organic and conventional dryland winter cereal crops in NE Spain', *Agriculture, Ecosystems & Environment*, 124(1–2), pp. 97-104.

Rösch, V., Tscharntke, T., Scherber, C. and Batáry, P. (2015) 'Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments', *Oecologia*, 179(1), pp. 209-222.

Roschewitz, I., Gabriel, D., Tscharntke, T. and Thies, C. (2005a) 'The effects of landscape complexity on arable weed species diversity in organic and conventional farming', *Journal of Applied Ecology*, 42(5), pp. 873-882.

Roschewitz, I., Thies, C. and Tscharntke, T. (2005b) 'Are landscape complexity and farm specialisation related to land-use intensity of annual crop fields?', *Agriculture, Ecosystems & Environment*, 105(1–2), pp. 87-99.

Rose, F. (1981) *The wild flower key- British Isles and N.W. Europe*. Frederick Warne LTD, London.

Rundlöf, M., Andersson, G.K.S., Bommarco, R., Fries, I., Hederström, V., Herbertsson, L., Jonsson, O., Klatt, B.K., Pedersen, T.R., Yourstone, J. and Smith, H.G. (2015) 'Seed coating with a neonicotinoid insecticide negatively affects wild bees', *Nature*, 521, p. 77.

Rundlöf, M. and Smith, H.G. (2006) 'The effect of organic farming on butterfly diversity depends on landscape context', *Journal of Applied Ecology*, 43(6), pp. 1121-1127.

Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G. and Ekbom, B. (2015) 'Predator body sizes and habitat preferences predict predation rates in an agroecosystem', *Basic and Applied Ecology*, 16(3), pp. 250-259.

Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G. and Ekbom, B. (2013) 'Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale', *Journal of Applied Ecology*, 50(2), pp. 345-354.

Rusch, A., Valantin-Morison, M., Sarthou, J.-P. and Roger-Estrade, J. (2010) 'Chapter six - Biological Control of Insect Pests in Agroecosystems: Effects of Crop Management, Farming Systems, and Seminatural Habitats at the Landscape Scale: A Review', in Sparks, D.L. (ed.) *Advances in Agronomy*. Academic Press, pp. 219-259.

Rushton, S.P. and Eyre, M.D. (1992) 'Grassland Spider Habitats in North-East England', *Journal of Biogeography*, 19(1), pp. 99-108.

Sanderson, R.A., Goffe, L.A. and Leifert, C. (2015) 'Time-series models to quantify short-term effects of meteorological conditions on bumblebee forager activity in agricultural landscapes', *Agricultural and Forest Entomology*, 17(3), pp. 270-276.

Sanderson, R.A., Rushton, S.P., Cherrill, A.J. and Byrne, J.P. (1995) 'Soil, Vegetation and Space: An Analysis of Their Effects on the Invertebrate Communities of a Moorland in North-East England', *Journal of Applied Ecology*, 32(3), pp. 506-518.

Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.-M., Bieringer, G., Milasowszky, N., Moser, D., Plutzar, C., Pollheimer, M., Storch, C., Tröstl, R., Zechmeister, H. and Grabherr, G. (2004) 'Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria', *Biological Conservation*, 117(2), pp. 181-190.

Schaffers, A.P., Raemakers, I.P., Sykora, K.V. and Ter Braak, C.J. (2008) 'Arthropod assemblages are best predicted by plant species composition', *Ecology*, 89(3), pp. 782-94.

Schmidt-Entling, M.H. and Döbeli, J. (2009) 'Sown wildflower areas to enhance spiders in arable fields', *Agriculture, Ecosystems & Environment*, 133(1), pp. 19-22.

Schmidt, M.H., Clough, Y., Schulz, W., Westphalen, A. and Tscharntke, T. (2006) 'Capture efficiency and preservation attributes of different fluids in pitfall traps', *Journal of Arachnology*, 34(1), pp. 159-162.

Schmidt, M.H., Roschewitz, I., Thies, C. and Tscharntke, T. (2005) 'Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders', *Journal of Applied Ecology*, 42(2), pp. 281-287.

Schmidt, M.H. and Tscharntke, T. (2005) 'The role of perennial habitats for Central European farmland spiders', *Agriculture, Ecosystems & Environment*, 105(1–2), pp. 235-242.

Schweiger, O., Maelfait, J.P., Van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekotter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M. and Bugter, R. (2005) 'Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales', *Journal of Applied Ecology*, 42(6), pp. 1129-1139.

Sharley, D.J., Hoffmann, A.A. and Thomson, L.J. (2008) 'The effects of soil tillage on beneficial invertebrates within the vineyard', *Agricultural and Forest Entomology*, 10(3), pp. 233-243.

Sharma, P., Laor, Y., Raviv, M., Medina, S., Saadi, I., Krasnovsky, A., Vager, M., Levy, G.J., Bar-Tal, A. and Borisover, M. (2017) 'Green manure as part of organic management cycle: Effects on changes in organic matter characteristics across the soil profile', *Geoderma*, 305, pp. 197-207.

Shearin, A.F., Reberg-Horton, S.C. and Gallandt, E.R. (2007) 'Direct Effects of Tillage on the Activity Density of Ground Beetle (Coleoptera: Carabidae) Weed Seed Predators', *Environmental Entomology*, 36(5), pp. 1140-1146.

Shepherd, M., Pearce, B., Cormack, B., Philipps, L., Cuttle, S., Bhogal, A., Costigan, P. and Unwin, R. (2003) 'An assessment of the environmental impacts of organic farming', *A review for DEFRA-funded Project OF0405*.

Siitonen, J. (1994) 'Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods', *Annales Zoologici Fennici*, 31(1), pp. 89-95.

Sjödin, N.E., Bengtsson, J. and Ekbom, B. (2008) 'The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects', *Journal of Applied Ecology*, 45(3), pp. 763-772.

Southwood, T.R.E. and David, J.C. (2002) 'Food Requirements of Grey Partridge Perdix perdix Chicks', *Wildlife Biology*, 8(3), pp. 175-183.

Sparks, T.C. (2013) 'Insecticide discovery: An evaluation and analysis', *Pesticide Biochemistry and Physiology*, 107(1), pp. 8-17.

Stace (1991) *Plant taxonomy and biosystematics*. Cambridge University press.

Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., Snoo, G.R.d. and Eden, P. (2001) 'Ecological impacts of arable intensification in Europe', *Journal of Environmental Management*, 63(4), pp. 337-365.

Stork, N.E., McBroom, J., Gely, C. and Hamilton, A.J. (2015) 'New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods', *Proceedings of the National Academy of Sciences*, 112(24), pp. 7519-7523.

Storkey, J., Brooks, D., Haughton, A., Hawes, C., Smith, B.M. and Holland, J.M. (2013) 'Using functional traits to quantify the value of plant communities to invertebrate ecosystem service providers in arable landscapes', *Journal of Ecology*, 101(1), pp. 38-46.

Storkey, J., Macdonald, A.J., Bell, J.R., Clark, I.M., Gregory, A.S., Hawkins, N.J., Hirsch, P.R., Todman, L.C. and Whitmore, A.P. (2016) 'Chapter One - The Unique Contribution of Rothamsted to Ecological Research at Large Temporal Scales', in Dumbrell, A.J., Kordas, R.L. and Woodward, G. (eds.) *Advances in Ecological Research*. Academic Press, pp. 3-42.

Symondson, W.O.C., Sunderland, K.D. and Greenstone, M.H. (2002) 'Can generalist predators be effective biocontrol agents? 1', *Annual review of entomology*, 47(1), pp. 561-594.

Takayuki, O. (2005) 'Indirect Interaction Webs: Herbivore-Induced Effects Through Trait Change in Plants', *Annual Review of Ecology, Evolution, and Systematics*, 36(1), pp. 81-105.

Tauber, C.A., Tauber, M.J. and Albuquerque, G.S. (2009) 'Chapter 181 - Neuroptera: (Lacewings, Antlions) A2 - Resh, Vincent H', in Cardé, R.T. (ed.) *Encyclopedia of Insects (Second Edition)*. San Diego: Academic Press, pp. 695-707.

Teja, T., Jason, M.T., Tatyana, A.R., Raphael, K.D., Lenore, F., Péter, B., Janne, B., Yann, C., Thomas, O.C., Carsten, F.D., Robert, M.E., Jochen, F., Robert, D.H., Andrea, H., Alexandra, M.K., David, K., Claire, K., Doug, A.L., William, L., David, L., Christoph, S., Navjot, S., Ingolf, S.D., Carsten, T., Wim, H.v.d.P. and Catrin, W. (2012) 'Landscape moderation of biodiversity patterns and processes - eight hypotheses', *Biological Reviews*, 87(3), pp. 661-685.

ter Braak, C.J.F. (1986) 'Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis', *Ecology*, 67(5), pp. 1167-1179.

Ter Braak, C.J.F. and Prentice, I.C. (1988) 'A Theory of Gradient Analysis', in Begon, M., Fitter, A.H., Ford, E.D. and Macfadyen, A. (eds.) *Advances in Ecological Research*. Academic Press, pp. 271-317.

Ter Braak, C.J.F. and Smilauer, P. (2002) *CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)*. www. canoco. com.

Thomas, C.F.G., Brown, N.J. and Kendall, D.A. (2006) 'Carabid movement and vegetation density: Implications for interpreting pitfall trap data from split-field trials', *Agriculture, Ecosystems & Environment*, 113(1), pp. 51-61.

Thomas, C.F.G. and Marshall, E.J.P. (1999) 'Arthropod abundance and diversity in differently vegetated margins of arable fields', *Agriculture, Ecosystems & Environment*, 72(2), pp. 131-144.

Thomas, J.A. (2005) 'Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1454), pp. 339-357.

Thorbek, P. and Bilde, T. (2004) 'Reduced numbers of generalist arthropod predators after crop management', *Journal of Applied Ecology*, 41(3), pp. 526-538.

Topping, C.J. and Lovei, G.L. (1997) 'Spider density and diversity in relation to disturbance in agroecosystems in New Zealand, with a comparison to England', *New Zealand Journal of Ecology*, 21(2), pp. 121-128.

Topping, C.J. and Sunderland, K.D. (1992) 'Limitations to the Use of Pitfall Traps in Ecological-Studies Exemplified by a Study of Spiders in a Field of Winter-Wheat', *Journal of Applied Ecology*, 29(2), pp. 485-491.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. and Thies, C. (2005a) 'Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management', *Ecology Letters*, 8(8), pp. 857-874.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. and Thies, C. (2005b) 'Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management', *Ecology Letters*, 8(8), pp. 857-874.

Tscharntke, T., Rand, T.A. and Bianchi, F.J.J.A. (2005c) *Annales Zoologici Fennici*. JSTOR.

Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A. and Bengtsson, J. (2014) 'Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis', *Journal of Applied Ecology*, 51(3), pp. 746-755.

Tylianakis, J.M., Tscharntke, T. and Klein, A.-M. (2006) 'Diversity, Ecosystem Function, and Stability of Parasitoid–Host Interactions across a Tropical Habitat Gradient', *Ecology*, 87(12), pp. 3047-3057.

UN (2003.) 'Department of Economic and Social Affairs – Population Division.', *HarperCollins, London*

Unwin, R.J. and Smith, K.A. (1995) 'Nitrate Leaching from Livestock Manures in England and the Implications for Organic Farming of Nitrate Control Policy', *Biological Agriculture & Horticulture*, 11(1-4), pp. 319-327.

Valtonen, A.K.S.J.J. (2006) 'Effect of different mowing regimes on butterflies and diurnal moths on road verges.', *Animal Biodiversity and Conservation* Vol. 29, p. Núm. 2.

van Elsen, T. (2000) 'Species diversity as a task for organic agriculture in Europe', *Agriculture, Ecosystems & Environment*, 77(1), pp. 101-109.

van Heezik, Y., Dickinson, K.J.M., Freeman, C., Porter, S., Wing, J. and Barratt, B.I.P. (2016) 'To what extent does vegetation composition and structure influence beetle communities and species richness in private gardens in New Zealand?', *Landscape and Urban Planning*, 151, pp. 79-88.

van Klink, R., van der Plas, F., van Noordwijk, C.G.E., WallisDeVries, M.F. and Olff, H. (2015) 'Effects of large herbivores on grassland arthropod diversity', *Biological Reviews*, 90(2), pp. 347-366.

Varchola, J.M. and Dunn, J.P. (1999) 'Changes in ground beetle (Coleoptera: Carabidae) assemblages in farming systems bordered by complex or simple roadside vegetation', *Agriculture, Ecosystems & Environment*, 73(1), pp. 41-49.

Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J.-M. and Baudry, J. (2013) 'The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations?', *Agriculture, Ecosystems & Environment*, 166, pp. 3-14.

Verburg, P.H., Overmars, K.P., Huigen, M.G.A., de Groot, W.T. and Veldkamp, A. (2006) 'Analysis of the effects of land use change on protected areas in the Philippines', *Applied Geography*, 26(2), pp. 153-173.

Wamser, S., Dauber, J., Birkhofer, K. and Wolters, V. (2011) 'Delayed colonisation of arable fields by spring breeding ground beetles (Coleoptera: Carabidae) in landscapes with a high availability of hibernation sites', *Agriculture, Ecosystems & Environment*, 144(1), pp. 235-240.

Wang, Y., Naumann, U., Wright Stephen, T. and Warton David, I. (2012) 'mvabund– an R package for model-based analysis of multivariate abundance data', *Methods in Ecology and Evolution*, 3(3), pp. 471-474.

Watson, C.A., Atkinson, D., Gosling, P., Jackson, L.R. and Rayns, F.W. (2002) 'Managing soil fertility in organic farming systems', *Soil Use and Management*, 18, pp. 239-247.

Weiher, E., der, v., Werf, A., Thompson, K., Roderick, M., Garnier, E. and Eriksson, O. (1999) 'Challenging Theophrastus: a common core list of plant traits for functional ecology', *J. Veg. Sci*, 10, p. 609.

Weiner, H.L. (2001) 'Induction and mechanism of action of transforming growth factor-beta-secreting Th3 regulatory cells', *Immunological Reviews*, 182(1), pp. 207-214.

Westerman, P.R., Liebman, M., Menalled, F.D., Heggenstaller, A.H., Hartzler, R.G. and Dixon, P.M. (2005) 'Are many little hammers effective? Velvetleaf (Abutilon theophrasti) population dynamics in two- and four-year crop rotation systems', *Weed Science*, 53(3), pp. 382-392.

Whittingham, M.J. (2006) 'Will agri-environment schemes deliver substantial biodiversity gain, and if not why not?', *Journal of Applied Ecology*, 44(1), pp. 1-5.

Wickramasinghe, L.P., Harris, S., Jones, G. and Vaughan Jennings, N. (2004) 'Abundance and Species Richness of Nocturnal Insects on Organic and Conventional Farms: Effects of Agricultural Intensification on Bat Foraging

Abundancia y Riqueza de Especies de Insectos Nocturnos en Granjas Orgánicas y Convencionales: Efectos de la Intensificación Agrícola sobre el Forrajeo de Murciélagos', *Conservation Biology*, 18(5), pp. 1283-1292.

Wickramasinghe, L.P., Harris, S., Jones, G. and Vaughan, N. (2003) 'Bat activity and species richness on organic and conventional farms: impact of agricultural intensification', *Journal of Applied Ecology*, 40(6), pp. 984-993.

Willer, H. and Yussefi, M. (2000) *Organic agriculture worldwide: statistics and perspectives*. Bad Dürkheim: Stiftung Ökologie & Landbau (SÖL).

William, D. and Terry, L.E. (1982) 'Responses in Abundance and Diversity of Cornfield Carabid Communities to Differences in Farm Practices', *Ecology*, 63(4), pp. 900-904.

Winkler, K., WÄCkers, F. and Pinto, D.M. (2009) 'Nectar-providing plants enhance the energetic state of herbivores as well as their parasitoids under field conditions', *Ecological Entomology*, 34(2), pp. 221-227.

Winkler, K., Wäckers, F.L., Termorshuizen, A.J. and van Lenteren, J.C. (2010) 'Assessing risks and benefits of floral supplements in conservation biological control', *BioControl*, 55(6), pp. 719-727.

Wissinger, S.A. (1997) 'Cyclic Colonization in Predictably Ephemeral Habitats: A Template for Biological Control in Annual Crop Systems', *Biological Control*, 10(1), pp. 4-15.

Witmer, J.E., Hough-Goldstein, J.A. and Pesek, J.D. (2003) 'Ground-Dwelling and Foliar Arthropods in Four Cropping Systems', *Environmental Entomology*, 32(2), pp. 366-376.

Woltz, M.J. and Landis, D.A. (2014) 'Coccinellid response to landscape composition and configuration', *Agricultural and Forest Entomology*, 16(4), pp. 341-349.

Woodcock, B.A., Potts, S.G., Westbury, D.B., Ramsay, A.J., Lambert, M., Harris, S.J. and Brown, V.K. (2007) 'The importance of sward architectural complexity in structuring predatory and phytophagous invertebrate assemblages', *Ecological Entomology*, 32(3), pp. 302-311.

Woodcock, B.A., Pywell, R.F., Roy, D.B., Rose, R.J. and Bell, D. (2005a) 'Grazing management of calcareous grasslands and its implications for the conservation of beetle communities', *Biological Conservation*, 125(2), pp. 193-202.

Woodcock, B.A., Westbury, D.B., Potts, S.G., Harris, S.J. and Brown, V.K. (2005b) 'Establishing field margins to promote beetle conservation in arable farms', *Agriculture, Ecosystems & Environment*, 107(2–3), pp. 255-266.

Wratten, S.D., Bowie, M.H., Hickman, J.M., Evans, A.M., Sedcole, J.R. and Tylianakis, J.M. (2003) 'Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land', *Oecologia*, 134(4), pp. 605-611.

Yi, W., Ulrike, N., Stephen, T.W. and David, I.W. (2012) 'mvabund– an R package for model-based analysis of multivariate abundance data', *Methods in Ecology and Evolution*, 3(3), pp. 471-474.

Young, B.G. (2006) 'Changes in Herbicide Use Patterns and Production Practices Resulting from Glyphosate-Resistant Crops', *Weed Technology*, 20(2), pp. 301-307.

Zaller, J.G., Moser, D., Drapela, T., Schmöger, C. and Frank, T. (2008) 'Insect pests in winter oilseed rape affected by field and landscape characteristics', *Basic and Applied Ecology*, 9(6), pp. 682-690.

Zimmermann, K., Fric, Z., Jiskra, P., Kopeckova, M., Vlasanek, P., Zapletal, M. and Konvicka, M. (2011) 'Mark–recapture on large spatial scale reveals long distance dispersal in the Marsh Fritillary, Euphydryas aurinia', *Ecological Entomology*, 36(4), pp. 499-510.