The impacts of agricultural intensification on arthropod assemblages at global and local scales

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Abstract

Agriculture has often resulted in large-scale habitat loss and simplification of ecosystems and the loss of biological diversity. However, agricultural landscapes can also provide habitat for a wide range of species. Whilst ecological research has tended to focus on natural habitats or native habitat components situated in agricultural systems, there is a growing realisation that production land can play an important role in ecological processes and conservation outcomes. In this thesis I explored a number of questions pertaining to the relationship between agriculture and biodiversity:

1. What drives agricultural change and how have different global patterns of agricultural development impacted upon biological diversity?
2. How do abundance and richness of different arthropod taxa and feeding guilds respond to land-use change globally?
3. How and why do Formicidae populations and assemblages vary among different land uses in a heterogeneous agricultural landscape?
4. Do body-size and morphological features of Araneae, Coleoptera and Formicidae assemblages differ among different land uses in an agricultural landscape?
5. How do arthropod assemblages of crops differ depending on the type of habitat that borders the crop field?
6. Does the rate of pest-predation in cropping vary depending on the adjacent habitat type?

Agricultural land-use change is often driven by an interacting combination of biophysical factors and socio-economic and political factors, and frequently impacts negatively on biodiversity. In this study I identified four broad patterns of how agriculture can impact on biodiversity globally, related to the history of agriculture in a region, and the trajectory of agricultural management intensification.

The impact of agriculture and the utilisation of agricultural land uses by arthropods are of particular importance, given the role that arthropods can play in driving fundamental ecosystem processes and functions upon which healthy agricultural systems depend. In order to examine global trends in responses of arthropod communities to land-use change, I undertook a series of meta-analyses incorporating data from over 250 studies from the scientific literature. From this I found that arthropod richness declined along a gradient of agricultural intensification from native vegetation to improved pasture, to reduced-input cropping, to intensive cropping. Within feeding guilds, both predators and decomposers exhibited this response, but not herbivores. The decline of arthropod richness was greater between native vegetation and agricultural land than it was between different categories of agricultural land, implying that on average, the retention of native vegetation may be a more effective strategy in maintaining arthropod species richness than wildlife-friendly farming. However, low-intensity agricultural land uses were consistently more biodiverse than their intensive counterparts, indicating that wildlife-friendly farming may also be an effective conservation strategy where retaining native vegetation is not feasible or cost effective, or where native vegetation is already sufficiently protected or managed.

Having identified a range of globally consistent patterns of arthropod assemblage responses to different agricultural land-use and management change scenarios, I examined these in a geographically localised context, in a heterogeneous mixed farming landscape in southern Queensland, Australia. I examined patterns of Formicidae abundance, richness, and assemblage composition in three land-use types (native woodland, grazed pastures and crops) and the interfaces between them. The patterns of richness decline amongst land-use types observed for ants in the field study were broadly similar to those found in the global analyses. However, whilst the native woodland sites were the most biodiverse and the intensively managed cropping was biologically very impoverished, the pasture treatment contributed to landscape-level ant diversity in having a distinctive ant assemblage and several morphospecies restricted to this land-use type. This indicated that not only remnants of woody vegetation, but also elements of the agricultural matrix, should be considered in biodiversity management in agricultural landscapes.

I also examined if assemblages displayed different morphological trait patterns among the land-use types, potentially due to the differing levels of habitat modification and disturbance in the land uses. There were more small-bodied beetles and spiders in intensively managed cropping areas than in pastures and woodlands, and the incidence of highly mobile macropterous beetles was greatest in intensively

managed cropping. This indicates that intensively managed land uses may create suitable conditions for, and confer an advantage on, taxa that have small body size and high degrees of vagility. Such findings could be attributable to a range of factors, such as highly vagile, winged taxa being better able to rapidly colonise crops following disturbance events.

The ecological influence of a land-use type can extend beyond its boundaries. I examined how arthropod assemblages differed in crop fields that were bordered by different habitats, and whether sites at the edge of the field differed in their assemblage to those in the interior. This was tested using pitfall trap stations at crop field edges and crop interiors that differed in whether they were bordered by a patch of native woodland/grassland or a linear grass strip. The richness, abundance and assemblage composition of ants was different at a cropping/woodland edge than it was between the edge formed by cropping and linear strips of vegetation. The ant assemblage in cropping field interiors differed depending upon which habitat type was adjacent to the field. Whilst I found differences in assemblage composition in cropping habitats, depending on whether the adjacent habitat type was native woodland or a linear grass strip, predation rates of *Heliothis armigera* (Lepidoptera: Noctuidae) eggs placed in crops bordered by different habitats did not differ. However, the distance from the edge (regardless of adjacent habitat type) did appear to influence predation rates, with removal of eggs being greater at the edges of crops than in the cropping field itself. This higher rate of egg predation appears to indicate that predator densities may be higher at edge habitats than in crops, and therefore edges may be important sources of predatory arthropods.

This study has contributed to an understanding of how arthropod assemblages are shaped by different agricultural land uses and habitat types in a part of the world where European-style agriculture is a relatively recent introduction (‘frontier’ regions). From this study I conclude that agricultural landscapes in frontier regions have considerable potential to support a range of arthropod groups, providing that they contain remnants of native vegetation, and some relatively low intensity land uses such as pastures. The distinct ant assemblages and treatment-specific taxa found in the pasture systems indicate that mixed-land use farming is likely to have greater biodiversity value than monocultural practices and hence should be encouraged at the policy and on-ground management levels. Furthermore, it appears that relatively low intensity habitat types such as the edges and boundaries of crops and other land-use

types may contribute to maintaining arthropod biodiversity and localised pest control potential. Finally, this study indicates that more attention given to examining the biodiversity attributes of agricultural land uses in frontier regions (where the focus of biodiversity research and conservation is often centred on remnants of native habitat rather than components of the agricultural matrix) may provide important insights into the roles that different farm environments can play in conserving biodiversity and maintaining ecosystem function.

Certification of Dissertation

I certify that the ideas, experimental work, results, analyses and conclusions reported in this thesis are entirely my own effort, except where otherwise acknowledged. I also certify that the work is original, and has not been previously submitted for any other award, except where otherwise acknowledged.

Signature of candidate **Date**

Endorsement:

Signature of supervisor **Date**

Signature of supervisor **Date**

Signature of supervisor **Date**

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Journal publications

Attwood, S.J., Park, S.E., Maron, M., Collard, S.J., Robinson, D., Reardon-Smith, K.R.S. & Cockfield, G. (2009) Declining birds in Australian agricultural landscapes may benefit from aspects of the European agri-environment model. *Biological Conservation*, **142**, 1981–1991.

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Conference presentations

Attwood, S J., M Maron, C Zammit, A. P. N. House. (2005) *A quantitative literature analysis of global invertebrate responses to agricultural intensification.* Ecological Society of Australia Conference, Brisbane, Australia.

Attwood, S J., M Maron, A. P. N. House, C Zammit. (2006) *Ant assemblage responses to agricultural intensification in heterogeneous landscapes.* Ecological Society of Australia Conference, Wellington, New Zealand.

Attwood, S J., M Maron, A. P. N. House, C Zammit. (2007) *Arthropod assemblage responses to agricultural intensification in heterogeneous landscapes – local testing of global patterns.* International Association of Landscape Ecology 25th World Congress, Wageningen, The Netherlands

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Chapter 1

Introduction—Agricultural development and its implications for biodiversity

The sections of this chapter outlining historical development of European agriculture underpinned part of the published paper:

Attwood, S.J., Park, S.E., Maron, M., Collard, S.J., Robinson, D., Reardon-Smith, K.R.S. & Cockfield, G. (2009) Declining birds in Australian agricultural landscapes may benefit from some aspects of the European agri-environment model. *Biological Conservation*, **142**, 1981–1991.

1.1 Introduction

1.1.1 Preamble

A typical agricultural field is brimming with life, a complex food chain that includes top-level predators and tiny, unheralded detritivores and fungivores. Whilst the incumbent fauna are generally small, often microscopic, the sheer numbers are staggering: a cubic metre of topsoil may contain 100,000 springtails (Larink, 1997), whilst an acre of pasture grassland may contain two million individual spiders (Bristowe, 1958; Wise, 1993), themselves devouring around 40 kg ha^{-1} yr^{-1} of prey (Kajak *et al.* 1971 in Nyfeller, 2000).

The complex array and intricate spatial arrangement of land-use types and disturbance processes associated with mosaic agricultural landscapes results in an equally complex assemblage of arthropods. Whilst agricultural practices and land uses shape arthropod assemblages in many ways, arthropods also play fundamental roles in the ecosystem processes that drive and influence agricultural production—arthropods are predators, pests, soil engineers and pollinators. It is a need to understand the response of arthropod communities to different land-use types (along a disturbance/modification gradient from natural to intensive) and the implications of these responses for conservation of arthropod diversity and arthropod-driven ecosystem processes that underpin much of this thesis.

As this study analyses global as well as local data, and given the enormously influential nature of land-use history and trajectory on faunal associations in agricultural landscapes, the impacts of agriculture on biodiversity are better understood in the context of bio-geographical and socio-political drivers and characteristics. Consequently, in this chapter I will present an overview of agricultural development and drivers of land-use and management change, examine global variation in the complex agriculture/biodiversity relationship, and identify how such factors may impact on biological diversity globally.

1.1.2 The origins and prehistoric dispersal of agriculture

The transition from a hunter-gatherer niche to one based on settlement and the deliberate production of food (rather than its periodic and intermittent acquisition) was arguably the most pivotal advance of modern humans (Harris, 1996). The development of agriculture liberated *Homo sapiens* from the need to locate and subdue or collect food and allowed longer periods of residency in the same locale. The area of resources needed to support a family or tribe was also greatly affected by the development of farming—from hunter-gatherer communities requiring several square kilometres to meet their resource requirements, to agrarian communities requiring only a few hectares (Bellwood, 2005).

This increase in resource productivity per unit area permitted an explosion in human populations. Estimates vary for different parts of the world, but Smith (1979, in Bellwood, 2005) suggests that the population of Southwest Asia may have increased from 100,000 to 5 million people between 8,000 and 4,000 BC. The societal impacts of such resource and population changes were considerable, and it has been hypothesised that agriculture formed the foundation upon which the 'modern' template for civilisation was constructed (Tudge, 2004; Bellwood, 2005) and thus catalysed the accelerated development of technology, art and culture (Atahan *et al*. 2007). However, the processes by which the cultivation of plants and the domestication of animals developed, and indeed when this development occurred, continue to be a source of debate and evolving opinion (Vasey, 2002).

It is thought that the cultivation of plants began in the Southwest Asian 'fertile crescent' (discernable via grains of wheat and barley different from those in the wild (Tudge, 2004)) and eastern Asia at the end of the last glacial maximum (the present interglacial beginning approximately 12,000 years BP). This development was determined to a considerable extent by two key elements—a change in climate to warm, wet and relatively stable conditions and the availability of wild food plants suitable for domestication (Bellwood, 2005; Atahan *et al*. 2007). Climatic conditions prior to this period would have been cold, dry and highly variable, and as such, any early attempts at cultivating and domesticating plants would eventually have failed (Bellwood, 2005).

Whilst it would appear that farming has a number of advantages over hunting and gathering, Tudge (2004) offers evidence that early farmers were not necessarily better off than their hunter-gatherer ancestors—for instance, rudimentary agriculture is relatively labour-intensive compared to hunting in a prey-rich environment. Tudge proposes that communities that had previously feasted on the bountiful wild fauna and flora of what is now the Persian Gulf would have been forced to inhabit the more barren uplands as melting glaciers began to flood the lowland. With hunting grounds submerged, they may have been forced into regularly cultivating the grasses that previously might only have a formed a limited part of their diet (and perhaps were sporadically cultivated).

Regarding the relative benefits of farming and hunting/gathering, Diamond and Bellwood (2003) propose three compelling reasons why agriculture may be a highly effective strategy, and why it subsequently expanded to neighbouring communities:

i) agriculture leads to higher and more predictable food yields per area of land, which can in turn support higher population densities, thus increasing the power, prestige and influence of a community;

ii) agriculture enables populations to be relatively sedentary and thus able to accumulate food surpluses, which in turn enables them to advance technologically and develop a more complex social, political and military culture;

iii) farmers, due to prolonged contact with domesticated stock that acted as vectors of disease, were able to acquire some level of immunity to diseases such as measles, whilst hunter-gatherer societies were less able to develop such immunity.

There are numerous theories regarding the spread of agriculture, including the dispersal of Neolithic farmers from Southwest Asia into (for instance) Europe (demic diffusion), and the adoption of farming practices by neighbouring hunter-gatherer communities (cultural diffusion) (Harris, 1996). Whilst it is outside the scope of this thesis to consider critically the main competing theories, a review by Diamond and Bellwood (2003) encapsulates a number of the recent ideas. Their basic hypothesis is that food production based upon the domestication of wild plants and animals developed independently a number of times globally, and spread outwards due to the advantages that agriculture conveyed. The authors, using linguistic analyses as a basis, maintain that the agrarian societies gradually expanded and replaced hunter-gatherer communities and their culture. This process would also have included some degree of interbreeding between hunter-gatherers and agriculturalists, some hunter-gatherers occasionally adopting farming practices and occasional reversion of some farmers to a hunter-gatherer existence. Whatever the means of spread, by approximately 4,000 years BP, agriculture had expanded to five continents, had transformed the human world and would begin to transform the non-human world.

In more recent times, agriculture has expanded rapidly. Around 1700, there were approximately 300–400 million ha of cropland, which rose to an estimated 1500–1800 million ha in 1990 (Lambin *et al*. 2003). The global area of permanent cropping and arable land increased by 11.3% between 1961 and 2003 (Food and Agriculture Organisation (FAOSTAT), 2008). However, this figure obscures the differing land-use change trajectories between developed and developing nations. In developed nations there was a total decrease in arable land area of 6.8%, whereas developing nations reported an increase in area of 24% (FAOSTAT, 2008). These figures included 57.4% and 32% increases from 1961–2003 for Brazil and China respectively (FAOSTAT, 2008). Meanwhile, the total area under pasture increased from some 500 million ha in 1700 to about 3100 million ha in 1990 (Lambin *et al.* 2003). The global area of permanent pasture increased by 9.1% between 1961 and 2003 (FAOSTAT, 2008). Similar geo-political differences were observed for pasture as for cropping—in developed nations there was a total decrease in pasture land area of 2.6%, whereas developing nations reported an increase in area of 15.2% (FAOSTAT, 2008). Again, increases were considerably greater for both Brazil and China, with increases of 38% and 40.5% respectively (FAOSTAT, 2008). Conversion to pasture was largely at the expense of forests/woodlands and natural grasslands, steppes and savannas. Forest area was reduced from 5000–6200 million ha in 1700 to 4300–5300 million ha in 1990, and grassland/steppe/savannah cover from approximately 3200 million ha in 1700 to around 1800–2700 million ha in 1990 (Lambin *et al*. 2003).

1.1.3 What drives agricultural land-use change?

There are many drivers of the historic spread and development of farming and associated spatio-temporal patterns of land-use change. However, they typically are related to a combination of the biophysical attributes of land (e.g. altitude, slope, or soil type) and social, economic and political factors (Veldkamp and Lambin, 2001). Biophysical attributes provide an explanation of why agriculture has a non-random distribution in the landscape, favouring lowlands, less-undulating terrain, and deeper, more productive soils, often resulting in native vegetation persisting in steeper, rocky areas. Lambin *et al*. (2001; 2003) greatly illuminated the underlying socioeconomic and political causes of several globally prevalent agricultural land-use change scenarios. For instance, tropical deforestation for agriculture is often attributed to rapid population growth, poverty and shifting cultivation pressures, which are underpinned by changing economic opportunities, often triggered or supported by government policies, settlement schemes, development projects or incentives and interests in plantation or extractive industry interests. Such drivers effectively lead to an opening up of forest frontiers through infrastructure development, population migration and displacement and disempowerment of indigenous peoples (Lambin *et al*. 2001; 2003).

Whilst agricultural expansion often involves the replacement or modification of native vegetation, agricultural intensification is the alteration, often through increased inputs per unit area, of management of land already used for farming. The intensification of agriculture, through a suite of processes such as increased agro-chemical use, increased mechanisation, increased fertilisation and irrigation, pasture improvement and the development of new crop cultivars, has resulted in greatly increased yields (Matson *et al*. 1997; Tilman *et al*. 2001). For instance, cereal yields (kg/ha) increased globally by c. 240% between 1961 and 2006, with yields in the developing world increasing by c. 190% and yields in the developed world by c. 275% during the same period (FAOSTAT, 2008). The causes of agricultural intensification include land scarcity, (often linked to high population growth/density) and increased market demand for, and value of, particular agricultural products. This can lead to a need for increased production per hectare and/or an increased area of production (Lambin *et al*. 2003).

Whilst the land-use changes discussed above are driven by national and regional influences, they are increasingly being driven by global dynamics, as global interconnectedness of economic and trade systems increases (Lambin et al. 2003). As such, land-use decisions and changes that previously operated at local scales are now determined by a wide range of global market, information, capital and policy processes (Yi *et al*. 2008).

1.2 Agriculture and biodiversity

1.2.1 Broad impacts of agricultural land-use change on biodiversity

1.2.1.1 Agriculture as a major threat to biodiversity

Land-use change from indigenous native vegetation systems to agricultural land exerts the greatest influence on biodiversity globally (Sala *et al*. 2000), with a broad swathe of taxa impacted, from birds (Waltert *et al*. 2004) to arthropods (Attwood *et al*. 2008 (Chapter 2 of thesis)). The loss of habitat is far from evenly distributed among habitat types, reflecting the productivity of the soil and the ease of conversion. For instance, a high percentage of tropical and sub-tropical dry broadleaved forests, grasslands and savannas, which tend to occur on more fertile soils, have recently been converted or heavily modified for agriculture (Millennium Ecosystem Assessment, 2005).

As introduced in section 1.1.3, there are two very broad ways in which agriculture can impact negatively upon biodiversity: i) the conversion of native vegetation to farmland, often causing substantial changes to vegetation structure and composition, soil processes, food chain interactions and a wide range of other physico-chemical and biological features and processes (Armbrecht and Perfecto, 2003; Waltert *et al*. 2005; Yimer *et al*. 2007); and ii) changes to the management of land that has already been modified for agricultural production. This latter mechanism frequently manifests as an increase in the intensification of management and operates through processes such as increased agro-chemical input, mechanisation and system homogenisation and simplification (Benton *et al*. 2003). This results in a loss of resources for taxa dependent upon traditional agricultural management. However, changes to management can also entail the abandonment of extensively managed agricultural land, leading to a loss of species associated with early successional semi-natural habitats (Schmitt and Rákosy, 2007).

The conversion of native systems to farmland today occurs primarily in tropical and sub-tropical regions (Green *et al*. 2005) and ecologically detrimental changes to existing farming systems are generally reported from the long-established, traditional farming systems in Europe. Despite this, there is an increasing realisation that the nature and intensity of agriculture and the presence or absence of particular agricultural land uses or features can have a considerable bearing upon biodiversity in more recently farmed regions such as Australia (Haslem and Bennett, 2008a; 2008b) and Costa Rica (Perfecto *et al*. 1997; Hughes *et al*. 2002; Sekercioglu *et al*. 2007).

1.2.1.2 Agricultural expansion and coincidence with areas of high biodiversity

There is a considerable degree of coincidence between areas of high biodiversity, human impacts and anthropogenic land-use change. In sub-Saharan Africa, there is a positive correlation between the species richness of birds, mammals, snakes and amphibians and human population density (Balmford *et al.* 2001). A similar relationship was found for neotropical bird richness and human population pressure (Fjeldså and Rahdek, 1998) and richness of plants, mammals, reptiles and amphibians and human population density in Europe (Araújo, 2003). Such spatial relationships often lead to the coincidence of habitat loss and biodiversity (e.g. Balmford and Long, 1994), and agriculture is a prevalent land use in areas of considerable biodiversity value such as Endemic Bird Areas (Scharlemann *et al.* 2004).

To explore and illustrate the relationship between biodiversity and agricultural production at the national scale, I investigated the relationships between three metrics of avian diversity (species richness, number of endemics and number of IUCN threatened species) and three measures of agricultural expansion and impact. Although my thesis is centered on arthropods, national species-level data for such groups are extremely sparse, whilst birds are among the most extensively studied and well-documented taxa. Lists of bird species richness data were compiled for each country using Avibase (Bird Studies Canada, 2008), which provides an account of the number of different bird species, number of endemic bird species and number of IUCN Threatened bird species recorded in each world country up to 2008 (see Appendix A.1). Data on cattle headage (absolute numbers to nearest thousand), total agricultural land area (hectares) and cropping land area (hectares) were generated for each country for the earliest available date (1961) and the most recent available date (2005) from FAO production data (FAOSTAT, 2008). Countries with <100,000 hectares of production land were excluded from analyses, as very small changes in actual production area tended to give large percentage changes in land-use cover, thus potentially skewing results. I calculated the percentage change in each agricultural metric between 1961 and 2005 and performed a series of Spearman's rho correlation tests to examine relationships between agricultural land-use trends expressed as percentage change in a given agricultural metric (e.g. percentage increase or decrease in number of cattle between 1961 and 2005) in a country and i) the total bird species richness, ii) number of endemic species and iii) number IUCN Threatened species in that country.

Despite using data at a rather coarse grain (i.e. based upon national boundaries rather than on spatial location or biogeographical parameters) there was a high degree of coincidence between the measures of biodiversity value and agricultural expansion over the last four decades (Table 1.1). This was particularly evident for percentage change in cattle headage and percentage change in agricultural land area, with countries that have high avian diversity, high numbers of endemics or many Threatened species, typically also exhibiting rapid rates of increase in cattle numbers and area of land under agricultural production. However, the relationship was far less evident for cropping (Table 1.1), with no correlation found between the increase in area of cropped land and number of endemics or number of threatened species. This implies that the spread of pasture has been far more pervasive than the spread of arable cultivation in nations with high biodiversity. In some regions, the conversion of native systems to agriculture appears to have decelerated, but this may be because so little habitat remains in many instances (Millennium Ecosystem Assessment, 2005). Given the recent demands for biofuels, the trend for land conversion may accelerate in regions with suitable land remaining.

This analysis indicates that for an important component of biological diversity, the threats from agricultural expansion (change in total agricultural area) and the expansion and intensification of cattle production (through increased pastoral area and/or increased headage per unit of area) continue to be significant global phenomena. Given there can be high correlation rates between bird hotspots and priority areas for other biodiversity (Brooks *et al.* 2001), applied research relating to biodiversity in agricultural systems globally is of paramount importance for informing both policy and management.

Table 1.1. Spearman's rho correlation results for three metrics of avian diversity at national scale (number of species, number of endemic species, number of threatened species) and three agricultural metrics (% change in cattle numbers, % change in area of agricultural land and % change in area of cropping).

Biodiversity measure	**Agricultural change measure**	**Spearman's Rho**	**d.f.**	**P (two-tailed)**
Species richness	% change in cattle headage (1961–2005)	0.308	134	0.001
	% change in agricultural land area (1961–2005)	0.309	138	0.001
	% change in cropped land area (1961–2005)	0.286	133	0.001
Endemic species richness	% change cattle	0.551	134	0.001
	% change agricultural land	0.402	138	0.001
	% change cropping land	0.063	133	0.473
IUCN threatened species richness	% change cattle	0.443	134	0.001
	% change agricultural land	0.430	138	0.001
	% change cropping land	-0.66	133	0.488

1.2.2 Global agricultural development scenarios and biodiversity impacts

It is evident from the literature and this analysis that agricultural land-use trends and impacts on biodiversity differ among world regions. In order to illuminate commonalities and differences in land-use trajectory and the likely implications for biodiversity, I consider four common scenarios of land-use change and biodiversity response. The four categories are:

Traditional & intensive—regions with a long historic association with extensive/traditional agriculture that have subsequently experienced recent intensification of management (e.g. north-western Europe);

Traditional & abandoned—regions with a long historic association with extensive/traditional agriculture that have subsequently experienced recent land abandonment and succession (e.g. south-western Europe);

Frontier & extensive—regions with a relatively brief historic association with agriculture, managed extensively (e.g. some Central American coffee plantations).

Frontier & intensive—regions with a relatively brief historic association with agriculture, managed intensively (e.g. cropping systems of SE & SW Australia).

1.2.2.1 Traditional & intensive (long history of traditional agriculture with recent intensification)

Figure 1.1a details the important changes in agricultural development and associated environmental impacts experienced in Britain and much of north-western Europe. This is a depiction of a long-farmed landscape, where a rich biota has adapted to, or followed the geographical advance of, extensively-practiced agriculture (Donald *et al.* 2002). This long historical trend is followed by recent social, economic and political drivers, resulting in a broadscale shift to intensified, even industrialised, farming in a homogenised and uniform landscape. In seeking greatly increased productivity, enormous changes were wrought upon the traditional farming landscapes from WWII onwards (Robinson and Sutherland, 2002). For instance, between 1961 and 2006 cereal yields per hectare increased by 300% in France, 270% in Germany and 230% in the UK (FAOSTAT, 2008). Changes to management and their consequences during this period include (Gillings and Fuller, 1998; Newton, 2004):

- Removal of habitat features such as hedgerows and other non-farmed habitats such as uncultivated field headlands and margins, small woodlands, ponds and ditches.
- The loss of species-rich habitats such as lowland grassland, calcareous grassland, fen and marshes.
- A switch from spring-sown to autumn-sown crops, resulting in reduced habitat suitability for a range of arable-dependent taxa.
- A loss of traditional cropping rotations and a specialisation of either cropping or grazing on farms that had formerly been mixed, thus reducing landscape heterogeneity and spatially segregating resources and habitats important to wildlife.
- The intensification and productive improvement of grasslands, through nitrogen and phosphorus input, increased stocking rates, use of fewer stock breeds (and hence more homogeneous grazing strategies), the replacement of hay production with silage production and the cessation of seasonal grassland flooding.
- The increased use of agro-chemicals such as herbicides and insecticides, with concomitant effects on botanical diversity and invertebrate abundance and diversity.

The impacts of this fifty-year wave of modernisation amount to both habitat loss (more on-farm land put into production) and habitat degradation (where changes to crop and grassland management result in loss of food resources and microhabitats) (Gillings and Fuller, 1998). This has resulted in population declines and local extinctions of a wide variety of taxa (Robinson and Sutherland, 2002), including plants (Green, 1990; Stoate *et al.* 2001), small mammals (Tew *et al.* 1992), birds (Gillings and Fuller, 1998; Newton, 2004) and invertebrates (Burel *et al.* 2004). Many of the species most severely impacted by these changes are those that are adapted to traditionally managed anthropogenic landscapes and land uses. These include open country specialists dependent upon a range of early- to mid-successional habitats (Sutherland, 2004), and species that have become gradually adapted over evolutionary time to low intensity farming. It is these 'farmland specialists' that have had food resources and habitat availability and suitability reduced by the recent advent of intensive agriculture.

The impacts of agricultural intensification on arthropods, whilst not commanding the same attention as impacts on farmland birds, have been considerable, if not greater (Thomas *et al.* 2004). For instance, a review of farming practice impacts on various arthropod groups indicated that insecticide commonly had detrimental impacts on non-target arthropods that can be beneficial to agriculture, such as carabid and staphylinid beetles, spiders and Hymenoptera. In another study, a move to monocultures impacted severely on beetles and spiders and intensive grazing or cutting of grass was shown to affect orthopterans detrimentally (Wilson *et al.* 1999). A host of other recent studies indicate that the intensification of agriculture and consequent habitat loss and deterioration are implicated in the declines of a wide range of taxa, including macro moths (Conrad *et al.* 2006), butterflies (Feber *et al.* 2007; Schmitt and Rákosy, 2007) and dung beetles (Hutton and Giller, 2003). Impacts not only reduce arthropod diversity and abundance, but also affect fauna dependent upon arthropods for food (Wickramasinghe *et al.* 2004) and ecosystem services vital for human food production, such as pollination (Steffan-Dewenter and Westphal, 2008).

Agro-environmental timeline for British Isles – 8,000 yrs BC to present (chronologically not to scale)

Year	c.10,000 – c.5,500 B.P.	c.5,500 B.P.	c.5,000 – c.3,000 B.P.	c.2,800 B.P. – c.500 AD	550 – 1086	1086 – 1700	1700 - 1800	1800 – 1900	1900 - 1950	1950 - present
Population	4000+	c.14,000	'tens of thousands'	c.200,000 to c. 2 million	<1 million to 1.75 million	1.75 million to 5 million	5 million to 9 million	9 million to 32.5 million	32.5 million to c.50 million	c.50 million to c.59 million
Milestones	Climate warming & glacial retreat	Introduction of agricultural practices from S & C Europe	First metal technology	Iron technology, Roman occupation & departure	Domesday Charter, 1086	Plague reduced European pop. by 35-40% 'Little Ice Age'	Beginnings of large scale fossil fuel use and industry	Transition to industrial society Fossil fuel dominance	Two World Wars Increased industrialisation & urbanization	>public access to countryside; spread of suburbia; globalization; environmental movement
Agricultural development	Hunter-gatherer Expand grassy areas for game Fire management of grass Ring-barking trees	Mixed farming adopted Early cropping; stock (sheep & goats) Woodland managed for grazing, fodder & poles	Agriculture dominant way of life in lowland Britain >range of crops Intensification via manure application Charcoal from woodland	Well-planned, enclosed fields in crop rotation, pasture and woodland Romans brought new crops and technology	Enclosed field system until post-Roman; open systems appeared in Dark Ages Likely advance of farmland Much of country well-ordered rural landscape	Agriculture expands Advances – e.g. water mill Intensification - new crops, legumes and fertilisation; yields up by 1/3 from C15 to C18	c. 4.5 million ha of crops and c.7 million of pasture Enclosure Act – 2800 acts of enclosure 1760-1850 >urban settlement	Intensification - continuous crop rotations Advances, e.g. steam ploughing Arable covers 6 million ha by 1870 >urban settlement	Crop area fluctuates; intensified grazing WWII – more tractors Govt. payments and price intervention Agro-chemicals	Agricultural intensification: > field size, hedge removal, > machinery, >chemical use, industrialized animal husbandry Common Agricultural Policy Production subsidies
Environmental outcomes	Natural responses of veg to climate change (> deciduous woodland) Opening-up of vegetation Natural & human processes	Devt. of small fields in woodland matrix Land clearing increased <mature trees, >open woodland structure	> lowland vegetation clearing Nutrient loss & soil erosion on cropping Wild cattle extirpated; large mammal decline Moorland and heath devt.	Clearing of upland vegetation By Iron Age, 50% of Mesolithic woodland cleared Increased 'edge' habitat and associated fauna/flora	Loss of woodland, heathland, wetlands; >woodland management Extensive woodland in parts of England (c.15% cover in Domesday)	Wildwood gone, managed woodlands remain Clearing of uplands (1600, Scotland 'very denuded') c.10% woodland cover by 1350	Last age of coppice, coal replaces charcoal 810,000 ha of woodland Hedgerow planting accumulates biodiversity Large losses of heathland	Non-native forests plantations Loss of wetlands and associated fauna (e.g. Ruff) Increase in some birds – e.g. skylark	Felling of woodland for WW, > forestry tree cover Land use still mostly agricultural Concern: demise of 'rural England'	Homogenised countryside & wildlife declines Concern over environment and sustainability of farming Agri-environmental payments Interest in organic production
Period	Mesolithic	Neolithic	Bronze Age	Iron Age & Roman	Anglo-Saxon & Norman	Medieval and beyond	18th Century	19th Century	Early 20th Century	Late 20th Century

Fig. 1.1.a Chronological sequence of agricultural and land-use development, and the environmental consequences for the British Isles. The region has a long history of traditional agricultural practices, whilst experiencing recent intensification. Based on information from Rackham, 1986; Buckland and Dinnin, 1993; Simmons, 2001.

Agro-environmental timeline for Australia – 60,000 yrs BP to present (chronologically not to scale)

Year	c.60,000 – 45,000 B.P.	c.10,000 B.P.	6,000-4,000 B.P. (continuing to 18th C)	1788 - 1800	1800 – 1900	1900 - 1950	1950 - present
Population	Possibly 100,000 in late Pleistocene	?	Uncertain, but > due to hunting technology and favourable climate	Estimated 6-700,000 Aborigines; ? Europeans	?/?	Aboriginal 67,000; ? European	c.20 million; 86% in urban centres
Milestones	First humans. Climate change, sea-level rise, drying of interior	Aboriginal occupation of much of continent Rising sea levels	Devt. stone tools, introduction of dingo, human population increase	European settlement; Displacement of Indigenous populations Introduction of disease (e.g. small pox)	Greatly increased European settlement < Aboriginal populations Land clearing, urban devt.	Two World Wars Increased industrialisation & urbanization	Vast scale of land clearing Urban and suburban devt. Environmental movement; land clearing legislation; Aboriginal land rights
Agricultural development	Hunter-gatherer (marine/littoral initially) Sea-level rise forced adaptation to inland systems	Fire-stick 'farming' – seasonal selective burning of vegetation creates mosaic of successional stages, promotes fauna – analogous to crop rotation Knowledge of spatio-temporal availability of and management of resources	Sustainable management of resources continued, but more effective hunting techniques (hunting with dogs, stone weapons) and higher human population densities	Initial introduction of domestic stock and small-scale cropping. Small scale vegetation clearing Convicts generally from urban environs, no experience of farming. Very real prospect of starvation for settlers	Cessation of aboriginal land management Broad establishment of cropping and grazing systems Irrigation enables expansion of agriculture Wool exportation – 16 million sheep by 1849	Post-WWI – soldier settlements on marginal lands WWII – >use of machinery Increased cropping Increase in national parks and reserves	Agricultural intensification (machinery; irrigation; agro-chemicals; intensive animal industries) 1990s: Landcare movement, focus on sustainable production and natural resource management Increased conservation on private land
Environmental outcomes	Natural responses of vegetation to climate change. Extinction of much of large-bodied megafauna – 85% of fauna >44kg extinct, all marsupials >100kg extinct	Vegetation systems influenced by anthropogenic burning (shift from fire-sensitive to fire-promoting species) Reduced transpiration and reduced rainfall Human populations limited by ecological constraints, e.g. climatic and physico-chemical constraints Tasmania cut-off (sea-level rise)	Mainland faunal continental extinctions – e.g. thylacine, Tasmanian Devil These species persisted on Tasmania, where dingo absent	Bush very hard to clear by hand and farming very rudimentary – impacts very localised	Broad loss, fragmentation and degradation of woodlands and forests Altered fire regimes – <frequent, >intensive Altered vegetation composition and soil erosion from grazing Fauna declines & extinctions	Large-scale habitat loss, degradation, species decline and extinction Soil erosion >species adapted to open agricultural environments Establishment of feral animal and pest plant populations	Massive habitat loss – 1962-75, 1.5m ha of Brigalow woodland cleared for agriculture Pop. declines and local extinctions Continued remnant habitat degradation and agricultural matrix intensification Nationwide community projects aimed at ameliorating impacts
Period	Late Pleistocene	Holocene	Holocene to 18th C	Late 18th Century	19th Century	Early 20th Century	Late 20th Century

Fig. 1.1.b Chronological sequence of agricultural and land-use development and environmental consequences for Australia. The region has a short history of agriculture, with recent intensification. Based on Flannery, 1994; Roberts *et al.* 2001; Dodson and Mooney 2002; Johnson and Wroe, 2003; Prideaux *et al.* 2007; Bryce Barker pers. comm.

1.2.2.2 Traditional & abandoned (long history of traditional agriculture with recent land abandonment)

The demise of traditional farmland and its characteristic fauna and flora due to the intensification of management practices has received a great deal of consideration from researchers, politicians, the media and the wider public. On the other hand, the issue of the deterioration of traditionally managed agro-ecosystems due to the abandonment of the land has received rather less attention. For instance, in Europe, habitats exist in many cases *because of* rather than *despite* traditional agricultural management (Sutherland, 2004). Accordingly, many species are dependent upon the maintenance of this relatively low-intensity anthropogenic intervention to maintain a diverse mosaic of early- to mid-successional habitats (Sutherland, 2004).

The abandonment of agricultural land may be attributed to a range of factors, including reform of the Common Agricultural Policy, EU expansion, the break-up of large collective or state farms, demographic shifts in the farming community, rural unemployment and depopulation, globalisation and climate change (MacDonald *et al*. 2000; DLG, 2005; Giupponi *et al*. 2006). The areas abandoned are often marginal, less-productive agricultural land that is more topographically difficult to access with farm machinery and is located further from population centres (Giupponi *et al*. 2006). This scenario appears to be particularly prevalent in central, eastern and southern Europe (Osterman, 1998; DLG, 2005).

Whilst the environmental consequences of agricultural land abandonment are highly variable and depend upon location-specific characteristics, the successional encroachment of scrub into areas which previously had an open structure (e.g. old fields, meadows) is a common biological response (MacDonald *et al*. 2000). Accordingly the response of biota is also likely to vary, but generally consists of a proliferation of ruderal species in the initial stages of succession, as pioneer species dominate recently abandoned areas. There is generally a later increase in diversity in mid-successional periods, followed by a reduction in diversity as the woodland canopy closes (MacDonald *et al*. 2000) and climax species dominate. In contrast to the impacts of agricultural intensification in traditional farming systems, which are expressed very quickly as biodiversity loss, the biodiversity effects of land abandonment are likely to take several years to be expressed for some taxa (Schmitt and Rákosy, 2007). The loss of species dependent on managed, early-successional habitats, due to land abandonment, has been recorded by numerous researchers in the

Spanish dehesas. The dehesas is an example of a traditional agrosilvopastoral agricultural system that supports very high biodiversity, consisting of managed holm oak *Quercus ilex* (L.) and cork oak *Quercus suber* (L.) woodlands interspersed with pastoral land and low-input cultivation (Plieninger and Wilbrand, 2001). These systems are threatened by both agricultural intensification and abandonment. The latter process has been identified as the major driving force affecting the ecology of Mediterranean forests (Fabbio *et al*. 2003), leading to scrub encroachment, reduced tree productivity, more intense and frequent forest fires and loss of small-scale habitat mosaics of different closely-aligned land-use types (Plieninger and Wilbrand, 2001; WWF, 2008). Peco *et al*. (2005) found considerable differences in the vegetation structure and composition of grassland sites in the Spanish dehesas that were grazed or abandoned, with the former being characterised by prostrate, early flowering species, and the latter by tall, late flowering species. The loss of traditional management leading to loss of structural and compositional integrity is also likely to have impacts upon a range of species that are dependent upon these diverse systems (Plieninger and Wilbrand, 2001). These include a number of threatened bird species, such as the Spanish imperial eagle *Aquila adalberti* (Brehm) and the Eurasian black vulture *Aegypius monachus* (L.), as well as wintering common cranes *Grus grus* (L.), and numerous passerine species (Tellería, 2001; Plieninger and Wilbrand, 2001).

Whilst the dehesas have been a subject of conservation and research focus, the abandonment of traditional agricultural lands and consequences for biodiversity is also an area of conservation concern in many parts of Eastern Europe (Cremene *et al*. 2005). For instance, vascular plants, gastropods, and diurnal and nocturnal Lepidoptera all exhibited different responses in species richness along a successional gradient from managed hay meadow, to abandoned hay meadow, to birch forest to mature forest in Romania (Baur *et al*. 2006). In particular, richness of diurnal Lepidoptera was greater in the two hay meadow treatments, whilst richness of nocturnal species was higher in the two forest types. This study demonstrates the complexity of responses of various taxa to agricultural land abandonment and subsequent succession.

1.2.2.3 Frontier & extensive (relatively recent introduction of modern agriculture, with low intensity management or land uses)

Despite the (often correct) assumption that the introduction of agriculture into native systems previously unaltered by large scale farming practices is strongly detrimental to biodiversity, there are some notable exceptions. These occur where the management is of low intensity or where much of the native system's structural and/or compositional integrity is retained. An example from the neotropics that has received considerable attention is that of rustic and shade coffee plantations, where the coffee plants are either planted into the existing forest (rustic) or form the 'understorey' of a relatively intact native forest, thus retaining habitat structure and (in some cases) plant diversity (Armbrecht and Perfecto, 2003). Several authors have reported that traditional, low intensity, rustic shade coffee plantations are able to support populations of wintering neotropical migratory birds that are comparable in richness and composition to native forest and richer than other anthropogenic land uses (e.g. Wunderle and Latta, 1994; Greenberg *et al.* 1997). Perfecto *et al.* (2003) also demonstrated that traditional coffee plantations had similar ant species richness as native forest, and considerably greater richness than intensive coffee plantations. The apparent success of biodiversity conservation in traditional and shade coffee plantations has created a market for 'bird-friendly' coffee and similar eco-labelling market strategies for growers and companies utilising these farming strategies (Philpott and Dietsch, 2003).

Similar research has also been conducted in cocoa plantations of differing management intensity in various world regions. Results have varied considerably among studies, taxa and regions, indicating that the introduction of low intensity agricultural disturbance into indigenous vegetation systems may elicit very complex biotic responses. For instance, in Sulawesi, arthropod abundance and diversity did not vary among cocoa plantations of differing management intensity, but the ratio of phytophagous and entomophagous arthropods shifted in favour of phytophages as cocoa production intensified (Klein, *et al.* 2002). Also in Sulawesi, ant community composition in forest and cocoa agroforestry was found to be relatively similar, whereas assemblages of beetles were markedly different between forest and cocoa plantations (Bos *et al.* 2007). The same study also examined the impact of changes in canopy shade cover (as a surrogate for management intensification) and found that ant richness declined greatly with increasing modification of the habitat. This indicates that by maintaining components of natural systems in production systems, some biotic elements can be retained, but as the production system intensifies, these elements may be lost. It may be that by retaining critical elements of native systems in low-intensity farming systems, the habitat still provides the necessary resources for many native biota adapted to natural systems, thus keeping the habitat within the niche parameters of many taxa. However, it is also possible that in some cases time-lags between land-use change (e.g. from forest to plantation with forest elements) and local species extinctions may be masking eventual assemblage composition changes. Finally, botanical diversity and carbon sequestration were found to decline along a gradient of cocoa production intensification in Cameroon, indicating that less intensively managed systems are likely to provide both biodiversity and other ecosystem service benefits compared to more intensively managed systems in tropical regions (Herve and Vidal, 2008).

1.2.2.4 Frontier & intensive (relatively recent introduction of modern agriculture, with highly intensive management or land uses)

The introduction of intensive agriculture to regions previously dominated by native vegetation systems has a particularly deleterious impact upon biodiversity (Aratrakorn *et al.* 2006; Attwood *et al.* 2008 (Chapter 2 of thesis)). A sobering example of this phenomenon is the agricultural landscapes in south-eastern and south-western Australia. European-style agriculture was only introduced to Australia a little over 200 years ago (see Fig. 1.1b), but in that time has come to dominate terrestrial systems, with almost 60% of Australia's land area supporting some sort of agriculture (FAOSTAT, 2008). In the south-east, the dominance of agriculture is even greater, with 81% of New South Wales being under agricultural management in 1996/97 (Australian Natural Resources Atlas, 2007).

Such a rapid transition from a system consisting entirely of native vegetation systems to one dominated by European-style agriculture has wrought enormous changes on native ecosystems. A stark example is that of the grassy box woodlands of south-east Australia, which prior to European settlement covered large areas of what is now the wheat-sheep belt of the south-east (Prober *et al.* 1998). These woodlands, consisting of an open canopy structure of tree species and an understorey of native grasses and herbs, have been severely fragmented and degraded by cropping and livestock grazing and now cover a tiny fraction of their former extent

(Prober *et al.* 1998). Other vegetation types have also been severely depleted, such as temperate native grasslands, reduced to 1.25% of their pre-European extent (Fensham and Fairfax, 1997). In Queensland, clearing rates of native vegetation were approximately 1% of coverage per annum between 1956–1994 (Fensham and Fairfax, 2003), with *Acacia harpophylla* (Muell. ex Benth.) forests reduced from 91.3% of their original area in 1956 to just 8.1% in 1994 (Fensham and Fairfax, 2003). The cleared areas are now largely used as broad acre cropping, cattle pasture, or have been abandoned to *A. harpophylla* regrowth (Bowen *et al.* 2009).

The impacts of habitat loss, fragmentation and degradation on fauna, attributable to agriculture, have been similarly dramatic. In particular, the decline of woodland birds continues to be a cause for conservation concern in Australian landscapes (Ford *et al.* 2001). Several of the correlates of declines are attributable to agricultural development and management practices. For example, the clearing of native vegetation for agriculture tends to occur on the most productive land (Robinson and Traill, 1996), therefore leading to the disproportionate loss of vegetation types that occur on that land (Ford *et al.* 2001). The rapid decline of populations of a range of taxa dependent upon native vegetation in Australia and other ‘frontier’ regions may in part be due to the discrepancy between environmental stimuli (e.g. habitat loss) and adaptive response. Many research papers and media articles have discussed the idea of ‘extinction debt’, whereby species’ populations have a response lag between the land clearing event and the populations reaching a new equilibrium (Cowlishaw, 1999). Such thinking has led to predictions of a 40% reduction in bird species richness for the Mount Lofty Ranges near Adelaide, due to a 90% reduction in native vegetation cover compared to pre-European estimated cover (Ford and Howe, 1980).

Another, more insidious, threat to wildlife populations in these recently farmed landscapes is that of agricultural intensification, effectively analogous to the intensification of farming systems that has been so ecologically damaging in western Europe. This can manifest in many ways, including a transition from grazing to cropping systems, the replacement of dryland cropping with irrigated cropping (NSW DECC, 2006) and the removal of habitat resources such as paddock trees (Maron and Fitzsimons, 2007; Fischer *et al.* 2009).

Compared to the vast number of studies in European farming systems, research into the impacts on biodiversity of agricultural intensification in Australia are rare in the literature. However, interesting results are reported in two separate studies that examined ant assemblages in native vegetation compared to farmed systems. Both Majer (1977) and Lobry de Bruyn (1993) found that ant richness was much higher in the native compared to the agricultural system. Other studies around the world have reported results that support the idea that biodiversity may decline with increased intensity of agriculture in regions of recent agricultural arrival, in a manner similar to declines observed in regions of long-established agriculture (e.g. Lavelle and Pashanasi, 1989; Perfecto *et al.* 1997; Escobar, 2004).

Whilst much of Australia's biodiversity conservation focus has been on the reserve system and native remnants on private land, there is a growing realisation that the agricultural matrix (i.e. land used predominantly for production) is the dominant form of land cover in many regions, and exerts a strong influence on native remnants embedded in the matrix (Fischer *et al.* 2005; Attwood *et al.* 2009). The value of the agricultural matrix for biodiversity may also have been underestimated (Fischer and Lindenmayer, 2002; Haslem and Bennett, 2008a). This, coupled with the importance of elements of biodiversity in providing ecosystem services, has alerted a number of researchers to the importance of undertaking ecological research in multiple elements of agricultural landscapes (Bridle *et al.* 2007; Haslem and Bennett, 2008a; 2008b).

1.2.3 Agriculture and arthropods

The expansion, contraction, intensification and extensification of farming have enormous and increasingly well-documented effects on a vast range of taxa, ranging from iconic threatened bird species to human populations. However, the greatest changes to ecosystem function and resilience and the most profound alterations to ecosystem service provision may occur through the impacts of agriculture on arthropods, 'the little things that run the world' (Wilson, 1987). Arthropods are one of the oldest extant groups of organisms. For instance, the earliest dated fossil insect specimen is that of *Rhyniognatha hirsti* (Tillyard), which dates back some 400 million years (Engel and Grimaldi, 2004). Such antiquity also gives testament to the resilience and evolutionary tenacity of arthropods, indicating that they survived and proliferated after the Permian and Cretaceous mass extinctions (Kim, 1993). Today, arthropods are the most diverse group of organisms with over one million described species (May, 1988), with estimates including 30 million tropical arthropod species, based upon extrapolations of beetle richness from tropical tree species (Erwin and

Scott, 1980). Arthropods are also the most abundant multi-cellular organisms on the planet and constitute by far the greatest faunal biomass in tropical rainforest (Wilson, 1987). In addition to richness, abundance and evolutionary longevity, terrestrial arthropods are also known to inhabit a wide range of systems and habitat types—insects and other arthropods are found in caves (Howarth, 1983), deserts (Cloudsley-Thompson, 1975), high montane areas (Edwards, 1987) and other extreme environments (Edwards, 1987).

Some of the most intriguing aspects of arthropods in production systems are the roles they play in ecosystem processes, the extent to which they maintain or inhibit the delivery of ecosystem services and how arthropod-driven processes are affected by changes in arthropod richness, abundance, community composition and feeding-guild representation. The debate over how biological diversity influences and supports ecosystem function is complex and controversial, but there is no doubt that continued ecosystem function is dependent upon the persistence of multiple components of a biotic assemblage. Furthermore, agriculture is, to a great extent, dependent upon the effective functioning of ecosystem processes such as nutrient cycling, soil aggregation, water movement and waste decomposition (Daily, 1997).

Two of the main theories pertaining to the relationship between biodiversity and ecosystem function (and therefore ecosystem services) are the rivet hypothesis (all taxa in a system have some effect on ecosystem function, so to lose any may impact upon system function) and the redundancy hypothesis (that only a sub-set of species in a community are significant contributors to system processes) (Ehrlich and Ehrlich, 1981; Lawton and Brown, 1993; Naeem *et al.* 1995; Wolters, 2001). The issue of functional redundancy is of particular interest, as it implies that ecosystem function will continue in a relatively unimpaired manner as long as the functionally important taxa are retained, or if previously ‘redundant’ taxa step into a vacant role when a functionally important taxon is lost from a system. A review of the relationship between arthropod assemblages and ecosystem function is beyond the scope of this chapter or thesis, but a wide range of responses of various ecosystem processes to altered arthropod assemblage richness and composition has been reported in the literature. These range from increased function with increased assemblage richness (Slade *et al.* 2007; Letourneau *et al.* 2009), decreased function with increased assemblage richness (Finke and Denno, 2004) and increased function with increased interspecific functional dissimilarity (Heemsbergen *et al.* 2004).

From both ecological and agronomic perspectives, arthropods and agriculture are inextricably linked, from insect pests to their arthropod predators and parasitoids, and from the highly mobile pollinators and the relatively sessile soil organisms that break down organic matter and play such a vital role in the nutrient cycle. It is therefore unsurprising that the study of arthropods in agricultural landscapes has culminated in a wealth of literature addressing a wide range of issues and topics. However, the responses of arthropods to land-use transition and evolving management, the complex interactions between arthropods and their environment, the biogeographical and geopolitical differences in land use, and the intricate relationship between biotic assemblages and ecosystem processes indicate that we still have much to discover and describe.

1.3 Research focus of thesis

1.3.1 Overview of research rationale

The research focus and selected questions were driven by several factors. Firstly, agriculture is the dominant terrestrial land-use type both globally and in Australia, with projections indicating that it will continue to expand in global area to meet growing demands for food and biofuels (Millennium Ecosystem Assessment, 2005). Furthermore, continued agricultural expansion and fragmentation of indigenous vegetation means that non-agricultural habitats will become increasingly spatially juxtaposed with agricultural land use. As a result, the impacts and influence of agricultural expansion and development on biodiversity is likely to be an area that will command increasing policy, research and conservation attention. Consequently, this research was conducted in mosaic, mixed-land use agricultural systems, in an attempt to describe and explain how arthropod assemblages are stratified by different degrees of habitat modification and management intensification and consider what implications this may have for both conservation and ecosystem processes.

Secondly, given the increased dominance of agricultural land uses, there is a growing need to establish if there are reliable global generalisations we can make about responses of different elements of biodiversity to commonly occurring land-use types. Whilst there are many thousands of individual studies examining the responses of various aspects of biodiversity to a wide range of agricultural land-use and management scenarios, the responses are often complex and sometimes contradictory among different biotic assemblages, biogeographical regions and management practices. Whilst assessing each interaction between biodiversity and agriculture on an individual case-by-case basis is very informative, there is a need to look for broader and more general patterns in the responses of biodiversity to some of the more frequently occurring agricultural land-use change and management scenarios. Such generalisations, if found, would be of considerable importance for land managers and researchers in rapidly assessing the likely impact of land-use change or altered agricultural management practices. To do this I employed meta-analytical techniques to determine global trends for arthropod biodiversity in response to commonly encountered agricultural land-use change scenarios.

Thirdly, disturbance processes are known to have impacts on both within-taxon and within-assemblage morphological responses, such as body size and dispersal capability (Magura *et al.* 2006). Given that morphological traits are so intimately linked to life history traits, function and interspecific interactions, changes to among-assemblage morphology, such as body size (often linked to nutritional status of habitat, vulnerability to disturbance-related mortality and taxon reproductive strategies) and wing morphology (linked to dispersal capabilities and post-disturbance colonisation) can provide insights into the many ways in which agricultural land uses affect arthropods. In particular, I wished to examine if assemblage morphological traits differed among land uses, or if the close proximity, frequent juxtaposition and complex spatial arrangement of different land uses resulted in a more homogenous distribution of morphological traits across the landscape. Given that studies examining assemblage morphological traits along urban intensification gradients have sometimes found differing results for different taxa (e.g. Alaruikka *et al.* 2002), the consistency of morphological responses among different taxonomic groups, and why certain groups may display certain trait responses to disturbance are also important considerations that I explored in this study.

Fourthly, edge habitats constitute a relatively large proportion of mosaic agricultural landscapes and are known to influence assemblages of many taxa (including arthropods) in a variety of ways. This can include concentrations of taxa at habitat edges, the movement of taxa across or parallel to edges, and high rates of predation or competition at edges. The degree of contrast between the habitats or land uses that constitute an edge can also greatly influence the ease with which organisms can pass from one habitat to another, and so can help shape the structure and composition of assemblages across landscapes. In agricultural systems these factors can manifest in differences in assemblages between intensive cropping fields and neighbouring land uses that are less intensively managed and more structurally complex, and the movement of organisms between these two habitat types, with implications for functional issues such as predation and pest invasion and suppression. Two common features of Australian agricultural landscapes are native vegetation remnants (valued for conservation) and linear strips of grassy vegetation that separate cropping fields (generally not valued for conservation). In this study I seek to examine how the influence of edge habitat type (native remnant and linear strip) on assemblages within crops influence arthropod movement between crops and edge habitats, various aspects (e.g. taxonomic, morphological) of arthropod assemblage composition and how edge habitats may influence rates of pest predation.

There are also many knowledge gaps which need urgently to be filled in relation to biodiversity and ecosystem function/services in agricultural systems in ‘frontier’ regions (i.e. regions that have had a relatively short association with farming). Much of the research that has investigated biodiversity responses in relation to agriculture in ‘frontier’ regions has focussed on the changes to biotic assemblages as a result of transitions from native vegetation systems (often forest) to pastoral or cropping systems. By contrast, much of the research examining the value of agricultural systems or discrete components of such systems has been undertaken in regions with a long-historic association with agriculture (chiefly Europe). Where there have been some exceptions (such as studies on coffee plantations of varying management intensity in Latin America), the results have been very useful in indicating where agriculture may be able to contribute to biodiversity conservation and maintenance of ecosystem services. Conducting research in multiple agricultural land-use types and features in a region that has only been farmed for approximately the last 150 years will lead to insights regarding the responses of taxa to different land-use types, and in particular how taxa utilise the agricultural matrix.

Finally, terrestrial arthropods are sometimes overlooked in biodiversity research, perhaps owing to difficulties of taxonomy in many regions of the world. However, any such difficulties are offset by the importance of arthropods in driving ecological processes and their positive and negative interactions with agricultural production.

By examining arthropods, I aim to investigate how arthropod functional groups are affected by land-use change and transition, and distance to habitat edges and edge habitat type in fields of crops. I intend to discuss results in terms of potential ecosystem function implications and provide information to participating landholders that they consider to be of direct interest and relevance to their production practices.

1.3.2 Primary research questions

The primary research questions addressed in this thesis are:

1. What are the dominant drivers of agricultural change and how have the different global patterns of agricultural development impacted upon biological diversity?

2. How do abundance and richness of different arthropod taxa and feeding guilds respond to land-use change globally?

3. How and why do Formicidae populations and assemblages vary among different land uses in an agricultural landscape in Australia, and are these responses consistent with global patterns of abundance, richness and functional group representation?

4. Do body-size and morphological features of Araneae, Coleoptera and Formicidae differ among different land uses in an agricultural landscape?

5. How do arthropod assemblages of crops differ depending on whether the crop field is bordered by native woodland or a linear vegetation strip, and do assemblages change with distance from the crop edge?

6. Does the rate of pest-predation in cropping vary with adjacent habitat type and distance from the crop edge?

Question 1 was explored as part of this introductory chapter (see in particular sections 1.1.3, 1.2.1, 1.2.2 and Figs. 1.1a & 1.1b)—the other questions were investigated during three distinct research stages:

1. *Global overview*: a series of meta-analyses that assess the responses of multiple arthropod taxonomic groups and feeding guilds to agricultural land-use change and cropping management scenarios globally.
2. *Intensification gradient study*: a field study in southern Queensland that examines variation in arthropod biodiversity and assemblage morphological traits along a gradient of agricultural land-use intensification, from grazed native woodland remnants, through pastures, to cropping.
3. *Influence of edge habitat*: a field study in southern Queensland that examines how arthropod assemblages at crop edges and interiors are influenced by the presence of either an adjacent native remnant (woodland/grassland complex) or a linear grassy strip (separating the study crop from an adjacent crop).

1.4 Chapter summaries

Chapter 2 is a quantitative and qualitative literature review in the form of a series of meta-analyses that examine the responses of various arthropod taxa to a range of land-use comparison scenarios in the scientific literature. Using richness and abundance data from over 250 studies, I examined whether there are general trends in the responses of arthropod groups and feeding guilds to different mechanisms of agricultural intensification (both land-use change and altered cropping management). I investigated whether arthropod richness and abundance, at both taxonomic and functional group levels, differed between less intensive and more intensive land-use types. Furthermore, I sought to inform the land sparing versus wildlife-friendly farming debate (*sensu* Green *et al*. 2005) by indicating the points along a land-use intensification gradient where the greatest declines in biodiversity occur—for instance, is the majority of biodiversity lost in the land-use transformation from a native vegetation system to an agricultural land-use system, or during the management intensification transition from one agricultural land-use type to another?

Chapter 3 is a landscape-specific field examination of the trends identified in the meta-analysis, focussed on the responses of ant assemblages (such as abundance, richness, community composition) to a gradient of agricultural intensification. The field work was conducted in a mosaic agricultural landscape in southern Queensland, using three of the land-use categories included in the meta-analysis (thus allowing direct local testing comparisons of global response patterns), namely native woodland, pasture and cropping. Of particular interest were whether the different land-use types had distinct assemblages, whether assemblages at land-use interfaces contained different assemblages to those in the two bordering habitats, and whether the pasture or cropping treatments contained taxa that were not present in the woodland treatment. The results of the fieldwork were compared to global patterns of abundance, richness and functional group responses to different land-use types, derived from a series of meta-analyses.

Chapter 4 enhances the taxonomic comparisons of other chapters by examining another aspect of arthropod assemblages likely to be affected by land-use change and disturbance—body size and morphology. Research on patterns of arthropod assemblage body sizes in response to land-use disturbance/modification has indicated a range of responses. These include trends such as increases in small taxa in highly disturbed land-use types and a decrease in small taxa in late-successional habitats. Therefore, the rationale for this chapter was to determine how body-size/morphological attributes of three taxonomic groups responded to agricultural land-use types of differing degrees of disturbance. I examined a range of body size (for spiders, beetles and ants) and wing morphology (for beetles) metrics along the land-use intensification gradient described for Chapter 3. These taxa were selected as they are known to be sensitive to environmental changes and other studies have indicated a range of morphological responses to other disturbance processes (e.g. urbanisation). The main aims of the study were to examine if morphological traits relating to resource availability, reproductive strategies and dispersal differed among land uses of differing levels of disturbance/modification, or if the traits were uniformly distributed across the landscape. I also wished to examine if responses differed among different broad taxonomic groups. From these findings I sought to provide insights into the potential mechanisms that influence arthropod assemblage patterns in mosaic agricultural landscapes and examine if responses differed among different broad taxonomic groups.

Having explored how arthropod assemblages differ across multiple land-use types, **Chapter 5** focuses on the arthropod assemblages of one particular land-use type (cereal cropping), and in particular how the nature and extent of the neighbouring land use affects arthropod community composition at crop edges and some distance into the crop itself. I compared the arthropod assemblages of cropping edge and interior habitats that differed in the type of habitat that bordered the crops (native vegetation remnant compared to a linear grass strip or margin). I also investigated biodiversity-driven ecosystem service provision in crops bordered by different habitat types by examining predation rates of an agricultural pest at the crop edges and crop interiors with different adjacent habitat types. The majority of field margin research has been restricted to European systems, where the importance of semi-natural habitats for biodiversity and ecosystem service maintenance is well recognised. In Australia, the value of such habitats is less certain. This chapter explores the potential for a habitat feature often considered to be classically European to provide similar biodiversity and ecosystem service benefits in a region where agricultural establishment has been relatively recent. This included investigating if linear vegetation strips have biodiversity value or a potential ecosystem service role, when compared to the edges of more extensive blocks of indigenous habitat.

Chapter 6 synthesises the chief findings and conclusions of each chapter and summarises how this research contributes to increased knowledge and understanding of the drivers of arthropod assemblages in complex agricultural landscapes, the impacts that agricultural management can have on arthropod taxa and the implications for the ecosystem processes that they help drive. Limitations of the study are discussed, as are the management and policy implications of the research. Finally, some potential avenues for future research are highlighted.

Chapter 2

Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management?

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Approximate percentage contributions of authors as follows:

Attwood – 90%, Maron – 5%, House – 2.5%, Zammit – 2.5%.

2.1 Introduction

A key focus in applied ecology and conservation is understanding the impact of agricultural intensification on biological diversity, environmental health and the sustainability of production (Tilman, 1999; Tilman *et al.* 2001). Factors such as increased human population pressure and demand for food, and shifts from small-scale independent producers to large-scale agri-businesses have all helped drive the intensification of global agriculture (Ormerod *et al.* 2003; Tudge, 2004). Intensified management practices contributed to an increase in global cereal yield per hectare of over 240% from 1961 to 2005 (FAO, 2006). During the same period, the area of cereal harvest in developing countries increased by 126% and the area under oil crops in the developing world rose by over 200% (FAO, 2006). The recent surge in demand for biofuels is also leading to increased pressure to clear native forests for palm oil and sugar cane production (Birdlife International, 2007; Carter *et al.* 2007). Given that global food demand is anticipated to more than double between 2005 and 2050 (Green *et al.* 2005), it is unlikely that the intensification and expansion of agriculture will abate in the short to medium term.

The impact of agricultural intensification on biological diversity is of particular concern (McLaughlin and Mineau, 1995; Benton *et al.* 2003), with intensively managed agriculture recognised as a major cause of global biodiversity loss (Ormerod *et al.* 2003). Practices such as clearing of native vegetation, agrochemical application, monocropping and overgrazing by livestock have all been implicated in the loss of biological diversity (Stoate *et al.* 2001; Tilman *et al.* 2001). Agriculture impacts on biodiversity via two broad processes: the conversion of natural systems into production land, and the intensification of management on land that is already human-dominated and highly modified (Foley *et al.* 2005; Donald and Evans, 2006). Examples abound of the impacts of both processes on biodiversity. Aratrakorn *et al.* (2006) reported a 60% reduction in avian species richness when Indonesian forest was converted to palm plantations and Sala *et al.* (2000) identified land-use change as the greatest threat to biodiversity in the 21st Century. The intensification of land management is believed to have caused the Corn Bunting *Miliaria calandra* L., a formerly abundant farmland bird in the UK, to decline by 89% between 1970 and 2001 (Gregory *et al.* 2004). In addition, there are biogeographical patterns to agricultural impacts on biodiversity. The majority of the transformation of native into agricultural systems is occurring in the developing world (Green *et al.* 2005). This translates into a considerable proportion of broad land-use change occurring at lower latitudes, where species richness is generally higher. Despite such well-documented impacts, landscapes dominated by agriculture can often be dynamic and complex mosaics of different land uses and habitats, capable of supporting an array of biological communities (Benton *et al.* 2003).

Arthropods constitute the vast majority of known species on the planet (Wilson, 1992), and some groups (e.g. ants) are known to be sensitive and reliable indicators of environmental change (Andersen and Majer, 2004). As such, arthropods may be useful in describing responses of a range of biological and environmental metrics to altered land use and shifting management practices. Many groups of arthropods are also important drivers of ecosystem functions such as nutrient cycling, pest control, pollination and soil structure maintenance (Petchey and Gaston, 2002; Tscharntke *et al.* 2005a). A potential impairment of ecosystem function due to arthropod diversity decline could have serious implications for primary production (Cardinale *et al.* 2004), and there are increasing concerns regarding the sustainability of ecologically simplified farming systems, dependent upon high levels of artificial inputs (Altieri, 1999).

Agriculture can affect arthropod assemblages in many ways. For instance, the transformation of native systems into pasture or cropping land usually has a dramatic effect on vegetation structure and composition, and habitat connectivity (Dunn, 2004). Such land-use conversion can result in considerable changes to the structure of arthropod communities (Decaens *et al.* 2004) and arthropod species interactions (Armbrecht and Perfecto, 2003). Furthermore, the direct and indirect impacts of agricultural management and inputs can also have a pronounced effect on arthropod diversity and abundance (Thorbek and Bilde, 2004), with concomitant implications for ecosystem function and key ecosystem services.

In this study, we sought to determine whether arthropod biodiversity displays globally consistent response trends to agricultural intensification. Although many individual studies show that biodiversity declines with agricultural expansion and intensification, we wished to establish if this pattern was evident across a range of regions, habitats, agricultural systems and taxa. To do this, we undertook a series of meta-analyses of the responses of arthropods to a range of agricultural land-use and management intensification scenarios presented in the scientific literature. Although there are various criticisms of meta-analytical approaches, not least the ‘file-drawer’ phenomenon (Roberts *et al.* 2006), whereby studies that find a significant effect are more likely to be published and cited, they remain a valuable means of gaining a quantitative overview of the often vast array of published results on a given topic.

Meta-analyses are often used for examining several studies focusing on a very specific question, particularly in the fields of medicine and psychology (Gurevitch and Hedges, 1993). However, our primary research premise, that agricultural intensification affects arthropod richness and abundance, is rather broad, and our information base comprises a wide range of habitats and methodologies. Consequently, we elected to use a range of meta-analytical approaches that allows comparisons of results across analytical techniques. Each represented a trade-off between the statistical robustness of the technique and the number of studies that could be considered using a particular approach.

The paper aims to address the following questions relating to both broad scale land use and cropping management:

(i) Is arthropod richness and abundance greater in native vegetation than in agricultural production land? (ii) Is there a general trend in arthropod richness and abundance along a land-use intensification/anthropogenic disturbance gradient from native vegetation to intensive cropping? (iii) Do patterns of richness and abundance among land uses differ among different feeding guilds and taxonomic groups? (iv) Are the identified patterns in richness and abundance consistent between meta-analytical techniques of differing robustness and sophistication?

2.2 Methods

2.2.1 Arthropod measures

Given the complexity of arthropod assemblages, the sheer wealth of literature examining arthropods in different land-use types, and our pragmatic concerns about keeping the paper to a manageable scale, we opted to omit some groups from our study. Highly mobile taxa (including Diptera, Hymenoptera (excluding Formicidae) and Lepidoptera), which we thought may be more influenced by landscape-scale factors than land-use type (Dauber *et al.* 2005), were omitted from the analyses (although see Schweiger *et al.* 2005, who found that taxa with different dispersal capabilities responded similarly to land-use intensity, albeit at a 4 x 4 km landscape rather than the patch scale generally used in this study). Whilst this obviously limits the scope of the study slightly, the authors feel that a sufficiently broad range of taxa are included to provide some insights into the general responses of arthropods to land-use change, particularly at the patch scale.

We used two basic measures of arthropod response to land-use and management intensification: abundance and richness. All were readily available in the studies sampled. Abundance was determined as the total number of individual organisms collected in a land-use treatment in a given study, whilst richness was the total number of different taxonomic or morphological units recorded in each treatment. For studies that only presented data in terms of diversity indices, we followed the approach of Bengtsson *et al.* (2005) and included them only in vote-counting analyses.

In order to determine feeding guild responses, we assigned taxa to one of three feeding guilds where applicable: predators, decomposers and herbivores. Feeding guild classification followed that described in the paper under examination (where possible), or a range of literature (e.g. Moran and Southwood, 1982). For some taxa, classification was straightforward (e.g. predators for Araneae), but for others was more ambiguous. Ultimately, we adopted a relatively conservative approach; for instance, we classified Formicidae as omnivorous, even though some taxa are predatory. Again, on occasions where the paper had already classified taxa according to a feeding guild, or where a specific taxon (e.g. at genus level) was predominantly predatory, herbivorous, etc., we favoured that categorisation.

2.2.2 Land-use comparisons

We divided abundance and richness responses to agricultural intensification into two categories: responses to broad land use and responses to different types of crop management. The former contrasted arthropod responses among land uses commonly found in mosaic landscapes: native woodland, native grassland, introduced/improved pasture and cropping, each representing a point along a gradient of increasing anthropogenic disturbance. The latter compared conventional cropping systems (e.g. tilled, pesticide-treated) with reduced-input alternatives such as no-till or organic systems. To reduce the complexity of land-use categorisation, we compared arthropod abundance and richness between the following land-use types:

1. Native vegetation (NV) compared to agricultural land (Ag);

2. Wooded native vegetation (WNV) compared to introduced/improved pasture (IP);
3. Native grassland (NG) compared to introduced/improved pasture (IP);
4. Introduced/improved pasture (IP) compared to cropping (C);
5. Reduced input cropping (RIC) compared to conventional cropping (CC).

Each land-use category contained the following land-use types from the literature:

WNV—woodland, forest, heathland, scrub (excluding restoration plantings);

NG—native grassland, unimproved meadows, native savannah and steppe.

NV—This category was compared to Ag (agricultural land – see below). In many cases, it was the WNV from WNV:IP comparisons or NG from NG:IP comparisons. It also applied when any native system was compared to cropping in a study.

Ag—pasture, cropping and horticulture (not forestry or silviculture). For studies where WNV or NG were compared to IP and C, Ag was calculated as the mean abundance or richness in IP and C for the vote-counting and proportional analyses;

IP—fertilised and/or introduced sown pastures (grazed and ungrazed). Included sown pasture on former arable land;

C—any cropped system that was not part of the RIC:CC comparison (i.e. IP:C, NV:Ag);

RIC—cropping that featured at least one of several management options: no/reduced-till, unfertilised, reduced-pesticide/herbicide/fungicide, organic, rotation, intercropping, mulched;

CC—conventional cropping that provided direct 'intensive' comparison in studies that investigated RIC management. Therefore, RIC and CC were paired comparisons.

2.2.3 Literature search

We sourced published literature relating to arthropods in agricultural landscapes up to September 2007 using the internet-based scientific literature search engine Scopus (www.scopus.com), searching the database using a series of keywords (Appendix B.1). Keywords were divided into thirty-five taxonomic terms representing our target taxa and fourteen land-use/management-related terms. The choice of search taxa was based upon reference to standard texts (e.g. Naumann, *et al.* 1991) and the authors' experience of which arthropods may be important in agricultural landscapes. We then paired each taxonomic term with each land-use term as the basis for our search (e.g. search conducted using 'Araneae' and 'crop'). Finally, we undertook further searches in general internet search engines to locate 'grey literature' (Roberts *et al.* 2006). Although unlikely to have detected all relevant studies, we feel that the techniques used were sufficient to obtain a substantial and representative sample. We located 259 studies (Appendix B.2) that presented data for arthropod abundance and/or richness in at least one of the chosen land-use comparisons. We then subjected the studies to three different meta-analytical techniques: a vote-counting method, a proportional approach and (where data allowed) a fixed-effects/random effects meta-analysis following the procedure in Gurevitch and Hedges (1993). The three approaches varied in their robustness and the level of detail that they demanded from the data in a given study.

2.2.4 Data extraction and analysis

We extracted abundance and richness data from the results section text, tables of means and other numerical data, appendices, graphs and figures from each of the papers.

In some studies, we found several treatments in a comparison that matched the categories forming our investigation. For example, a woodland (WNV) site being compared to three different pasture (IP) treatments (*WNV1*, *IP1*, *IP2* and *IP3*, where numerical suffix refers to order in which *IP* site is reported in the study results) could be treated as a single comparison (*WNV1* compared to *IP1* or *WNV* compared to mean of *IP1*, *2* & *3*) or as three distinct comparisons (*WNV1* compared to *IP1*, *WNV1* compared to *IP2*, etc). Several authorities have highlighted the importance of maintaining independence between comparisons within studies (e.g. Gurevitch and Hedges, 1993; Bengtsson *et al.* 2005). Similar issues arose regarding the independence of data from the same locality over multiple time periods and whether different taxonomic groups from the same study could be treated independently. We therefore devised a set of decision rules to deliver a consistent and conservative approach to addressing potential independence issues:

1. Our chief aim was to examine taxon responses and feeding guild responses (as well as combined responses) among different land uses. Therefore, we opted to follow the lead of Bengtsson *et al*. (2005) and treat different taxa within the

same study as independent samples. Where possible, and in the overwhelming majority of cases, we analysed taxa at the taxonomic level of order or family.

2. For all studies that presented means, standard errors/standard deviations/confidence limits and sample sizes we used only paired land-use comparisons, in order to avoid potential inaccuracies from pooling or averaging standard errors or standard deviations. For example, for arthropod richness in WNV1 compared to IP1, IP2 and IP3, we used WNV1 richness compared to IP1 richness. In this instance, we would omit data from IP2 and IP3. Similarly, when means, variances and sample sizes were presented for multiple time-periods, we used the final time-period only (again to avoid calculating an incorrect pooled or averaged standard error or standard deviation) (Gurevitch and Hedges 1993). We deviated from this rule only for studies that examined arthropod responses to a particular disturbance event in cropping (e.g. a tillage event, pesticide application). In this instance, we selected the first sample following the disturbance event in order to capture the immediate assemblage response. To be as consistent as possible, we also used the means from these approaches for the vote-counting and proportional techniques.
3. Some studies did not include the data necessary for conducting a fixed/random-effects meta-analysis, and therefore were only suitable for the vote-counting and proportional analyses (see below). In such instances, we were able to include data for multiple samples of land-use types (e.g. WNV1 compared to the mean of IP1, IP2 and IP3) and the mean of all time periods for a sample. We waived this latter rule only for studies examining arthropod responses to a particular disturbance event in cropping, following the approach described above and selecting only the data immediately following the disturbance event.

2.2.5 Data analysis

All studies were included in the vote-counting and proportional analyses. Those containing measures of variance and sample sizes were also analysed using the fixed/random-effects meta-analysis.

For the vote-counting analysis, we attributed a (+) or (-) to each land-use comparison, depending on whether the arthropod abundance or richness was greater in the less intensive or the more intensive land-use/management regime. This resulted in a total of (+) and (-) scores for each comparison, the frequency of which we compared to a random distribution of responses using the binomial sign test (Siegel and Castellan, 1988). We conducted the sign tests using SPSS Version 14.0 for Windows.

For the proportional analysis, we transformed the abundance and/or richness data for each land-use comparison in a study into the proportion of abundance or richness in the less intensive compared to the more intensive land uses. We then calculated the average proportional abundance or richness across all studies. If the resulting average proportion in the less intensive land use was greater than 0.5, then the richness or abundance was greater in the less intensive land-use/management regime, indicating both the direction and the magnitude of the average effect size. Conversely, if the resulting average was less than 0.5, then richness or abundance was greater in the more intensive land use. To examine whether higher proportions of abundance or richness were found in the less intensive treatments across studies, we calculated 95% confidence intervals on the mean value for each across-study land-use comparison. If the 95% confidence intervals did not include 0.5, then we considered richness or abundance to differ between the land-use categories.

For the ‘formal’ meta-analysis, we employed both the fixed-effects and random-effects models as appropriate. For each land-use category comparison, we tabulated mean abundance and/or species richness, the standard deviation and the sample size for each study. The pooled SD for each comparison was then calculated following the methods in Bengtsson *et al*. (2005). We then calculated Hedges’ d effect size and the variance of d for each study (Gurevitch and Hedges, 1993; Rosenberg *et al*. 2000). We divided the effect size by the pooled SD and multiplied by a term that adjusts for small sample size (Gurevitch and Hedges, 1993). A positive d value indicated greater abundance or richness in the less intensive land use, and a negative value greater abundance or richness in the more intensive land use.

To assess the average effect size across the studies, we combined the effect sizes for each individual study in a fixed-effects model (Gurevitch and Hedges, 1993; Rosenberg *et al*. 2000). If the average effect size $E{+}{+}$ was greater than zero, this indicated that abundance or richness was higher in the less intensive land use for a given comparison. The upper and lower limits of the 95% confidence intervals were also established and we considered the effect size was significant if the 95% C.I. limits of the overall effect size $E{+}{+}$ did not include zero (Gurevitch and Hedges, 1993; Rosenberg *et al*. 2000; Bengtsson *et al.* 2005). The fixed-effect model also calculated a homogeneity test statistic *Q*. Where *Q* was significant, the effect sizes comprising *E*++ were heterogeneous, differing among the studies. In this event, we recalculated the average effect size *E*++ using a random effects model that assumes random variation among studies in a class (Gurevitch and Hedges, 1993). The random-effects model also calculated the 95% confidence intervals and *Q*. We conducted all meta-analytical calculations using MetaWin (Rosenberg *et al.* 2000).

2.3 Results

2.3.1 Arthropod richness

2.3.1.1 Combined taxa richness

Richness was greater in less intensive compared to more intensive land uses when all arthropod data were combined (Fig. 2.1a & 2.1d; Table 2.1). All three meta-analytical techniques reported significantly greater arthropod richness in native vegetation (NV) compared to agricultural land (Ag). We found similarly consistent results for the other land-use comparisons, with significantly greater arthropod richness in the less intensive land use for wooded native vegetation compared to pasture (WNV:IP), native grassland compared to pasture (NG:IP), pasture compared to cropping (IP:C) and reduced-input cropping compared to conventional cropping (RIC:CC) (Figure 2.1a; Table 2.1).

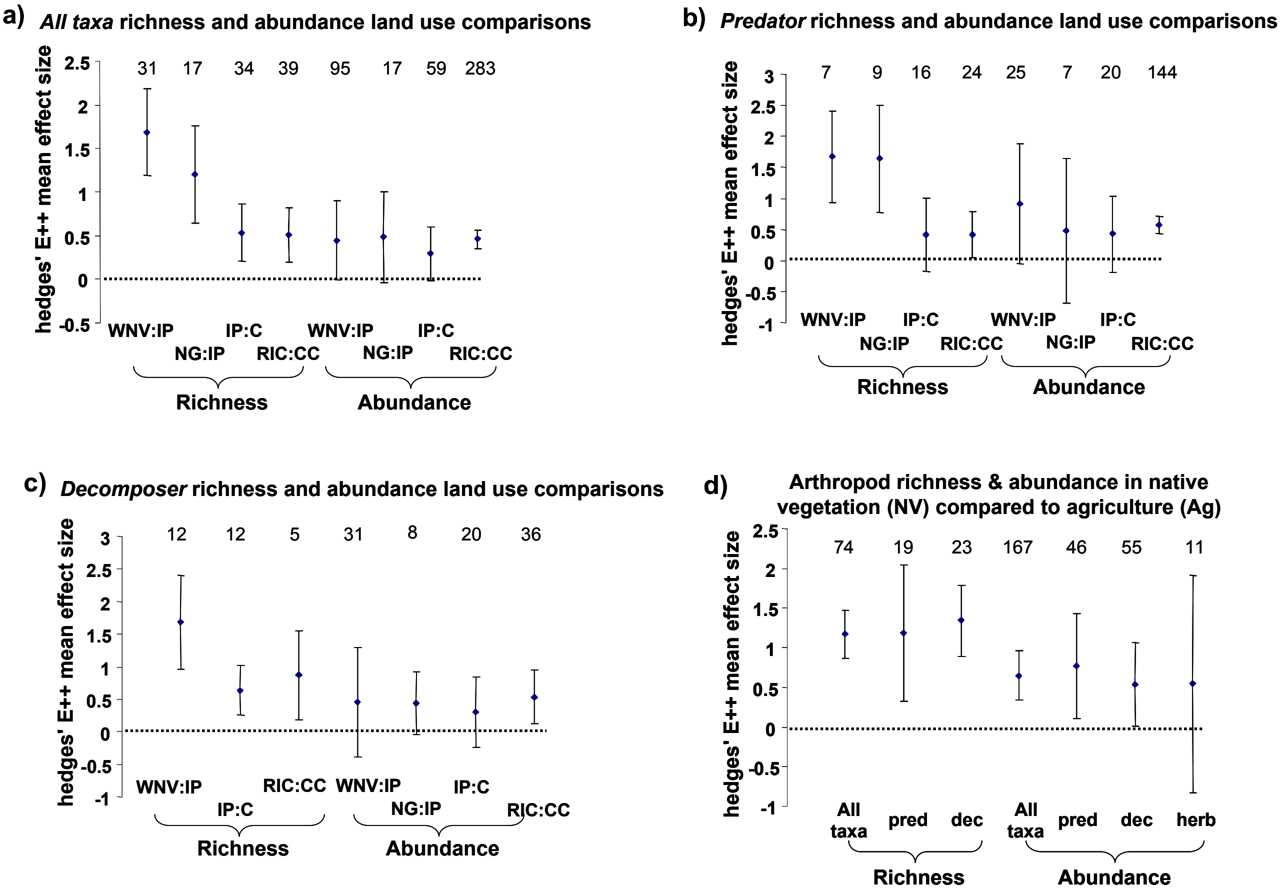

Fig. 2.1.

The Hedges' *E*++ average effect size (mean effect size averaged across all studies in a land-use comparison) for fixed and random effects meta-analyses of arthropod abundance and richness responses for various land-use comparisons (+/- 95% C.I.). Figs. 2.1 (a), (b) & (c) depict the responses of all taxa combined, predators and decomposers, respectively for multiple land-use comparisons. Fig. 2.1 (d) depicts the abundance and richness responses in native vegetation compared to agricultural land for all taxa, predators, decomposers and herbivores. The dashed line indicates the point at which richness/abundance are equal between the two land-use comparisons. Comparisons where the 95% C.I.s do not cross zero are considered to exhibit significantly greater richness or abundance in the less intensive land-use type (α = 0.05). The number above the data points is the number of different taxa analysed for each land-use comparison.

Abbreviations: **WNV:IP** = wooded native vegetation compared to improved/introduced pasture; **NG:IP** = native grassland compared to improved/introduced pasture; **IP:C** = improved/introduced pasture compared to cropping; **RIC:CC** = reduced-input cropping compared to conventional cropping; pred – predators; dec – decomposers; herb – herbivores.

Table 2.1. Combined arthropod and feeding guild richness results for vote-counting, proportional and fixed/random effects meta-analyses for land-use and cropping management comparisons. Vote-counting/binomial sign test columns contain number of studies for each comparison (percentage of studies that found greater arthropod richness in less intensive land use in parentheses). Proportional analysis columns contain the richness proportion in the less intensive land use averaged across all studies, +/- 95% confidence intervals. The fixed/random-effects meta-analysis columns contain the Hedges' *E*++ (the mean effect size averaged across all studies in a land-use comparison) +/- 95% confidence intervals, Q heterogeneity statistic and number of studies used in each comparison.

* P = <0.05. ** = significant among-study heterogeneity (where Q was significant for fixed-effects meta-analysis, random effects meta-analysis was used).

NV:Ag = native vegetation compared to agriculture; **WNV:IP** = wooded native vegetation compared to improved/introduced pasture; **NG:IP** = native grassland compared to improved/introduced pasture; **IP:C** = improved/introduced pasture compared to cropping; **RIC:CC** = reduced input cropping compared to conventional cropping.

		Binomial sign test		**proportional meta-analysis**			**fixed effects/random effects meta-analysis**			
		N studies (% > in less intensive land use)	Signif. (P value)	mean proportion in less intensive land use	+/- 95% C.I.	ratio of richness in less intensive compared to more intensive land use	Hedges' *E*++ (average effect size)	+/- 95% C.I.	Q	N
All taxa	NV:Ag	173 (81)	<0.001*	0.62*	0.03	1.62	1.17*	0.30	114.0**	74
	WNV:IP	85 (79)	<0.001*	0.62*	0.04	1.60	1.69*	0.5	40.24	31
	NG:IP	27 (85)	0.001*	0.62*	0.05	1.64	1.20*	0.56	19.57	17
	IP:C	73 (69)	0.001*	0.57*	0.03	1.33	0.54*	0.34	43.87	34
	RIC:CC	132 (67)	<0.001*	0.55*	0.02	1.20	0.51*	0.31	37.55	39
predators	NV:Ag	45 (82)	<0.001*	0.64*	0.07	1.79	1.19*	0.86	15.17	19
	WNV:IP	21 (95)	<0.001*	0.70*	0.01	2.30	1.67*	0.74	5.76	7
	NG:IP	12 (100)	<0.001*	0.65*	0.07	1.84	1.64*	0.86	9.64	9
	IP:C	32 (66)	0.071	0.54	0.05	1.19	0.42	0.59	25.09**	16
	RIC:CC	66 (62)	0.64	0.55*	0.04	1.23	0.41*	0.37	29.61	24
decomposers	NV:Ag	43 (86)	<0.001*	0.64*	0.05	1.81	1.34*	0.54	37.77**	23
	WNV:IP	20 (100)	<0.001*	0.64*	0.08	1.77	1.68*	0.72	11.57	12
	NG:IP	5 (100)	0.063	0.75*	0.14	3.02	N/A	N/A	N/A	N/A
	IP:C	18 (72)	0.096	0.59*	0.05	1.44	0.64*	0.39	9.77	12
	RIC:CC	18 (78)	0.031*	0.56*	0.05	1.29	0.87*	0.68	6.50	5
herbivores	NV:Ag	18 (50)	1	0.55	0.12	1.23	N/A	N/A	N/A	N/A
	WNV:IP	10 (30)	0.344	0.50	0.19	0.99	N/A	N/A	N/A	N/A
	NG:IP	5 (60)	1	0.50	0.03	1.01	N/A	N/A	N/A	N/A
	IP:C	3 (100)	0.25	0.60*	0.10	1.54	N/A	N/A	N/A	N/A
	RIC:CC	7 (29)	0.453	0.43	0.13	0.76	N/A	N/A	N/A	N/A

For both quantitative analytical techniques, the difference in richness between the less intensive and the more intensive land use was greatest in the comparison between native and agricultural systems. This pattern was particularly pronounced for the random-effects meta-analysis, where the average effect size was much greater between WNV:IP (Hedges' $E{+}{+} = 1.69 \pm 0.5$, df = 30) and NG:IP (Hedges' $E{+}{+} = 1.2 \pm 0.56$, df = 16) than between IP:C (Hedges' $E{+}{+} = 0.54 \pm 0.34$, df = 33) and RIC:CC (Hedges' $E{+}{+} = 0.51 \pm 0.31$, df = 38) (Fig. 2.1a; Table 2.1). This indicates that the differences in arthropod richness between native systems and agricultural systems are greater than those between different categories of agricultural land use.

2.3.1.2 Feeding guild richness

The results for predatory taxa were very similar to those for the combined taxa, with all analytical techniques indicating greater richness in the less intensive land uses for NV:Ag, WNV:IP, NG:IP and RIC:CC (Fig. 2.1b & 2.1d; Table 2.1). However, we found there was no significant difference in predator richness between improved/introduced pasture and cropping (IP:C) for all three analyses (Fig. 2.1b; Table 2.1). We detected elements of this trend in individual taxa, such as spiders, which displayed significantly greater richness in WNV:IP for all analyses, and exhibited no differences in richness between IP:C (Table 2.2).

We calculated that decomposer richness responses were similar overall to the combined and predatory taxa results (Fig. 2.1c & 2.1d; Table 2.1). Richness was greater in the less intensive land use for NV:Ag, WNV:IP and RIC:CC for all three techniques and greater in the less intensive land use for IP:C for two of the three approaches.

We did not find the same clear decrease in richness of herbivores with increasing land-use intensity that we found for combined taxa, predators and decomposers. Insufficient studies were available to use the fixed/random-effects meta-analysis, and we found only one instance where there was significantly greater herbivore richness in a less intensive land-use type using the other techniques (IP:C using the proportional analysis, see Table 2.1). We detected no other significant differences between land-use types.

2.3.2 Arthropod abundance

2.3.2.1 Combined taxa abundance

We found greater combined arthropod abundance in native vegetation than agricultural land (NV:Ag) on average for all three analyses (Fig. 2.1d; Table 2.3). However, our fixed/random-effects meta-analysis reported no difference in overall arthropod abundance between WNV:IP, NG:IP and IP:C (Fig. 2.1a). Results for these land-use comparisons were similarly equivocal for the vote-counting and proportional techniques, with only WNV:IP showing significantly greater abundance in the less intensive land-use type using these two approaches (Table 2.3) and greater abundance in pasture than cropping for the proportional approach. This suggests that arthropod abundance responds less consistently to land uses of differing management intensity than arthropod richness. Conversely, we found considerable concordance among the techniques in finding significantly greater arthropod abundance in reduced-input compared to conventional cropping (RIC:CC) (Fig. 2.1a; Table 2.3).

2.3.2.2 Feeding guild abundance

Both the random-effects and the proportional meta-analyses indicated significantly greater predator abundance in native vegetation than agricultural land (Fig. 2.1d; Table 2.3). We also found significantly greater predator abundance in reduced-input compared to conventional cropping (RIC:CC) (Fig. 2.1b; Table 2.3). The predatory taxa spiders, carabids, coccinellids, neuropterans and staphylinids also exhibited significantly greater abundance in reduced-input compared to conventional cropping (Table 2.4). We obtained mixed results for predator abundance in the other land-use comparisons (Fig. 2.1b; Table 2.3).

We found that decomposers tended to exhibit a similar response to predators, with significantly greater abundance in reduced-input compared to conventional cropping (RIC:CC) and significantly greater abundance in native vegetation compared to agriculture (NV:Ag) found in all analyses (Fig. 2.1c & 2.1d; Table 2.3). Again, we found mixed results for the other land-use comparisons (Fig. 2.1c; Table 2.3).

In contrast to the results of the combined data, predators and decomposers, herbivore abundance differed little between the land-use categories. There were no differences in herbivore abundance among any of the broad land-use comparisons (NG:Ag, WNV:IP, NG:IP & IP:C) and only one of three analyses found greater herbivore abundance in reduced-input compared to conventional cropping (Fig. 2.1d; Table 2.3). Analyses of chrysomelids, curculionids and homopterans supported these findings (Table 2.4).

2.3.3 Analytical technique

Results from different meta-analytical approaches were largely consistent for both arthropod richness and abundance. The vote-counting approach reported significant differences in 45% of comparisons (55% for richness, 35% for abundance), the fixed/random-effects approach found significant differences in 63% of comparisons (93% for richness, 39% for abundance) and the proportional approach delivered significant differences in 70% of comparisons (75% for richness, 65% for abundance).

Table 2.2. Taxonomic richness results for vote-counting, proportional and fixed/random effects meta-analyses for land-use and cropping management comparisons. Vote-counting columns contain percentage of studies that found greater richness of focal taxon in less intensive land use (binomial sign test not conducted due to typically small sample sizes). Proportional analysis columns contain the richness proportion in the less intensive land use averaged across all studies (+/- 95% confidence intervals). The fixed/random-effects meta-analysis columns contain the Hedges' *E*++ (the mean effect size averaged across all studies in a land-use comparison) (+/- 95% confidence intervals). * P = <0.05. NV:Ag = native vegetation compared to agriculture; WNV:IP = wooded native vegetation compared to improved/introduced pasture; IP:C = improved/introduced pasture compared to cropping; RIC:CC = reduced input cropping compared to conventional cropping.
– denotes insufficient studies to conduct analyses.

Taxa	**NV:Ag**			**WNV:IP**			**IP:C**			**RIC:CC**		
	% of studies where richness > in less intensive land use	mean proportion in less intensive land use	Hedges' *E*++	% of studies where richness > in less intensive land use	mean proportion in less intensive land use	Hedges' *E*++	% of studies where richness > in less intensive land use	mean proportion in less intensive land use	Hedges' *E*++	% of studies where richness > in less intensive land use	mean proportion in less-intensive land use	Hedges' *E*++
Acari	80	0.61 (0.10)*	–	–	–	–	–	–	–	–	–	–
Araneae	93	0.66 (0.07)*	1.28 (0.64)*	100	0.72 (0.12)*	1.65 (1.01)*	73	0.60 (0.13)	2.19 (2.44)	50	0.56 (0.05)*	0.20 (0.51)
Carabidae	78	0.61 (0.14)	–	–	–	–	38	0.49 (0.09)	–	74	0.55 (0.04)*	0.75 (1.10)
Chilopoda	80	0.73 (0.18)*	–	–	–	–	–	–	–	–	–	–
Collembola	–	–	–	–	–	–	83	0.59 (0.06)*	–	80	0.55 (0.07)	–
Diplopoda	100	0.74 (0.07)*	–	–	–	–	40	0.59 (0.14)	–	–	–	–
Formicidae	80	0.61 (0.05)*	1.28 (0.54)*	82	0.62 (0.08)*	1.75 (2.26)	67	0.63 (0.10)*	–	90	0.58 (0.04)*	–
Isoptera	83	0.63 (0.27)	–	80	0.58 (0.31)	–	–	–	–	–	–	–
Scarabaeidae	89	0.60 (0.04)*	1.43 (1.00)*	82	0.60 (0.06)*	1.83 (1.35)*	–	–	–	–	–	–
Staphylinidae	100	0.76 (0.13)*	–	–	–	–	71	0.55 (0.04)*	–	46	0.51 (0.03)	-0.06 (0.61)

Table 2.3. Combined arthropod and feeding guild abundance results for vote-counting, proportional and fixed/random effects meta-analyses for land-use and cropping management comparisons. Vote-counting/binomial sign test columns contain number of studies for each comparison (percentage of studies that found greater arthropod abundance in less intensive land use in parentheses). Proportional analysis columns contain the abundance proportion in the less intensive land use averaged across all studies, +/- 95% confidence intervals, and the ratio of abundance in less intensive compared to more intensive land use. The fixed/random-effects meta-analysis columns contain the Hedges' *E*++ (the mean effect size averaged across all studies in a land-use comparison) +/- 95% confidence intervals, Q heterogeneity statistic and number of studies used in each comparison.

		Binomial sign test		**proportional meta-analysis**			**fixed effect/random effects meta-analysis**			
		N studies (% > in less intensive land use)	Signif. (P value)	mean proportion in less intensive land use	+/- 95% C.I.'	ratio of abundance in less intensive compared to more intensive land use	Hedges' *E*++ (average effect size)	+/- 95% C.I.'	Q	N
All taxa	NV:Ag	320 (64)	<0.001*	0.61*	0.03	1.53	0.65*	0.31	239.24**	167
	WNV:IP	189 (63)	<0.001*	0.61*	0.04	1.55	0.44	0.45	158.63**	95
	NG:IP	33 (61)	0.296	0.55	0.06	1.20	0.48	0.52	20.26	17
	IP:C	134 (55)	0.261	0.55*	0.05	1.23	0.29	0.31	74.39	59
	RIC:CC	539 (70)	<0.001*	0.59*	0.02	1.43	0.46*	0.10	385.20**	283
predators	NV:Ag	88 (58)	0.165	0.59*	0.06	1.43	0.77*	0.65	37.11	46
	WNV:IP	55 (62)	0.105	0.64*	0.08	1.77	0.91	0.96	25.24	25
	NG:IP	10 (50)	1	0.55	0.11	1.23	0.48	1.16	6.97	7
	IP:C	55 (49)	1	0.50	0.07	1.00	0.43	0.61	23.31	20
	RIC:CC	274 (78)	<0.001*	0.63*	0.02	1.69	0.58*	0.14	146.57	144
decomposers	NV:Ag	88 (70)	<0.001*	0.64*	0.06	1.77	0.536*	0.531	110.34**	55
	WNV:IP	57 (75)	<0.001*	0.68*	0.08	2.08	0.46	0.84	67.70**	31
	NG:IP	10 (70)	0.344	0.61*	0.09	1.58	0.44	0.47	7.50	8
	IP:C	36 (61)	0.243	0.58	0.10	1.37	0.30	0.54	21.91	20
	RIC:CC	73 (66)	0.01*	0.57*	0.06	1.34	0.53*	0.41	72.80**	36
herbivores	NV:Ag	38 (50)	1	0.52	0.10	1.08	0.54	1.37	20.57**	11
	WNV:IP	22 (45)	0.832	0.52	0.13	1.07	0.27	3.22	5.15	5
	NG:IP	5 (60)	1	0.44	0.15	0.78	N/A	N/A	N/A	N/A
	IP:C	14 (57)	0.791	0.59	0.14	1.41	N/A	N/A	N/A	N/A
	RIC:CC	114 (45)	0.303	0.51	0.04	1.03	0.26*	0.22	99.45**	63

* P = <0.05. ** = significant among-study heterogeneity (where Q was significant for fixed-effects meta-analysis, random effects meta-analysis was used).

NV:Ag = native vegetation compared to agriculture; **WNV:IP** = wooded native vegetation compared to improved/introduced pasture; **NG:IP** = native grassland compared to improved/introduced pasture; **IP:C** = improved/introduced pasture compared to cropping; **RIC:CC** = reduced input cropping compared to conventional cropping.

Table 2.4. Taxonomic abundance results for vote-counting, proportional and fixed/random effects meta-analyses for land-use and cropping management comparisons. Vote-counting columns contain percentage of studies that found greater abundance of focal taxon in less intensive land use (binomial sign test not conducted due to typically small sample sizes). Proportional analysis columns contain the abundance proportion in the less intensive land use averaged across all studies (+/- 95% confidence intervals). The fixed/random-effects meta-analysis columns contain the Hedges' *E*++ (the mean effect size averaged across all studies in a land-use comparison) (+/- 95% confidence intervals).

Taxa	**NV:Ag**			**WNV:IP**			**IP:C**			**RIC:CC**		
	% of studies	mean proportion	Hedges' *E*++	% of studies	mean proportion	Hedges' *E*++	% of studies	mean proportion	Hedges' *E*++	% of studies	mean proportion	Hedges' *E*++
Acari	56	0.55 (0.09)	0.52 (0.63)	56	0.51 (0.10)	–	67	0.58 (0.14)	–	69	0.55 (0.07)	0.62 (0.26)*
Araneae	52	0.54 (0.08)	1.35 (1.30)*	63	0.60 (0.11)	1.73 (1.83)	81	0.67 (0.11)*	0.796 (1.445)	79	0.62 (0.03)*	0.62 (0.26)*
Carabidae	46	0.60 (0.18)	-0.05 (1.43)	–	0.49 (0.25)	–	18	0.40 (0.16)	–	73	0.6 (0.04)*	0.72 (0.38)*
Chilopoda	85	0.73 (0.16)*	0.73 (2.11)	90	0.80 (0.14)*	0.76 (2.61)	–	–	–	40	0.49 (0.17)	–
Chrysomelidae	–	–	–	–	–	–	–	–	–	40	0.46 (0.18)	–
Coccinellidae	–	–	–	–	–	–	–	–	–	84	0.70 (0.09)*	0.69 (1.06)
Collembola	50	0.48 (0.18)	0.16 (1.28)	–	–	–	67	0.63 (0.14)	0.964 (1.223)	72	0.56 (0.04)*	0.80 (0.53)*
Curculionidae	–	–	–	–	–	–	–	–	–	50	0.48 (0.24)	–
Dermaptera	38	0.41 (0.30)	-1.06 (2.33)	–	–	–	–	–	–	64	0.69 (0.16)*	0.06 (0.25)
Diplopoda	86	0.71 (0.17)*	0.88 (0.41)*	90	0.72 (0.18)*	-0.58 (2.66)	67	0.72 (0.24)	–	–	–	–
Formicidae	69	0.61 (0.10)*	0.82 (0.67)*	52	0.51 (0.12)	-0.11 (0.87)	58	0.64 (0.15)	0.294 (1.136)	80	0.62 (0.07)*	0.55 (0.40)*
Homoptera	25	0.36 (0.17)	–	–	–	–	–	–	–	43	0.50 (0.05)	0.36 (0.40)

Isopoda	55	0.58 (0.24)	0.45 (0.95)	83	0.67 (0.35)	–	–	–	–	–	–	–
Isoptera	87	0.71 (0.08)*	0.13 (1.92)	83	0.72 (0.17)*	0.04 (2.90)	25	0.41 (0.34)	–	–	–	–
Neuroptera	–	–	–	–	–	–	–	–	–	80	0.69 (0.15)*	–
Orthoptera	33	0.43 (0.18)	0.025 (2.55)	–	–	–	–	–	–	63	0.56 (0.27)	–
Scarabaeidae	81	0.60 (0.13)	0.20 (0.95)	64	0.61 (0.13)	0.25 (0.74)	63	0.51 (0.26)	–	71	0.57 (0.23)	–
Staphylinidae	67	0.57 (0.20)	–	100	0.67 (0.17)*	–	33	0.43 (0.11)	–	71	0.58 (0.07)*	0.72 (0.36)*
Thysanoptera	–	–	–	–	–	–	–	–	–	62	0.53 (0.08)	0.02 (0.66)

* P = <0.05. **NV:Ag** = native vegetation compared to agriculture; **WNV:IP** = wooded native vegetation compared to improved/introduced pasture; **IP:C** = improved/introduced pasture compared to cropping; **RIC:CC** = reduced input cropping compared to conventional cropping.

– denotes insufficient studies to conduct analyses.

2.4 Discussion

All three meta-analytical approaches found significantly higher richness in the less intensive land use for all land-use and management comparisons. These findings upheld our expectation that arthropod richness would decline as land-use and management intensity increased. This trend appeared to be consistent across a wide range of regions, biomes, management systems and taxa, with the exception of herbivorous taxa. A decline in biological richness may therefore be a general response (for most groups) to both the conversion of native vegetation into agricultural systems and the intensification of agricultural management. However, we found the response of arthropod abundance to land-use intensification somewhat more variable. Overall arthropod abundance was significantly greater in native vegetation than agricultural land and in reduced-input cropping than in conventional cropping in all three meta-analyses. We obtained broadly similar results for predators and decomposers, but not herbivores. For the other land-use comparisons, we found few differences in abundance between the less intensive and more intensive land uses.

In addition to exploring arthropod responses to land-use type, this review also illustrates the capacity for different meta-analytical techniques to accommodate studies depending on the amount of information provided in published research. For instance, the fixed/random-effects method requires the most information (mean, variance and sample size) for a study to be included in the analysis. Whilst the most rigorous approach, it is also the most exclusive – numerous studies that we included in the vote-counting and proportional approaches were necessarily omitted from the fixed/random-effects approach due to a lack of information. Whilst the vote-counting and proportional approaches are rapid and convenient options, they have evident limitations. Vote-counting only gives the direction of the trend between treatments, offering no indication of the magnitude of difference. The proportional approach accounts for the magnitude of difference, but includes no provision for variance or sample size. This approach may therefore also tend to report a higher rate of type-1 errors. However, the ease of calculation makes it a useful ‘first-pass’ precursor to a more formal meta-analysis.

2.4.1 Arthropod richness

We observed a general decline in arthropod richness with increasing land-use and management intensity. The broad process of agricultural intensification from intact, indigenous vegetation associations, through fragmented mixed-agricultural landscapes, to highly intensive, monotypic grazing or cropping systems can lead to a reduction in biological diversity via a range of impacts and threats. For instance, clearing native woody vegetation radically alters and simplifies habitat structure and composition, changes resource availability, unravels complex ecological associations, increases soil insolation and temperature, changes nutrient cycles, reduces niche availability, destabilizes microclimates and greatly alters soil structure and attributes (Gade, 1996; Barros *et al.* 2004). The introduction of domestic stock impacts further through soil compaction, accelerated nutrient inputs, cessation of plant regeneration, altered botanical composition and simplified sward structure (Abensperg-Traun *et al.* 1996; Reid and Hochuli, 2007). A change from pasture to cropping may simplify the structure and composition of the system still further, particularly if the land-use change is from a relatively heterogeneous grazing system to a monocultural cropping system. Common cropping management practices such as deep tillage, agro-chemical application and mechanical harvesting may all serve to increase the frequency and severity of disturbance regimes in the new system (Thorbek and Bilde, 2004). The change from wooded native vegetation to pasture arguably represents the greatest degree of structural vegetation contrast between our focal land uses. Accordingly, the loss in richness from wooded native vegetation to pasture was the largest of all land-use comparisons.

There are a number of possible explanations for higher arthropod richness in less intensive land uses. Areas of low to moderate modification/intensification (such as native vegetation and pasture) are likely to have greater habitat complexity, due in part to less exposure to intensive and uniform management than many cropping systems. Therefore, in complex land uses, niche opportunities are likely to be numerous, whilst fewer niches may be available in structurally and compositionally less-complex systems. (Bardgett, 2002; Willis *et al.* 2005). Consequently, opportunities for coexistence through resource partitioning, are likely to be reduced in simplified systems, resulting in lowered species richness. More complex habitat composition and structure may allow greater access to a wider range of alternative food resources (Langellotto and Denno, 2004), thus supporting more omnivorous and non-obligate predatory taxa. Increased predator density in areas of moderate to low disturbance (Landis *et al.* 2000) may also increase overall community richness through predator-mediated coexistence (Shurin and Allen, 2001).

Another potential explanation for greater richness in less-disturbed habitats is that in frequently or intensely disturbed environments, community composition cannot progress beyond early pioneer stages. This frequent ‘resetting of the successional clock’ in areas of high disturbance results in environments that favour early successional species, while disadvantaging later successional species (Büchs *et al.* 2003). If the disturbance is sufficiently severe and frequent (such as in intensive cropping), it could feasibly exclude all but the most ruderal of taxa, thus potentially leading to overall lower species numbers.

That the herbivore feeding guild did not show the characteristic richness decline we observed for combined taxa, predators and detritivores is surprising. As herbivore diversity would be expected to increase with plant diversity (Siemann *et al.* 1998), we expected herbivore richness to be highest in heterogeneous land uses such as native vegetation. However, the finding may be related to the small sample sizes of studies (e.g. WNV:IP, n = 10 studies for vote-counting and proportional analyses) which also precluded the use of the fixed/random-effects analysis.

The results from all three analytical approaches indicate that the reduction in arthropod richness from a native (wooded or grassland) system to an agricultural one (improved pasture or cropping) is greater than that from one agricultural system to another (improved pasture to cropping or reduced-input cropping to intensive cropping). The structural and compositional differences between complex native systems and simplified agricultural systems could represent a threshold of habitability for many species, whereas the differing degrees of modification in already altered agricultural habitats may represent less of an obstacle for the remaining taxa. Thus, many biological components of a native system are lost when it is transformed into an agricultural system. Further richness declines occur when the agricultural system is further modified (e.g. pasture to cropping), but the losses are of a smaller magnitude, possibly due to the tolerance of the remaining taxa to more frequent and intense disturbances.

2.4.2 Arthropod abundance

Arthropod abundance decreased from native vegetation to agricultural land for combined taxa, predators and, to a lesser extent, decomposers. Many of the potential causal factors could be attributed to the land-use change process discussed for richness decline above, and have also been extensively explored by Langellotto and Denno (2004). The natural enemies hypothesis predicts that vegetatively and structurally complex habitats should support greater predator abundance than simplified habitats (Andow, 1991). Our results support this view. More complex habitats may offer greater and more varied food resources, allow refuge from intra-guild predation and cannibalism, provide favourable microclimates and enable access to alternative food resources (Langellotto and Denno, 2004).

We also found statistically greater abundance of predatory, decomposer and combined arthropod taxa in reduced-input cropping compared to conventional cropping. The reduced intensity, frequency and scale of physical disturbances (e.g. tillage) could lead to lower mortality and post-disturbance emigration of predatory arthropods in reduced-input cropping systems (Stinner and House, 1990; Thorbek and Bilde, 2004), whilst a reduction in the use of pesticides, or a move towards pest-specific chemicals, could reduce non-target arthropod mortality (Hummel *et al.* 2002). Arable weeds have also been reported as an important resource and source of habitat heterogeneity that may benefit arthropods (Kromp, 1989). Arthropods, including predators of phytophagous species, have been observed to increase in ‘weedy’ crops (Brooks *et al.* 2005). Therefore, a reduction in general herbicide application could increase weed prevalence in cropping systems, resulting in increased habitat heterogeneity and greater arthropod abundance. The reduction of chemical inputs to cropping systems can also have positive impacts on adjacent non-cropped habitats (Boutin and Jobin, 1998), improving the condition of refugial habitats and potentially increasing arthropod immigration into cropping systems (Bell *et al.* 2002).

For native grassland compared to pasture and pasture compared to cropping, there were only two instances of significantly greater abundance in the less intensive land use (both using the proportional analysis). There are various possible explanations for this apparent lack of response. In some instances, there may have been species turnover changes in assemblage composition between land-use comparisons, but little change in overall abundance. As can be seen from the feeding guild and taxonomic results (Tables 2.3 & 2.4), different taxa may respond to agricultural disturbance and management in various ways (Fuller *et al.* 2005). For instance, as disturbance increases, generalists may increase in abundance, whereas specialists may decline (Tejeda-Cruz and Sutherland, 2004), leading to assemblage change with relatively unchanging net abundance.

As with richness, herbivores did not exhibit the same abundance responses between native vegetation and agriculture (NV:Ag) and reduced-input and conventional cropping (RIC:CC) as combined taxa, predators and decomposers (with the sole exception of increased abundance in RIC compared to CC for the random-effects approach). For instance, only 45% of our studies found greater herbivore abundance in reduced-input compared to conventional cropping and 75% of studies found greater homopteran densities in agricultural land compared to native vegetation. It is interesting to compare these responses to those reported by Tonhasca and Byrne (1994) whose meta-analysis suggested that increased crop diversity reduced herbivorous arthropod abundance.

2.4.3 Practical implications

Arthropods are one of the most important groups in the delivery of vital ecosystem services to agriculture (Goehring *et al.* 2002). Increased arthropod richness may have utilitarian benefits given that arthropods are linked to a range of ecosystem functions, and a reduction in arthropod biodiversity may be expressed in reduced ecological function or impairment of ecosystem processes (Naeem *et al.* 1994; Wolters, 2001). Although there is debate over the extent to which biological diversity and the effective functioning of ecosystem processes are entwined (Tilman, 1999; Tscharntke *et al.* 2005a), and evidence that increased predator diversity can lead to reduced herbivore suppression (Finke and Denno, 2004), a precautionary approach should be taken to the decline of functionally significant taxa, such as arthropods. Their conservation and retention in production landscapes should therefore be a high priority. Arthropods in production-dominated systems are also an intrinsic component of the food chain of species with a high conservation profile such as birds. For example, declines in insect larvae are considered a major factor in the population declines of birds such as the Grey Partridge *Perdix perdix* L. (Gates and Donald, 2000) and the provision and management of arthropod habitat in production systems is central to the recovery of this species (Thomas *et al.* 2001).

An increase in arthropod abundance, particularly predatory arthropods, in reduced-input cropping could also have desirable outcomes for agricultural production (Östman *et al.* 2003). For instance, predatory arthropod and pest invertebrate populations in cotton under integrated pest management (IPM) and non-IPM cotton were investigated by Bambawale *et al.* (2004), who found fewer predators and greater bollworm damage in non-IPM pesticide plots. Spiders in particular are valued for their role as predators of within-crop pests and there are numerous experimental examples of their impacts on some pest species in agricultural systems (Marc *et al.* 1999; Sunderland and Samu, 2000). We found that spider abundance was significantly greater in reduced-input compared to conventional cropping for the proportional and random-effects analyses, indicating that reduced cropping management intensity may result in positive pest control outcomes.

The non-linear biodiversity decline along our land-use intensification gradient (Figure 2.1a) may offer an insight into the effects of two prominent strategies for addressing the conservation of wild nature in agricultural landscapes (see Green *et al.* (2005), Fig. 3b). 'Wildlife-friendly farming' proposes that reduced intensity of farming practices (through the provision of semi-natural habitats and reduction in management inputs such as pesticides) can increase the biodiversity value of production land (McNeely and Scherr, 2002; Balmford *et al.* 2005) whilst simultaneously reducing external impacts on non-farmed habitat. However, Green *et al.* (2005) indicate that in some instances such practices may result in yield reduction, which in turn may require a greater area of land to be under agricultural production to compensate for any production deficit. Alternatively, intensive agriculture leads to higher yields, thus reducing the need to transform natural systems into production land ('land sparing') (Balmford *et al.* 2005; Green *et al.* 2005). Our findings indicate that natural systems contain the majority of arthropod richness, and that the bulk of biodiversity is lost when native vegetation is converted to agriculture. Therefore, where considerable native vegetation remains, its retention should be a priority conservation strategy. However, in relatively low intensity compared to high intensity agricultural land uses (IP:C, RIC:CC - Fig. 2.1a) richness was greater in the less intensive land use. This would indicate that where little native vegetation remains, such as in intensively farmed landscapes, the inclusion of pastures and low input cropping, is likely to be an effective conservation strategy.

Chapter 3

Ant diversity decline and habitat preference along an agricultural intensification gradient

3.1 Introduction

Agriculture has been identified as a serious threat to biological diversity from local to global scales via processes such as habitat loss, fragmentation, land-use change and intensive land management (Matson *et al*. 1997; Tomich *et al*. 1998; Reidsma *et al*. 2006). Remnants of native habitat in agricultural landscapes have often been portrayed as distinct from, and embedded in, a homogenous matrix of production land, consistent with the theories of island biogeography and metapopulation dynamics (Revilla *et al*. 2004). This has sometimes resulted in a rather narrow perspective of native remnants as a beleaguered source of dwindling biological diversity, with the agricultural matrix depicted as biologically impoverished and a source of exogenous threatening processes (Haila, 2002). Whilst there is evidence to support this view in some instances and for some taxa (Cook *et al*. 2002; Branch *et al*. 2003; Driscoll, 2005), examples abound where the relationship between land use and the persistence and spatio-temporal distribution of taxa is far less straightforward (e.g. Cook *et al*. 2002; Driscoll, 2005). Production landscapes often support diverse biological assemblages, especially where the landscape consists of a mosaic of land-use types undergoing different levels of disturbance (Benton *et al*. 2003; Eggleton *et al*. 2005). Areas of high heterogeneity may provide a rich array of habitats and resources for a wealth of taxa that address both their spatial and temporal requirements (Law and Dickman, 1998; Delgado and Moreira, 2000; Holland *et al*. 2005; Clough *et al*. 2007).

In many regions, a multiplicity of land uses, habitats and other landscape features can occur in a fine-grained and intricate spatial arrangement within a relatively small geographical area. This arrangement is often accompanied by, and frequently due to, a complex history of land-use change and management. This is the case in much of eastern Australia, where a mosaic of native vegetation types, many managed for millennia using traditional aboriginal techniques such as periodic burning (Flannery, 1994; Bowman, 1998), have been impacted in recent times (c. last 200 years) by European-derived agricultural practices (Henzell, 2007). These practices initially included grazing of stock and clearing of native systems (Griffiths, 2002) coupled with a cessation of traditional fire management (Ward *et al*. 2001a). More recently, management has included broad-scale mechanical land clearing, pasture improvement and both dryland and irrigated cropping (Landsberg and Wylie, 1988; Cogger *et al.* 2003; Maron and Fitzsimons, 2007).

Establishing the distribution, habitat preferences and requirements of particular taxa in such areas can be a daunting task. However, whether management objectives are biodiversity conservation, the maintenance of critically important taxa for the delivery of ecosystem goods and services such as nutrient cycling, or the control of pest species, understanding the distributional relationships between taxa and the production environment is of considerable importance (Holland *et al.* 2005; Blackshaw and Vernon, 2006).

The study of arthropods has become increasingly popular as a means for landscape ecologists and conservation biologists to investigate the complexities of agricultural land-use change and its implications for biological communities (Duelli *et al.* 1999). This interest is reflected, for instance, in the scientific literature; since 1985, the number of journal papers referring to arthropods and insects as indicators or in an agricultural context has greatly increased (Fig. 3.1).

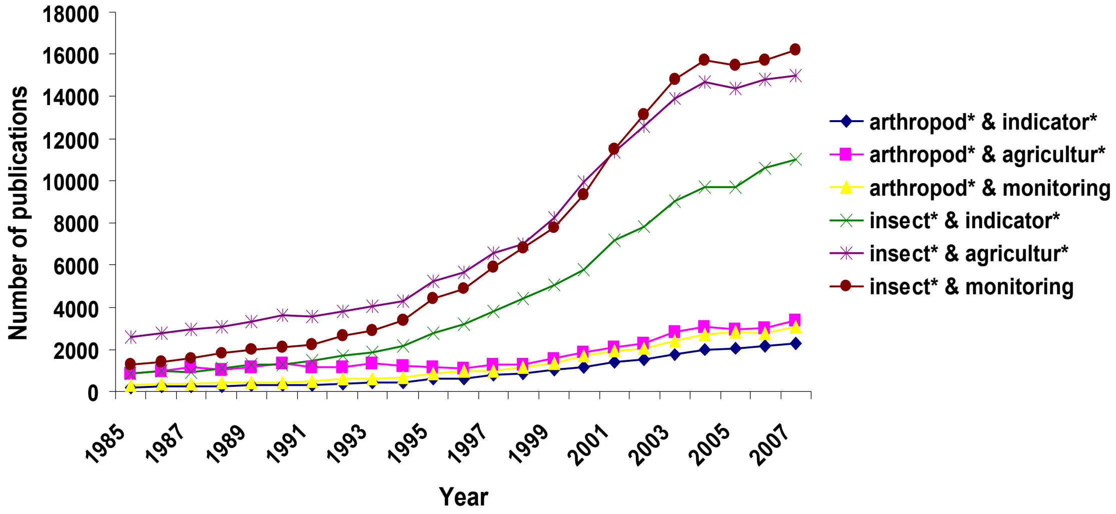

Figure 3.1. Number of journal articles found by Google Scholar that contained the search combinations “arthropod* & agricultur*”, “arthropod* & indicator*”, “arthropod* & monitor*”, “insect* & agricultur*”, “insect* & indicator*”, “insect* & monitor*” in the body of the text for the years 1985-2007 (accessed 19th June 2009).

This increasing focus on arthropods may reflect greater awareness that many taxa contribute to the functioning of a range of ecosystem processes (Holland *et al.* 2005). Some groups are also known to exhibit reliable responses to a range of environmental and management stimuli, rendering them useful ‘indicators’ of system change, condition and trajectory (Andersen and Majer, 2004). Advances in taxonomy and rapid identification techniques are also leading to more rapid processing of large samples, thus easing a number of pragmatic obstacles to the study of arthropods (Oliver and Beattie, 1996; Andersen and Majer, 2004). Formicidae (ants) is one group that has received considerable attention in a variety of ecological research situations around the world (Andersen and Majer, 2004). They play important roles in production landscapes as ecosystem engineers (Folgarait, 1998), predators (Abera-Kalibata *et al.* 2007) and through the association of some species with homopteran pests (Buckley and Gullan, 1991). Ants are also near-ubiquitous in terrestrial landscapes (Ratchford *et al.* 2005), particularly in Australia, occurring in great abundance and with great diversity (Hoffmann and Andersen, 2003). Whilst Dauber *et al.* (2005) are correct in stating that single indicator taxon studies may be limited in their usefulness, there is sufficient evidence to suggest that ants in particular remain an excellent group to use for assessing management actions and ecosystem changes (Underwood and Fisher, 2006).

I aimed to investigate whether, and how, ant assemblages changed along a gradient of increasing agricultural intensification. I considered this question at two different scales: i) globally, using data from published studies that examined ant abundance and/or richness and ant functional group composition in native and anthropogenic habitats in agricultural landscapes, and ii) locally, via field sampling of livestock-grazed remnants of native woodland (least disturbed), grazed pastures/grassland, and cereal cropping (most disturbed) in a sub-tropical eastern Australian landscape. For the field study, in addition to examining ant fauna in the core of each land-use type, I wished to examine changes in ant assemblages at the interfaces between the patches of different land uses. Edges make up a considerable proportion of both fragmented native systems and multiple-land use agricultural systems, and are an increasingly abundant physical feature of landscapes undergoing ongoing fragmentation. As such, they are thought to play important roles in shaping biological communities through environmental changes at the habitat boundaries, and also via the interactions between the taxa frequenting edges and those attempting to cross them (Dauber and Wolters, 2004; Ries *et al.* 2004). The ability or willingness of organisms to cross from one habitat to another can be influenced by the degree of contrast between neighbouring land uses, with ‘hard edges’ (high degree of contrast) often being less permeable to organism movement than ‘soft edges’ (low degree of contrast) (Duelli *et al.* 1990; Ries *et al.* 2004). Such relationships have implications for the ability of some organisms to traverse and occupy a landscape that consists of a) a mosaic of different land uses with differing structures and disturbance levels, and b) consequent differing degrees of contrast between neighbouring land-use types (and hence an array of ‘hard’ and ‘soft’ edges). In this study I examined if ants that were found in the core of a particular land use were also evident at the edge of that land use where it interfaced with a neighbouring land use. Edges can also support edge-specialist taxa that tend to favour edge habitats. This can be due to favourable physical conditions such as habitat structure or the concentration of resources along edges (Ries *et al.* 2004). Consequently, I also wished to discover if any ant taxa were present predominantly at edge habitats where two land uses interfaced, but largely absent from the land-use core areas.

Specifically, I addressed the following research questions:

1. Do ant richness, diversity, abundance and assemblage composition vary along a gradient of increasing land-use intensification/disturbance?
2. Do interfaces between land uses have a distinct ant assemblage, or one intermediate between those of the two adjacent land uses?
3. Do ant functional groups vary among different land-use types?
4. Are particular morphospecies of ants influenced by particular physical and structural characteristics of the habitat and landscape in the field study?
5. Are the abundance/richness/functional group responses of ants to agricultural land use at the local scale (field study) in southern Queensland consistent with predictions based on the meta-analyses?

3.2 Method

3.2.1 Literature analyses

I adopted two analytical approaches to determining whether broad global generalisations could be drawn regarding the impacts of agriculture on ant diversity, abundance and assemblage composition:

a) A series of formal meta-analyses that examined abundance and richness responses among several land-use comparisons: native vegetation compared to agriculture, wooded native vegetation compared to improved pasture, improved pasture compared to cropping and reduced-input cropping compared to conventional cropping (for further details of the methods employed and the studies included, please see Attwood *et al.* 2008 and Chapter 2 of this thesis).

b) A quantitative but non-statistical assessment of the relative functional group composition of wooded native vegetation compared to agricultural land, using data from field comparisons contained in the scientific literature. To do this I searched Web of Science and Scopus for papers using the search terms "Formicidae and agri*", "Formicidae and pasture*" and "Formicidae and crop*". I compiled papers that compared ants in wooded native vegetation to those in an agricultural land-use type. I then retained only those that provided a list or other account of the number of individuals per taxon of the ants that occurred in each land use (see Appendix C.2). Each taxon (where possible) was then assigned to one of eight functional groups (Cold Climate Specialists, Cryptic Species, Dominant Dolichoderinae, Generalised Myrmicinae, Hot Climate Specialists, Opportunists, Specialist Predators and Subordinate Camponotini), using a range of authorities to assist in the classification (such as Hoffmann and Andersen, 2003, but see Appendix C.2 for complete functional grouping references). This functional grouping approach to classifying ants was developed in order to increase the utility of ants as bioindicators of environmental stress, and to better capture the likely responses of ant community dynamics to disturbance (and other stimuli) in the absence of taxon-specific responses (Andersen, 1995; Hoffmann and Andersen, 2003; Majer *et al.* 2004). The approach is designed to predict responses at both biogeographical scales and responses to disturbance and group interactions at individual sites. For greater detail of the biogeographical, disturbance and inter-group interactions of each functional group classification, see Hoffmann and Andersen, 2003, Table 1.Tropical Climate Specialists were not included in the analysis, as they a) did not occur in the field study area, and therefore could not be used in the literature/field responses comparison, and b) occurred very infrequently or in low numbers compared to other functional groups, and were therefore very unlikely to skew the results by being omitted (TCS represented 0.04% of the total abundance of all ants in the literature analysis). For each study I calculated the percentage contribution that each functional group made to the overall assemblage composition for both the native vegetation and agricultural land treatments. This resulted in a ‘functional group profile’ for each land-use type in each study. I then calculated the mean percentage contribution that each functional group made across all studies for both native vegetation and agricultural land, and plotted the results.

3.2.2 Study area and Study sites

The field study was performed in the rural areas around Pittsworth, Felton, Cambooya and Mt Tyson, to the immediate west and south-west of Toowoomba in south-east Queensland, Australia (420–560 m a.s.l., 27°26′–47′S, 151°33′–51′E) (See Fig. 3.3). The climate is sub-tropical, with a mean annual daily maximum temperature of approximately 24.5 °C and mean annual precipitation of 700 mm, the majority of which falls from October to March (Bureau of Meteorology, 2007). The area forms part of the eastern Darling Downs, a region to the west of the Great Dividing Range, situated within the Condamine River basin. The area was first discovered by Europeans in 1827, first settled in 1840, and opened up to commercial sheep production in 1847 (Vandersee, 1975). Since then, the region has seen the expansion of wheat production and cattle for dairying and beef, with the region now supporting a range of summer and winter cereal crops (e.g. wheat, sorghum), beef and dairy, and sheep, pig and intensive poultry production (Vandersee, 1975; Australian Bureau of Statistics, 1994; 2008a; 2008b. Fig 3.2).

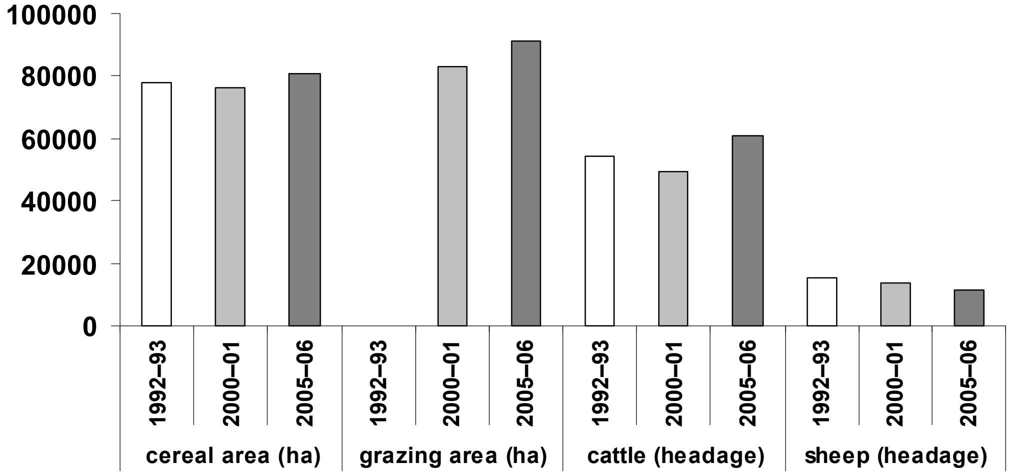

Fig. 3.2. Agricultural statistics summed for Cambooya Shire, Clifton Shire and Pittsworth Shire, of i) total area of land under cropping (ha), ii) total area of land under stock grazing (ha), iii) total number of cattle, and iv) total number of sheep and lambs for 1992–93, 2000–01 and 2005–06 (source data Australian Bureau of Statistics 1994; 2008a; 2008b). Grazing area data unavailable for 1992–3.

The soils are black vertisols and the remaining hill slope vegetation is cattle-grazed open woodland, largely consisting of canopy species *Eucalyptus orgadophila* (Maiden & Blakely) and *Eucalyptus crebra* (F. Muell.), with understorey components including a variety of native and introduced grasses, forbs and scattered shrubs. Vegetation types for woodland were restricted to the Regional Ecosystems 11.8.5 (*E. orgadophyla* open woodland), 11.8.4 (*E. melanophloia* woodland) and 11.9.2 (*E. melanophloia* ± *E. orgadophyla* woodland) (as per Sattler and Williams, 1999).

Three broad land-use or land-cover types were examined: grazed remnants of native woodland, grazed pasture/grassland and cereal crops. The woodlands are almost entirely restricted to mid-upper hill slopes and hill tops, on soils generally considered unsuitable for agriculture. Woody vegetation has been removed from other parts of the landscape through a combination of land clearing and ring-barking, with a current woody vegetation cover of approximately 11–20 % in the Condamine region (of which the study area forms a part), compared to estimated pre-European cover (Accad *et al*. 2008). No lower area size limit was set for the inclusion of woodland patches, as small areas of native woodland are a predominant feature of the region. The size of woodland patches ranged from 7 ha to approximately 100 ha. All woodland remnants were grazed by cattle during or close to the time of sampling, which is a standard agricultural practice in this region.

Pasture/grassland sites were areas of formerly grassy woodland systems that had been historically cleared of wooded native vegetation. Since clearing, the grasslands had been subjected to various histories of fertilisation, reseeding and stocking rates, but all consisted of a combination of exotic and native grass species and all were grazed during or close to the time of sampling.

Cropping sites were restricted to those used for cereal cropping (barley, oats, wheat or sorghum), but owing to prolonged drought (and therefore reduced cropping activity) this included both standing winter crops and stubble from the previous summer’s crop. The area of cropping fields ranged from 3.3 to 67 ha, with a mean area of 25 ha (± 21 ha S.D.).

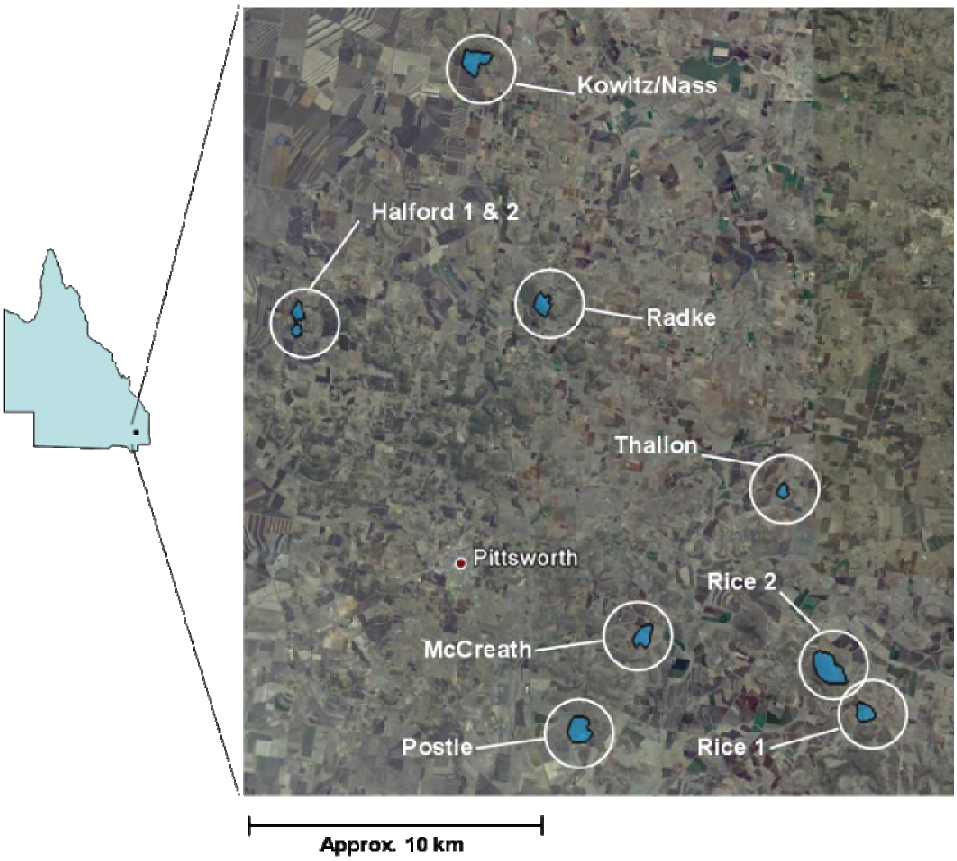

Fig. 3.3. Map of study area in southern Queensland. Each blue polygon is a sampling site of three core land uses and two habitat interfaces (see Fig. 3.4). Each site identified by landholder surname (and number if more than one site sampled under same tenure). Property where sampling sites destroyed by cattle not depicted. 'Pittsworth' is nearest town.

3.2.3 Experimental design

The spatial arrangement of the landscape mosaic in the region followed a consistent pattern: woodland remnants invariably remained on higher, rockier ground, segueing into grassland/pastures on the mid-slopes, which in turn abruptly adjoined cropping land on the lower slopes and deeper soils. This allowed a block design for the study, but because of the consistent landscape arrangement, this was non-randomised. A transect was established that represented a gradient of land-use intensification, incorporating the three land-use types. This transect was replicated a total of ten times across the region spanning eight different properties (Figures 3.3 & 3.4). Due to trampling by cattle during sampling, all sampling points along one complete transect were destroyed, as well as the cropping core and cropping/pasture edge from another site. This resulted in nine replicates each of woodland core, woodland/pasture edge and pasture core and eight replicates of cropping core and cropping/pasture edge.

Sampling points were located at five positions along the transect: the core of each land-use type and the two edges. The sampling point in the core of each land-use type was randomly located along the transect, but with the criterion that it must be situated a minimum of 50 m from adjoining land uses. Therefore, each land-use core sampling point was at least 100 m from the next core sampling point. For the edges, a sampling point was randomly located along the land-use edge. The edge of pasture and cropping was easily determined as the point where the pasture abutted the complex of crop plants and bare ground that constituted the outermost perimeter of the crop field (generally c.0.5 m in width). The interface between the edge pasture edge and the woodland edge was determined as the edge of the tree line.

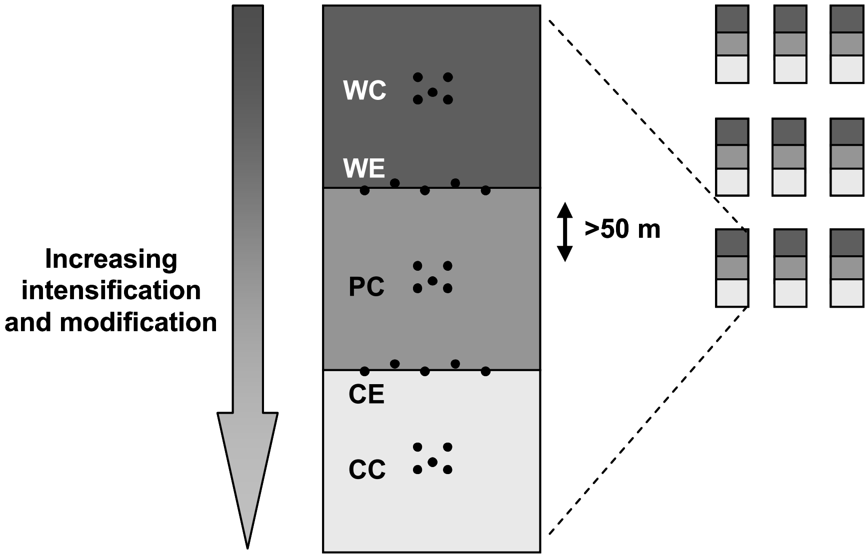

Figure 3.4. Experimental design and spatial arrangement of sampling points in relation to land-use gradient. WC = Woodland core, WE = Woodland/pasture edge, PC = Pasture core, CE = pasture/cropping edge, CC = Cropping core.

3.2.4 Ant sampling

Surface-dwelling arthropods were sampled using pitfall traps. Whilst there are known limitations and biases to pitfall trapping (Melbourne, 1999; Ward *et al.* 2001b), the technique is also recognised as a valid and useful approach to collecting large quantities of data for certain groups, including ants (Andersen, 1991). This technique was considered suitable for the comparative study as the aim was not to produce an exhaustive categorisation of site fauna. Pitfall traps consisted of plastic containers with an opening diameter of 115 mm and a depth of 80 mm. Five traps were placed 5 m apart from each other at each sampling point in a given land-use type (see Fig. 3.4) and allowed to settle with lids on for seven days to reduce digging-in effects

(Greenslade, 1973). In order to capture a comprehensive picture of each edge, traps were placed either side of the line of land-use division (see section 3.2.3 for how edges were determined), but no more than 0.2 m into the adjacent land use. Traps were then half-filled with 30% ethylene glycol solution and a few drops of household detergent. All traps were simultaneously opened for four days and nights in November 2005. Traps were then removed, and the contents transferred to a 70% ethanol solution.

All ant specimens were identified to genus and morphospecies using a stereomicroscope and standard reference works (Shattuck 1999; Andersen, 2000; Shattuck and Barnett, 2001) and morphospecies identification was confirmed by staff at the Queensland Museum and compared to voucher specimens from other studies in the region. Specimens were attributed to functional groupings after Hoffmann and Andersen (2003) and Majer *et al.* (2004).

3.2.5 Independent variables

In order to determine the relationship between ant assemblage composition and habitat factors, a number of variables relating to stand structure, ground cover and canopy cover were recorded at each sampling point (Table 3.1). Stand structure was measured within a 25 m^2 quadrat at each sampling point. Ground and canopy cover measures were estimated within four randomly located 1 m^2 quadrats (located within the 25 m^2) at each sampling point and the mean calculated. Tree canopy cover (for both above and below 10 m in height) was estimated as the percentage cover of branches and foliage covering the 1 m^2 quadrat, when the observer was standing in the middle of the quadrat and looking vertically upwards. Shrub cover was estimated in a similar manner but with the observer lying down face upwards in the quadrat. Amount of each ground cover variable was estimated by standing above the quadrat and estimating percentage cover of each variable. The estimation process was aided by having the metal quadrat divided into one hundred equally sized squares by attaching ten pieces of cord to the vertical and horizontal borders of the quadrat. This made it easier to visualise quantities in percentage terms. Both litter depth and graminoid height were measured 20 times (at random points) in each 1 m^2 quadrat by placing a 1 m rule (marked in mm) vertically on the ground and measuring at eye level. The mean of these 20 measurements was taken for each quadrat. In addition to the fine scale cover measurements, four landscape level variables were calculated, from digitally rectified aerial photographs, for each sampling point: the percentage cover of i) woodland, ii) pasture and iii) cropping within 500 m of each sampling point, and the linear distance of cropping edge (i.e. cropping/pasture interface) within 500 m of each sampling point. This latter variable represents the quantity of 'hard-edge' (edge with a high degree of contrast between the two bordering land-use types).

Table 3.1. Environmental variables measured at each sampling point, with units of measurement and number of samples taken. * = variable used in multivariate analysis (see Table 3.6); † = variables combined and used in multivariate analysis (see table 3.6).

Variable	Measure/units	Number of readings at each sampling point
Tree stand structure	Count within 25 m^2	1
Shrubs >2 m height	Count within 25 m^2	1
Shrubs <2 m height	Count within 25 m^2	1
Trees canopy cover 10-30 m height †	% cover within 1 m^2	4
Trees canopy cover <10 m height †	% cover within 1 m^2	4
Shrubs >2 m height *	% cover within 1 m^2	4
Shrubs <2 m height *	% cover within 1 m^2	4
Forbs/herbs (non-woody) *	% cover within 1 m^2	4
Graminoids (tussock and mat separated) *	% cover within 1 m^2	4
Coarse Woody Debris (logs diameter >50 mm) *	% cover within 1 m^2	4
Coarse litter (debris diameter >10 mm <50 mm) *	% cover within 1 m^2	4
Fine litter (debris <10 mm) *	% cover within 1 m^2	4
Litter depth	mm within 1 m^2	20
Graminoid height	mm within 1 m^2	20
Graminoid density	None, low, medium, high	4
Bare ground *	% cover within 1 m^2	4
Crop residue	% cover within 1 m^2	4
Standing crop	% cover within 1 m^2	4
Cryptogams	% cover within 1 m^2	4
Rock cover *	% cover within 1 m^2	4
Cover of woodland in landscape	% cover within 500 m radius	1
Cover of pasture in landscape *	% cover within 500 m radius	1
Cover of cropping in landscape *	% cover within 500 m radius	1
Quantity of 'hard edge' (cropping pasture interface) in landscape *	Linear measure within 500 m radius	1

3.2.6 Data analyses

3.2.6.1 Richness, abundance and diversity

Total morphospecies richness and grand mean abundance (mean abundance in each trap and grand mean of this across all replicates of a particular treatment) were calculated for each sampling point (across the five traps). Two diversity indices were calculated using the PRIMER® software package (Clarke and Gorley, 2001): the Shannon diversity index (H) and the Margalef index. Two indices were selected as each index is known to have its own limitations and benefits; for instance, the Shannon index is less sensitive to rare species, whereas the Margalef index is more sensitive to species represented by few individuals (Southwood, 1966; Jameson, 1989).

Prior to analysis, abundance and richness data were tested for normality of distribution and transformed where required. To test for differences in ant richness, abundance and diversity measures among treatments, I used repeated measures ANOVAs, with land-use type as the repeated measure. Where Mauchly's assumption of sphericity was violated, a re-evaluation of the F-ratio was conducted using new degrees of freedom, calculated using the Huynh-Feldt epsilon. Where a significant within-subject effect was detected (i.e. among land-use type), differences between each treatment were tested using paired t-tests. Differences among treatments in the mean abundance of individuals belonging to selected genera, individual morphospecies and functional groups were investigated using repeated measures ANOVAs. All univariate analyses were performed using SPSS 14.0 for Windows (SPSS for Windows, 2005).

3.2.6.2 Assemblage composition

To examine if ant assemblage composition and relative abundance differed among treatments, I calculated a Bray-Curtis similarity matrix from the fourth root transformed morphospecies data for each sampling point (this transformation was used as there were very large abundance differences among taxa, treatments and replicates of treatments). The primary reason for this analysis was to determine if the ant assemblages exhibited greater similarity within land-use type or within their block location (e.g. was the ant assemblage at WC1 more similar to that at WC2, WC3, WC4, etc., than that at WE1, PC1, etc.). To reduce data 'noise', I excluded all morphospecies that occurred at fewer than three sampling points, thus reducing the influence of rare species. Non-metric multidimensional scaling ordination was then used to try to visualise the patterns from the similarity matrix in two dimensions. The differences among ant assemblages for both treatment type and block were tested using ANOSIM, with 9999 permutations. The morphospecies contributing most to the observed differences were calculated using SIMPER. A similar procedure was used for the functional group data. All calculations were undertaken using PRIMER$^{®}$ (Clarke and Gorley, 2001).

3.2.6.3 Morphospecies occurrence and environmental variables

To ascertain which of the measured environmental variables appeared to be driving the variation in species occurrence among sites I used canonical correspondence analysis (CCA). Prior to analysis I removed all morphospecies that occurred at fewer than five sites, leaving 45 morphospecies (Debuse *et al*. 2007). In order to then determine if the morphospecies data had a linear or Gaussian (i.e. < or > than three lengths of gradient; Ter Braak and Šmilauer, 2002) distribution, I performed a detrended correspondence analysis (DCA). Before conducting CCA I used a ranging approach to standardising the environmental data (some measures were percentage cover, some heights, some distances, etc.) to a value between 0 and 1, by dividing each measure in an environmental variable category by the highest scoring measure in that category. I then calculated a correlation matrix of the environmental variables. Where there was a Spearman rank correlation of greater than 0.6, I carefully considered the ecological implications of these findings and the potential removal or combining of variables. For instance, tree stand density within 25 m^2 of each sampling point was highly correlated ($>R = 0.6$) with canopy cover of trees >10 m height, canopy cover of trees <10m height, litter cover, litter depth and percentage woodland cover within 500 m. Adopting a case-by-case approach, I omitted tree stand structure and derived a combined (mean) value for cover of both tree height classes, thus reducing the number of tree-related patch-scale variables to one measure. Despite litter cover being correlated with tree density and cover, I considered that these variables may influence ant assemblages in different ways—e.g. tree cover influencing the degree of sunlight reaching the ground layer, leaf litter directly influencing food webs, resource availability and microclimatic conditions. Consequently, I retained leaf litter cover, but discarded the highly correlated leaf-litter depth. Similarly, whilst woodland cover was also correlated with these variables, it was retained as it operated at a much larger spatial scale than the patch scale-variables (500 m radius compared to 4 m²). As the three area-based landscape variables were auto-correlated, I retained the two that a preliminary CCA found exerted the strongest influence on the morphospecies occurrence variability. I conducted a CCA for all remaining variables ($n = 14$) and the 45 most frequently recorded ant morphospecies, using logN transformed ant data, manual forward selection of environmental variables and 5,000 unrestricted Monte Carlo permutation tests.

To determine the amount of species variability attributable to a) patch-scale environmental variables and b) landscape-scale environmental variables, I performed variance partitioning partial ordinations with patch-scale measures (e.g. tree canopy cover) as the environmental variables and landscape-scale measures (e.g. crop area cover) as covariables, and then landscape scale measures as the environmental variables and patch-scale measures as covariables. This approach was based upon the methods of Borcard *et al*. (1992) and Debuse *et al*. (2007). All were performed with CANOCO Version 4.5 for Windows (Ter Braak and Šmilauer, 2002)

3.2.6.4 'Indicator' taxa

In order to determine if any of the taxa were characteristic of a land-use type, I conducted analysis using IndVal (Dufrêne and Legendre, 1997), which calculates the rate of occurrence in each habitat type and assesses whether a species is present predominantly in one habitat type. By incorporating both the abundance of a taxon within a land-use type as well as the number of sites of that land-use type in which the taxon occurs, it offers a realistic appraisal of a taxon's habitat specificity (Dufrêne and Legendre, 2004). The dataset used for this analysis was the same as for the CANOCO analysis. Thus, it only included morphospecies that occurred at more than five sampling points ($n = 45$ morphospecies to be tested). Only the land-use type was used as a typology (analogous to an independent variable), and 499 iterations of the analysis were performed. Any significant results were used as the basis for illustrating the distributions of target taxa along the land-use gradient. This was done by calculating the proportion of a taxon's total occurrence (e.g. proportion of abundance of individuals of that taxon in CC: $n_{CC}/ (n_{CC} + n_{CE} + n_{PC} + n_{WE} + n_{WC})$) in each land-use type, where a taxon occurred at two or more different sites. Graphics were then produced for a taxon's abundance occurrence in each land-use type based upon percentage of the total occurrence in each land-use type (0%, >0%–20%, >20%–40%, >40%–60%, >60%–80% and >80%–100%) (see Fig. 3.11).

3.3 Results

3.3.1 Meta-analysis (richness and abundance)

Averaged across all studies, both ant abundance and morphospecies richness were significantly greater in native vegetation (NV) than agricultural land (Ag), abundance and richness were significantly greater in reduced-input (RIC) conventional cropping (CC), and richness but not abundance was significantly greater in improved pasture (IP) than cropping (C) (Fig. 3.5). Despite the greatest mean disparity in richness being between wooded native vegetation (WNV) and improved pasture (IP), high among-study heterogeneity precluded this result being statistically significant. No other differences between treatments were found.

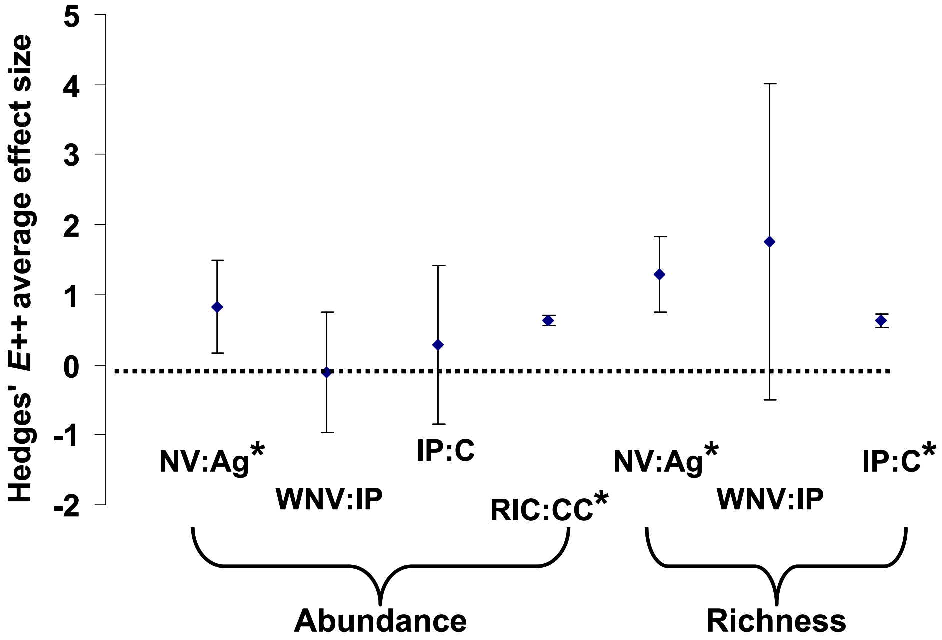

Fig. 3.5. The Hedges' *E*++ average effect size (mean effect size averaged across all studies in a land-use comparison) for fixed and random effects meta-analyses of ant abundance and richness responses for various land-use comparisons (+/- 95% C.I.). Comparisons where the 95% C.I.s do not cross zero (denoted by * in the legend) are considered to exhibit significantly greater richness or abundance in the less intensive land-use type ($\alpha = 0.05$).

Sample sizes: **Abundance**: NV:Ag = 24 comparisons from 17 studies; WNV:IP = 13 comparisons from 11 studies; IP:C = 6 comparisons from 5 studies; RIC:CC = 14 comparisons from 12 studies; **Richness:** NV:Ag = 20 comparisons from 15 studies; WNV:IP = 7 comparisons from 7 studies; IP:C = 5 comparisons from 4 studies.

Abbreviations: **WNV:IP** = wooded native vegetation compared to improved/introduced pasture; **NG:IP** = native grassland compared to improved/introduced pasture; **IP:C** = improved/introduced pasture compared to cropping; **RIC:CC** = reduced-input cropping compared to conventional cropping.

3.3.2 Ant richness, abundance and diversity in field

A total of 12,968 ants were collected, representing 85 morphospecies from 27 genera and 6 sub-families (see Appendix C.1). Mean morphospecies richness declined significantly along the land-use intensification gradient (Table 3.2), with paired t-tests reporting significant differences between CC & CE, CC & PC, CC & WE, CC & WC, CE & WE, CE & WC, PC & WE and PC & WC (see Table 3.3 and Fig. 3.6).

Richness was no different between an interface and the less intensive neighbour (e.g. WC:WE; PC:CE), but was significantly different between an interface and the more intensive neighbour (e.g. WE:PC; CE:CC), displaying a drop in richness with increasing intensification (Table 3.3).

A significant difference among treatments was reported for the repeated measures ANOVA of mean ant abundance (Table 3.2). However, paired t-tests revealed ant abundance was only significantly different between CC & PC ($t_7 = -3.118$; $P = 0.017$) and between CC & WE ($t_7 = -3.237$, $P = 0.014$) (Fig. 3.7).

Comparisons of the Margalef index mirrored the richness results with diversity declining with increasing intensification (Table 3.2). When comparing paired land uses, there were significant differences between CC & CE, CC & PC, CC & WE, CC & WC, CE & WE, CE & WC, PC & WE and PC & WC (Table 3.4 and Fig. 3.8). The ANOVA results for the Shannon index found an overall significant trend of diversity declining with land-use intensity (Table 3.2). Subsequent paired tests reported significant differences in ant Shannon diversity between WC & CC ($t_7 = -3.506$, $P = 0.010$); and WE & CC ($t_7 = -2.604$, $P = 0.035$) (see Fig. 3.8).

Table 3.2 Repeated measures ANOVA results for ant richness, abundance, Margalef diversity and Shannon diversity among different land uses. d.f. = 4,28 in all cases.

Measure	**F**	**Significance**
Ant morphospecies richness	19.2	0.001
Ant abundance	3.7	0.015
Ant Margalef diversity	19.3	0.001
Shannon diversity	3.2	0.01

Table 3.3 Paired t-test results between each land-use type for ant morphospecies richness. d.f. = 7 in all cases.

Paired land–use comparison	**t**	**Significance (2-tailed)**
CC & CE	-4.2	0.004
CC & PC	-6.3	0.001
CC & WE	-8.7	0.001
CC & WC	-6.9	0.001
CE & PC	-1.3	0.245
CE & WE	-3.8	0.006
CE & WC	-3.5	0.01
PC & WE	-2.8	0.022
PC & WC	-2.4	0.04
WE & WC	-0.8	0.94

Table 3.4 Paired t-test results between each land-use type for ant morphospecies Margalef diversity

Paired land–use comparison	**t**	**d.f**	**Significance (2-tailed)**
CC & CE	-3.7	7	0.008
CC & PC	-5.8	7	0.001
CC & WE	-11.9	7	0.001
CC & WC	-7.3	7	0.001
CE & PC	-1.2	7	0.285
CE & WE	-3.9	7	0.006
CE & WC	-4.6	7	0.003
PC & WE	-2.5	8	0.04
PC & WC	-3.9	8	0.05
WE & WC	-1.6	8	0.2

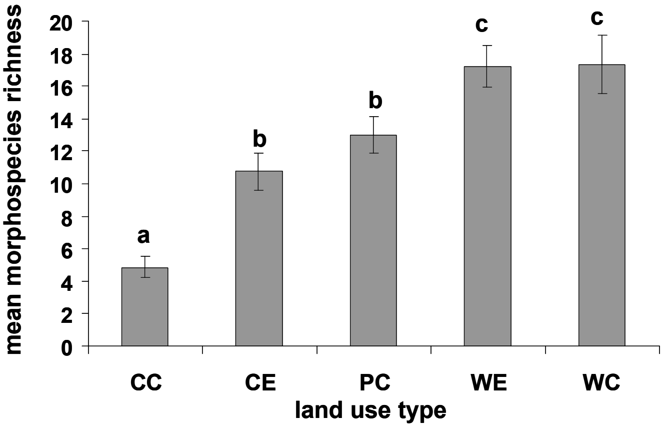

Fig. 3.6. Mean ant morphospecies richness in core land uses and edge habitats. WC = Woodland core, WE = Woodland/pasture interface, PC = Pasture core, CE = pasture/cropping interface, CC = Cropping core. Different letter denotes significant difference for paired t-tests among treatments at α = 0.05. N = 8 replicates for CC & CE, N = 9 replicates for PC, WE & WC.

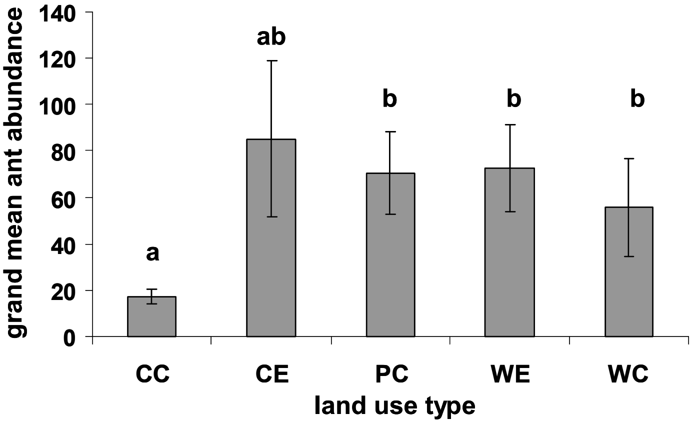

Fig. 3.7. Grand mean ant abundance in core land uses and edge habitats. Different letter denotes significant difference for paired t-tests among treatments at α = 0.05.

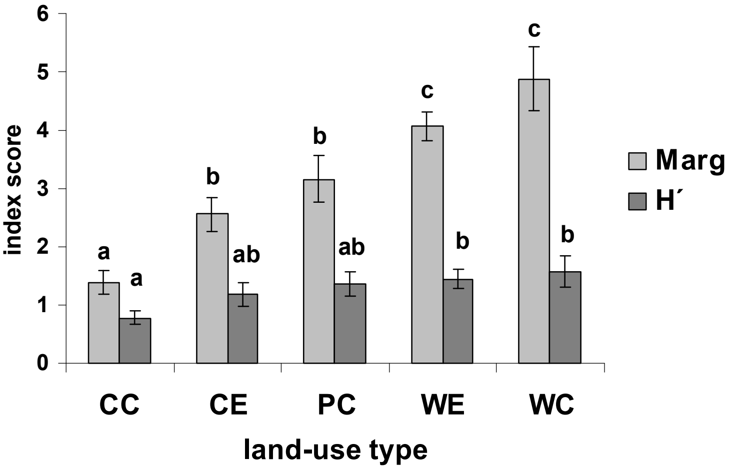

Fig. 3.8. Margalef and Shannon (H') diversity indices for core land uses and edge habitats. Different letter denotes significant difference for paired t-tests among treatments at α = 0.05. N = 8 replicates for CC & CE, N = 9 replicates for PC, WE & WC.

3.3.3 Assemblage composition

The non multi-dimensional scaling and ANOSIM comparing assemblages among land-use type showed that the core land uses supported significantly different ant morphospecies assemblages (Global R = 0.482, p = <0.01; pairwise comparisons: WC & PC: R = 0.45, p = <0.01; WC & CC: R = 0.955, p = <0.01; PC & CC: R = 0.558, p = <0.01; Fig. 3.9). For edge habitats, no assemblage differences were apparent in the pairwise comparisons between WC:WE, WE:PC and CE:PC. However, significant differences were found between WE:CE (R = 0.55, p = <0.01), CE:WC (R = 0.714, p = <0.01) and CE:CC (R = 0.392, p = <0.01) (Fig. 3.9).

The same data stratified by block (Fig. 3.10) showed a non-significant difference among assemblages of different blocks (Global R = 0.17, p = 0.06). Despite this weaker effect, overall, ant assemblages appeared to have been influenced predominantly by land-use type rather than due to spatial proximity of treatments or other local within-block factors.

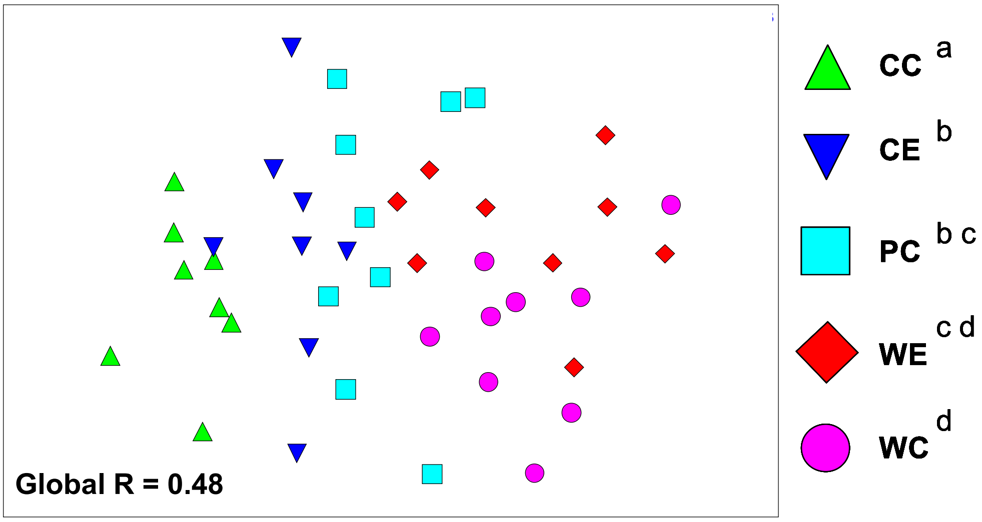

Fig. 3.9. nMDS of 4th rt transformed ant morphospecies assemblage data, Bray-Curtis similarity matrix, stratified by land-use type. CC = cropping core, CE = cropping/pasture edge; PC = pasture core; WE = woodland pasture edge; WC = woodland edge. Stress = 0.23. Different superscript letter denotes significant difference in assemblage composition (α = 0.05).

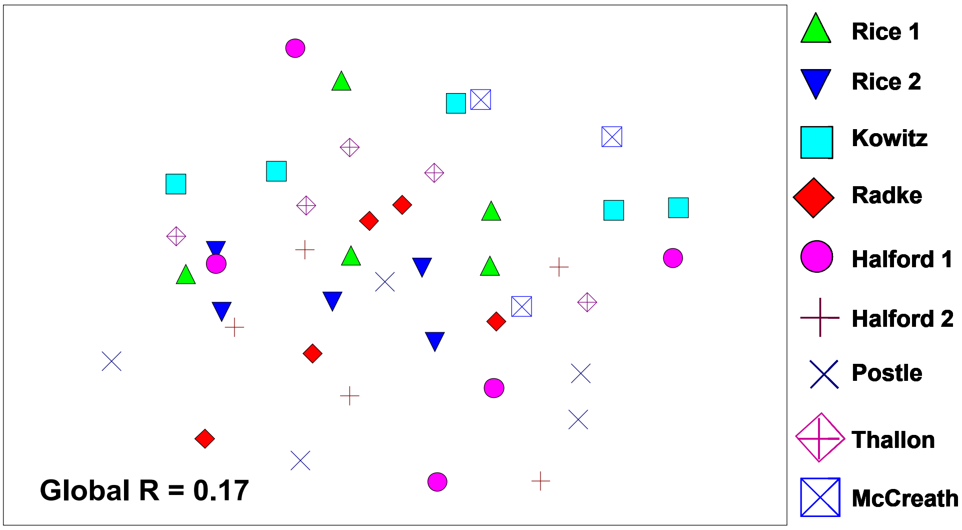

Fig. 3.10. nMDS of 4th rt transformed ant morphospecies assemblage data, Bray-Curtis similarity matrix, stratified by block/farm. Stress = 0.23. Differences were non-significant, so no pairwise tests were conducted.

Using SIMPER in PRIMER®, several morphospecies were consistently found to contribute most to differences between land-use types, including *Iridomyrmex* sp. 1 (*rufoniger* group), *Pheidole* sp. 3, and *Paratrechina* sp.1 (See Table 3.5 for all paired land-use comparisons).

Table 3.5. Paired land-use type comparisons depicting the three morphospecies in each comparison that contributed the highest between-land-use dissimilarity (percentage contribution to between-treatment dissimilarity in brackets), derived from SIMPER analyses.

Land use	CC	CE	PC	WE	WC
CC	N/A	*Iridomyrmex* 1 (11.2) *Paratrechina* 1a (6.8) *Pheidole* 3 (6.7)	*Iridomyrmex* 1 (8.7) *Pheidole* 3 (6.4) *Notoncus* 2 (4.4)	*Iridomyrmex* 1 (7.2) *Pheidole* 2 (6.2) *Iridomyrmex* 3 (5.9)	*Iridomyrmex* 1 (DD) (6.6) *Monomorium* 1 (GM) (5.3) *Pheidole* 5b (GM) (4.9)
CE	*Iridomyrmex* 1 (11.2) *Paratrechina* 1a (6.8) *Pheidole* 3 (6.7)	N/A	*Iridomyrmex* 1 (8.6) *Pheidole* 3 (5.2) *Paratrechina* 1a (4.9)	*Iridomyrmex* 1 (7.2) *Iridomyrmex* 3 (5.0) *Pheidole* 2 (5.0)	*Iridomyrmex* 1 (6.9) *Pheidole* 3 (5.2) *Paratrechina* 1a (4.0)
PC	*Iridomyrmex* 1 (8.7) *Pheidole* 3 (6.4) *Notoncus* 2 (4.4)	*Iridomyrmex* 1 (8.6) *Pheidole* 3 (5.2) *Paratrechina* 1a (4.9)	N/A	*Iridomyrmex* 1 (7.2) *Iridomyrmex* 3 (4.8) *Pheidole* 3 (4.8)	*Iridomyrmex* 1 (6.7) *Pheidole* 3 (5.4) *Melophorus* 2a (3.2)
WE	*Iridomyrmex* 1 (7.2) *Pheidole* 2 (6.2) *Iridomyrmex* 3 (5.9)	*Iridomyrmex* 1 (7.2) *Iridomyrmex* 3 (5.0) *Pheidole* 2 (5.0)	*Iridomyrmex* 1 (7.2) *Iridomyrmex* 3 (4.8) *Pheidole* 3 (4.8)	N/A	*Iridomyrmex* 1 (7.3) *Iridomyrmex* 3 (5.1) *Pheidole* 2 (3.8)
WC	*Iridomyrmex* 1 (6.6) *Monomorium* 1 (5.3) *Pheidole* 5b (4.9)	*Iridomyrmex* 1 (6.9) *Pheidole* 3 (5.2) *Paratrechina* 1a (4.0)	*Iridomyrmex* 1 (6.7) *Pheidole* 3 (5.4) *Melophorus* 2a (3.2)	*Iridomyrmex* 1 (7.3) *Iridomyrmex* 3 (5.1) *Pheidole* 2 (3.8)	N/A

The IndVal analysis found only five morphospecies that were significantly associated with a particular land-use type (Fig. 3.11 a-e). Four of these morphospecies were associated with an edge habitat, *Camponotus* 2 and *Paratrechina* 1a were associated with the pasture/cropping edge, and *Pachycondyla* 1 and *Melophorus* 2a were associated with the woodland/pasture edge.

Differences in the abundance and distribution of different morphospecies along the gradient could be better conceptualised and visualised by calculating how many individuals of a taxon occurred in each land-use type compared to that taxon's total abundance across all land uses. This was done by calculating the percentage of a taxon's total abundance in each land-use type, where a taxon occurred at two or more different sites. For example, to calculate what percentage of a taxon's total abundance was present in the cropping core I used the formula: $n_{CC}/ (n_{CC} + n_{CE} + n_{PC} + n_{WE} + n_{WC})$ to deliver a proportional figure and multiplied by 100 to derive a percentage ('n' is the total abundance of a taxon in each land use). As an illustration, *Rhytidoponera* 6 was trapped a total of 58 times, with the distribution among land-use types being 15 individuals in WC, 26 in WE, 8 in PC, 6 in CE and 3 in CC. Using the above formula, this translated into 26 % of individuals being caught in WC, 45 % in WE, 14 % in PC, 10 % in CE and 5 % in CC. Diagrams a) to e) in Fig. 3.11 show the patterns in occurrence of taxa which had a significant 'indicator value' for a particular land-use type ($P = <0.05$), and diagrams f) to l) are included to illustrate the range of habitats utilised and the interspecific differences in distribution within the landscape. In order to better demonstrate these points a range of the ant taxa that typify each land-use association are illustrated.

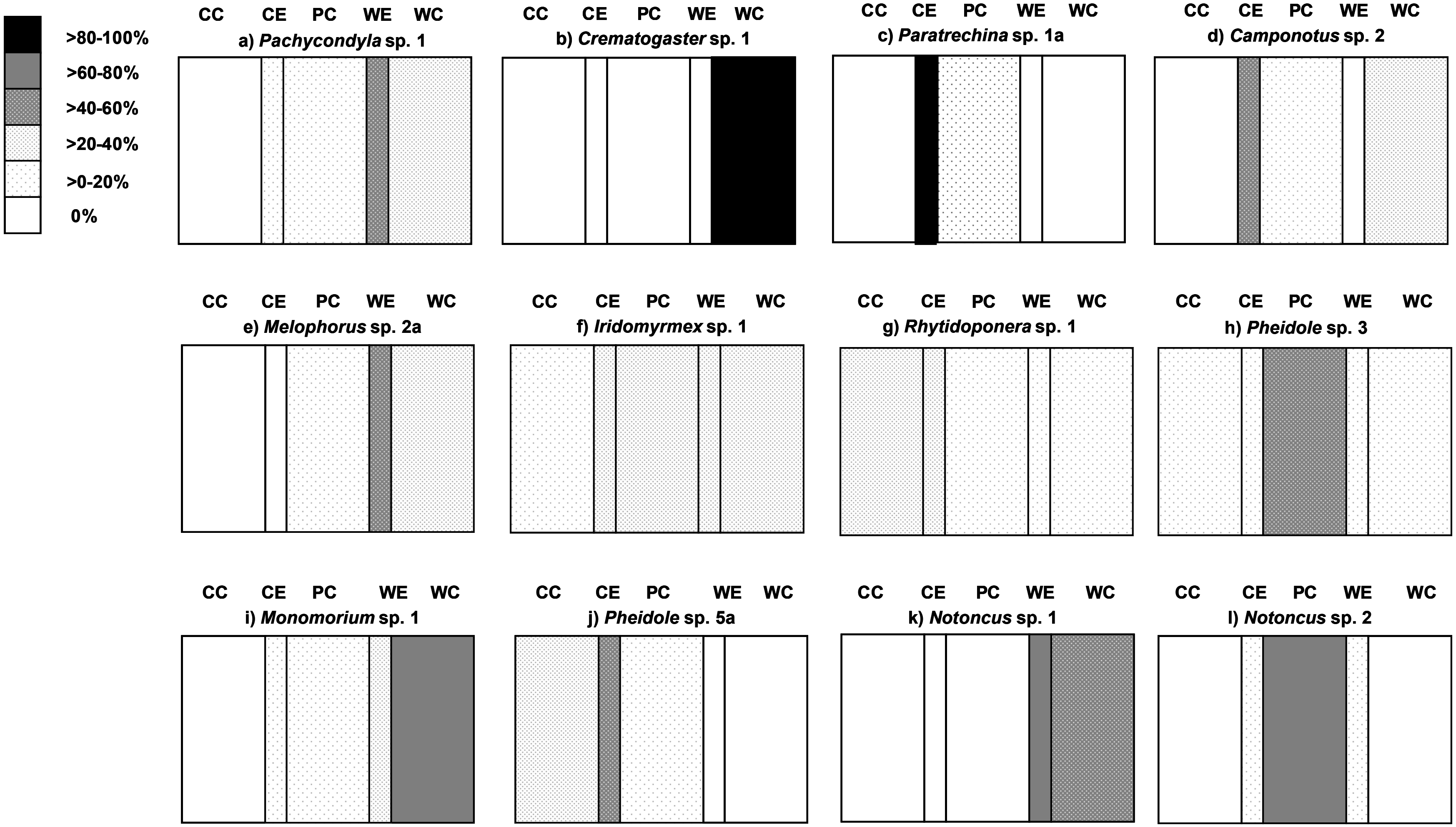

Fig. 3.11. Distributions of selected morphospecies based upon the proportion of the total occurrences that were recorded in each land-use type. Diagrams a–e are the taxa found to exhibit a significant ‘indicator value’ for a particular land-use type (α = 0.05). Diagrams f–l were taxa that showed non-significant responses, but have been illustrated in order to convey the wide range of ant taxa distributions along the intensification gradient.

3.3.4 Functional groups

3.3.4.1 Literature analysis

Comparing ant functional group assemblage changes between native vegetation and agricultural land uses derived from the scientific literature, Fig. 3.12 indicates that certain functional groups make up a greater part of an ant assemblage in native systems whilst others are more proportionately abundant in agricultural systems. For instance, the Dominant Dolichoderine group was higher in proportional abundance in wooded native vegetation compared to agricultural land (n = 10 studies), although this result was driven to a considerable extent by three studies reporting very high abundance of the DD group in native vegetation compared to agriculture (see Appendix C.2). A less dramatic, though more consistently reported, decline from native to agricultural systems was found for the Subordinate Camponotini group (n = 13 studies), indicating that this group may generally be negatively affected by agriculture. Conversely, two groups displayed a marked increase from native to agricultural systems, the Generalised Myrmicinae and the Opportunists. The former (n = 16 studies), whilst showing an overall proportional assemblage increase when averaged across all studies, displayed a range of responses in individual studies, including greater proportional abundance in native vegetation. Opportunists, however, displayed greater proportional abundance in the agricultural treatment of comparisons in 70% of cases (n = 17 studies).

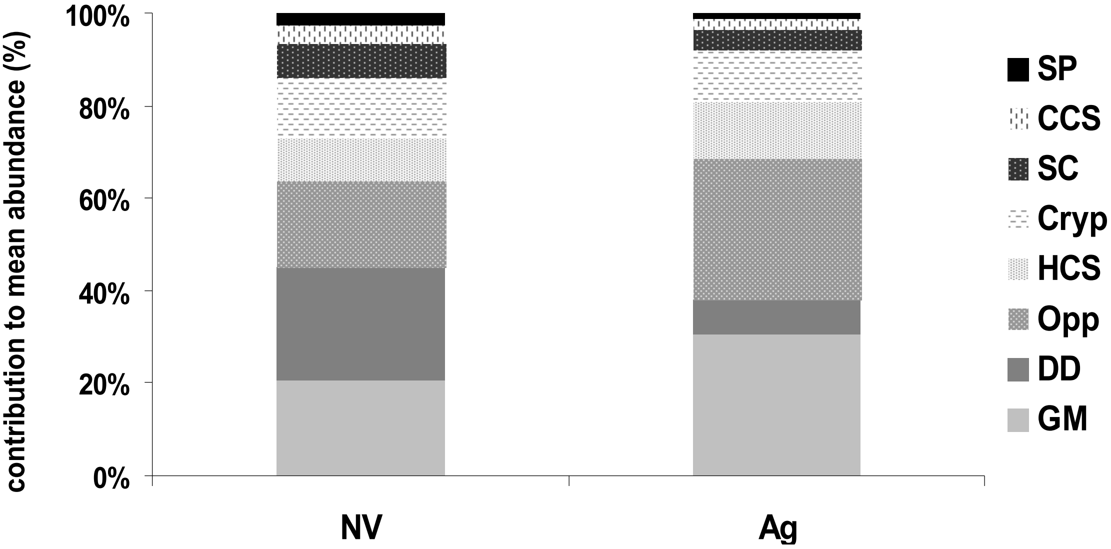

Fig. 3.12. Contribution of ant functional groups to overall assemblage composition in wooded native vegetation (NV) and agricultural land uses (Ag) averaged across 17 studies. Functional group abbreviations are: SP–Specialist predator; CCS–Cold Climate Specialist; SC–Subordinate

Camponotini; Cryp–Cryptic species; HCS–Hot Climate Specialist; Opp–Opportunist; DD–Dominant Dolichoderinae; GM–Generalised Myrmicinae. Details of studies and authorities used for assigning functional groups in Appendix C.2.

3.3.4.2 Field data

ANOSIM showed that functional group assemblage composition differed among land-use treatments (Fig. 3.13) (Global R = 0.34, p = 0.01; pairwise comparisons: WC & PC: R = 0.238, p = 0.003; WC & CC: R = 0.862, p = 0.01; PC & CC: R = 0.471, p = 0.01; CC & CE: R = 0.312, p = 0.03; CE & WE: R = 0.26; p = 0.007). There were no assemblage differences between WC:WE, WE:PC and PC:CE. There were no assemblage differences among blocks (Global R = 0.009, p = 0.399; Fig. 3.14).

SIMPER analysis indicated that the Dominant Dolichoderine, Cold Climate Specialist and Subordinate Camponotini groups contributed greatly to the distinction between WC and PC, whereas Hot Climate Specialists, Dominant Dolichoderines and Generalised Myrmicinae were the most influential in distinguishing between PC and CC.

Of the individual functional groups, Dominant Dolichoderines (largely represented by members of the genus *Iridomyrmex*) constituted 77% and 71% of the assemblage in WC and WE compared to 56%, 63% and 56% in PC, CE and CC respectively, but the differences were not significant. Only the Generalised Myrmicinae differed significantly in abundance among land uses ($F_{4, 28} = 4.940$; P = 0.004); pairwise t-tests: CC & PC ($t_7 = -3.051$; P = 0.019); CC & WE ($t_7 = -3.892$; P = 0.006); CC & WC ($t_7 = -3.574$; P = 0.009). Other groups (e.g. Subordinate Camponotini, Cold Climate Specialists) did not differ among treatments (possibly due to high within-treatment heterogeneity) or were recorded too infrequently from some treatments to allow statistical analysis. The proportional representation of each functional group in each land-use type is depicted in Figs. 3.15 and 3.16. Of the groups tested statistically, only the proportion of Opportunists differed among land-use types ($F_{4,28} = 3.129$; P = 0.03), with 31% of individuals being found in the CC treatment and 5 % in WC. Despite these findings, subsequent paired t-tests yielded no significant between land use difference—the nearest being greater proportion of Opportunists in CC compared to WC ($t_7 = 2.322$; P = 0.053).

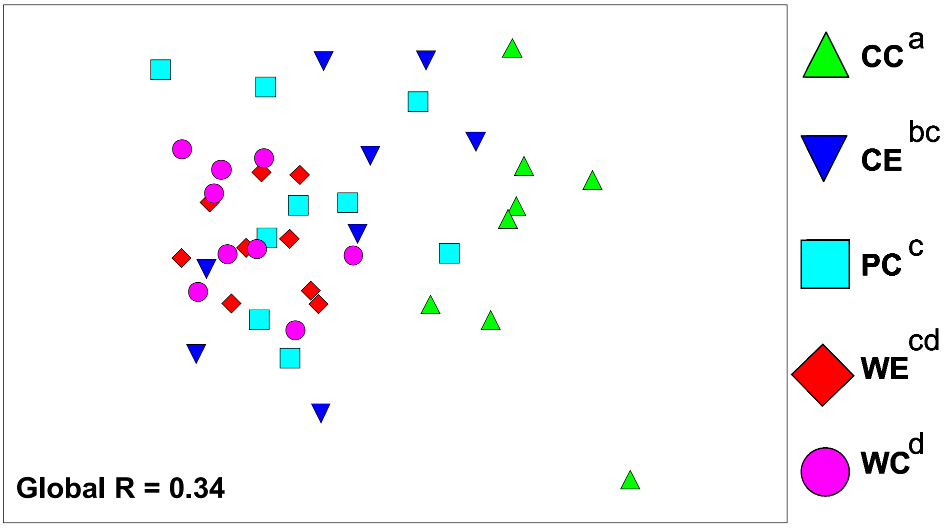

Fig. 3.13. nMDS of 4th rt transformed ant functional group assemblage data, Bray-Curtis similarity matrix, stratified by land-use type. CC = cropping core, CE = cropping/pasture edge; PC = pasture core; WE = woodland pasture edge; WC = woodland edge. Stress = 0.18. Different suffix letter denotes significant difference in assemblage composition (α = 0.05).

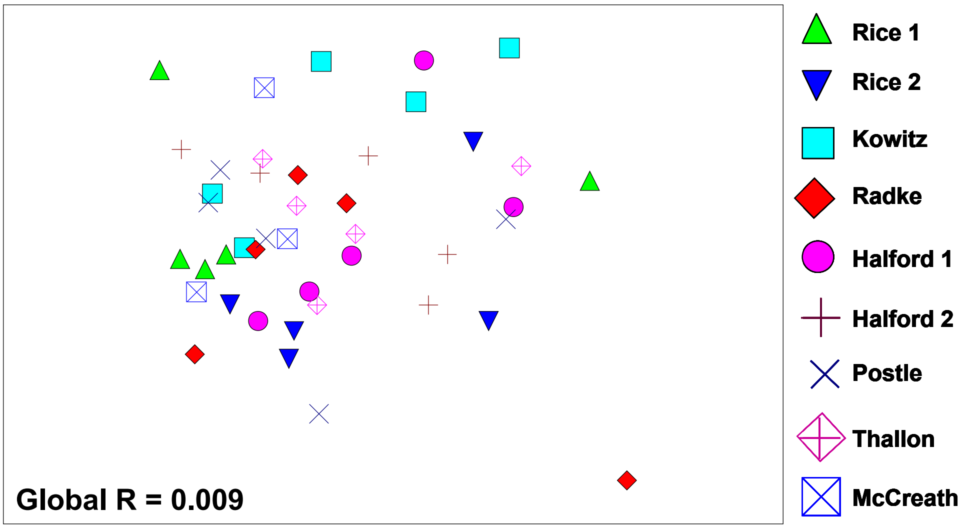

Fig. 3.14. nMDS of 4th rt transformed ant morphospecies assemblage data, Bray-Curtis similarity matrix, stratified by block/farm. Stress = 0.18. Global R non-significant, so no pairwise tests conducted.

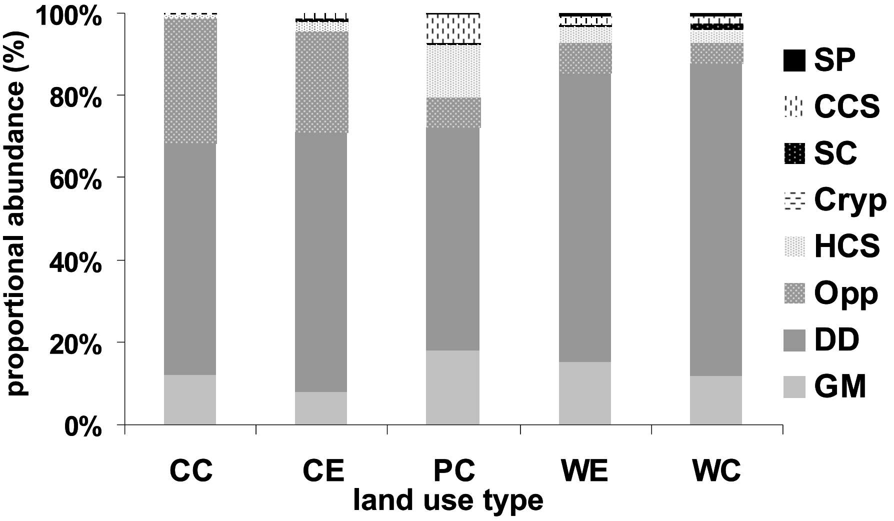

Fig. 3.15. Mean relative abundance of each functional group in five land-use treatments (expressed as a proportion of total abundance in each land use). CCS = Cold Climate Specialist; Cr = Cryptic; DD = Dominant Dolichoderine; GM = Generalised Myrmicinae; HCS = Hot Climate Specialist; Opp = Opportunist; SP = Specialist Predator; SC = Subordinate Camponotini.

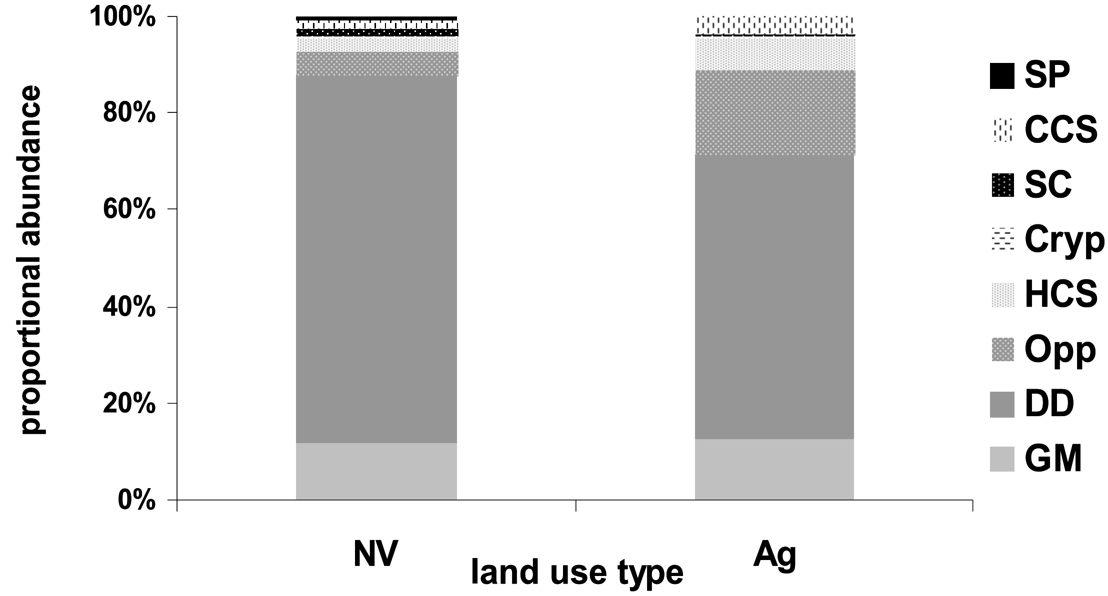

Fig. 3.16. Relative abundance of each functional group in native vegetation (WC) and agricultural land use (derived from summing data from CC, CE & PC) for field data (expressed as a proportion of total abundance in each land use). CCS = Cold Climate Specialist; Cr = Cryptic; DD = Dominant Dolichoderine; GM = Generalised Myrmicinae; HCS = Hot Climate Specialist; Opp = Opportunist; SP = Specialist Predator; SC = Subordinate Camponotini.

3.3.5 Morphospecies occurrence and environmental variables

The combined effects of patch-scale habitat attributes (tree canopy cover, etc) and landscape-scale measures (area of pasture within a 500 m radius, etc.) accounted for an eigenvalue of 1.31 from a total eigenvalue of 2.96, indicating that about 45% of the variance was accounted for by the environmental variables measured (Fig. 3.17 and Table 3.6). Much of the variation that was explained by the measured variables was attributable to patch-scale habitat factors, rather than landscape factors (Fig. 3.17 and Table 3.6).

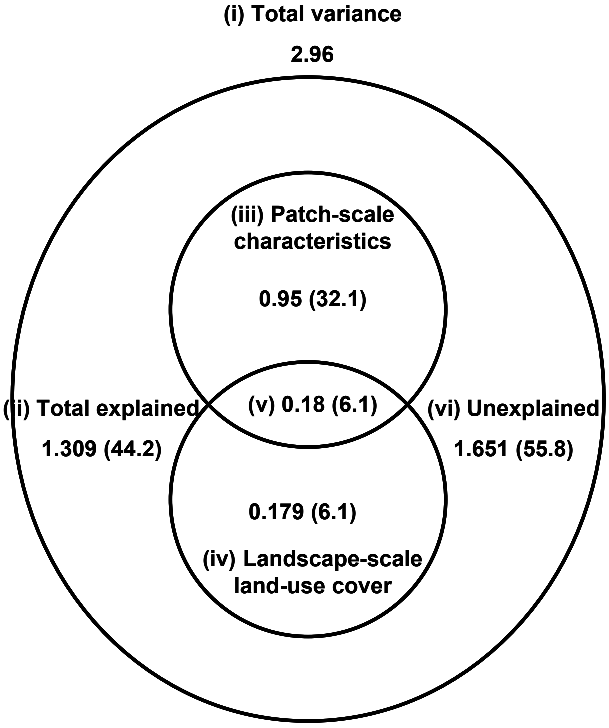

Fig. 3.17. Variation (as eigenvalues and percentage of total variation in parentheses) explained of ant morphospecies assemblage composition as determined by variance partitioning for (i) total variance, (ii) variance explained by all the environmental variables, (iii) variance explained by the patch-scale habitat attributes independently, (iv) variance explained by the landscape-scale attributes independently, (v) variance explained by interaction of patch-scale and landscape-scale attributes and (vi) variance due to unexplained factors.

Table 3.6. Variation in ant morphospecies assemblage composition explained by each of fourteen environmental variables as determined by manual variance partitioning (5,000 permutations in each case). The first eleven variables are patch scale attributes (total variation explained = eigenvalue of 0.95, 32.1% of total variation) and the final three are landscape-scale attributes (total variation explained = eigenvalue of 0.179, 6.1% of total variation).

Variable	**Eigen value**	**Percentage of total variation**	**F ratio**	***P* - value**
Rock cover (RC)	0.184	6.2	2.801	<0.001
Tree canopy cover (Tcov)	0.149	5.0	2.322	0.009
Fine litter cover (FL)	0.102	3.4	2.165	0.006
Coarse litter cover (CL)	0.084	2.8	1.775	0.099
Bare ground cover (BG)	0.078	2.6	1.705	0.02
Shrub cover over 2m (SCo2m)	0.077	2.6	1.258	0.223
Forb cover (FC)	0.066	2.2	1.116	0.31
Shrub cover under 2m (SCu2m)	0.056	1.9	1.012	0.398
Coarse woody debris (CWD)	0.053	1.8	0.924	0.51
Tussocky grass cover (TGC)	0.051	1.7	0.859	0.64
Mat-forming grass cover (MGC)	0.05	1.7	0.63	0.854
Crop/pasture edge in 500 m radius (CPedge)	0.061	2.1	1.001	0.438
Crop cover within 500 m radius (cropcov)	0.069	2.3	0.905	0.592
Pasture cover within 500 m radius (pastcov)	0.48	1.7	0.718	0.822

Several taxa were positively associated with attributes of woodland (e.g. '*Meranoplus* 3' and tree canopy cover, '*Pachycondyla 1*' and low shrub cover), whilst others appeared to be more positively influenced by broad-leaved ground cover ('*Notoncus* 2'), bare ground ('*Melophorus* 1') or the amount of cropping edge in the landscape ('*Tapinoma* 1' and '*Meranoplus* 1') (Fig. 3.18). Some morphospecies also exhibited negative associations with certain habitat attributes, such as '*Notoncus* 2' being negatively influenced by coarse litter cover and '*Meranoplus* 1' being negatively influenced by a range of variables associated with woodland (e.g. fine litter cover).

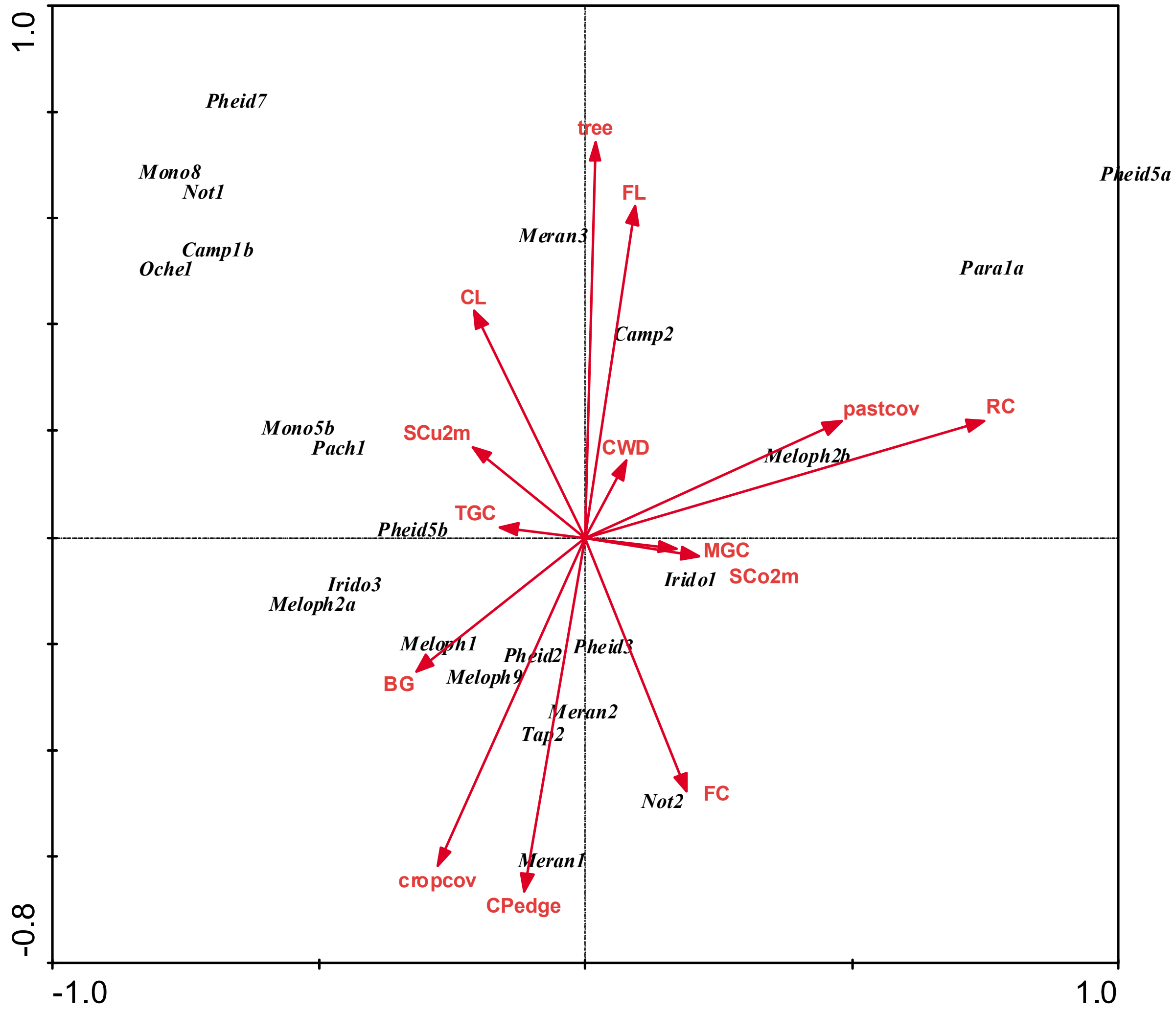

Fig. 3.18. Biplot based upon canonical correspondence analysis of ant morphospecies LN abundance using measures of patch-scale habitat attributes and landscape-scale land-use cover. Only morphospecies (in italics) showing minimum fit to the model of 10% are displayed. Habitat/landscape variable (plain type) arrows display strength and direction of correlation with morphospecies occurrence. The longer the arrow, the greater the power of that variable to explain variation in morphospecies occurrence. Arrows and taxa on similar trajectories display high degree of correlation; arrows and taxa on opposing trajectories display high negative correlation. Environmental variable abbreviations are: tree – tree canopy cover; FL – fine litter cover; CL – coarse litter cover; RC – rock cover; CWD – coarse woody debris cover; TGC – tussocky grass cover; SCu2m – shrubs (under 2 m) cover; SCo2m – shrubs (over 2 m) cover; MGC – mat-forming grass cover; BG – bare ground cover; FC – forb cover; pastcov – area of pasture cover in 500 m radius; cropcov - area of crop cover in 500 m radius; CPedge – cropping/pasture interface distance. Ant genus abbreviations (with numerical suffix denoting morphospecies) are: Camp – *Camponotus*; Irido – *Iridomyrmex*; Meloph – *Melophorus*; Meran – *Meranoplus*; Mono – *Monomorium*; Not – *Notoncus*; Oche – *Ochetellus*; Pach – *Pachycondyla*; Para – *Paratrechina*; Pheid – *Pheidole*; Tap – *Tapinoma*.

3.4 Discussion

3.4.1 Diversity and assemblage composition

In the field study, ant morphospecies richness declined significantly with increasing land-use intensity. This accorded with a) the global meta-analysis findings of significantly greater ant richness in native vegetation than agricultural land, and generally greater richness in the less intensive land use of a land-use comparison (e.g. pasture compared to cropping) and b) the many studies reporting similar patterns for a wide range of arthropod taxa (e.g. spiders, Baldiserra *et al*. 2004; centipedes, Nakamura *et al*. 2003). These results indicate that loss of arthropod diversity with increased habitat simplification and modification, stemming from agricultural development, is a general phenomenon globally.

Turnover of taxa among land uses also resulted in the formation of distinct ant assemblages evident in the woodland, pasture and cropping treatments. The results indicate that two basic mechanisms of assemblage change are apparent: i) taxon loss along the gradient leading to an impoverished ant assemblage in cropping, and ii) taxon turnover between the woodland and pasture/grassland treatments (i.e. both woodland and pasture exhibited habitat-specific species). The decline in taxonomic richness along the intensification gradient could be due to a range of interacting threats and processes. For instance, the relatively high levels of habitat complexity in the woodland and grassland are likely to provide greater resources, niche availability and opportunities for co-existence than the intensively disturbed and uniformly managed cropping land (Landis *et al*. 2000; Langellotto and Denno, 2004; Sarty *et al*. 2006), where microclimates and habitat structure have been dramatically altered. That land-use type was more influential in shaping ant assemblages than block-level factors is in accordance with the findings of Dauber *et al*. (2005) and Debuse *et al*. (2007), who found that ants were strongly affected by local habitat characteristics such as insolation and soil type, rather than broader landscape effects. These findings are further supported by the greater influence of patch-scale habitat attributes than landscape-scale habitat cover in explaining variation in the ant assemblages. However, although not tested, it is possible that landscape level factors were diluted on occasions where a particular patch of a land-use type (e.g. a patch of woodland or a cropping field), was so large that it effectively dominated the landscape at the 500 m radius scale used in this study. This could potentially be overcome by using larger measurement parameters (e.g. radii of 1000 m, 5000 m) to assess landscape composition.

There were no differences in richness, abundance, or assemblage composition between habitat interfaces and their less intensively managed neighbour (i.e. WC ≈ WE; PC ≈ CE). One possible explanation is that some taxa preferring a particular land-use type may be willing to venture short distances into a neighbouring, more intensively managed and modified land use. However, they may be unwilling or unable to venture any substantial distance (e.g. in the case of this study, 50–200 m) into the less hospitable land use. This phenomenon of ecological filtering (*sensu* Gascon *et al.* 1999) was prevalent in the cropping systems of this study, with thirty-three taxa occurring in the WC and WE treatments only and a further thirty-five taxa occurring in WC, WE, PC and CE, but not CC. This indicates that for many taxa, cropping is an inhospitable land use, analogous to a filter with small pore diameter (*sensu* Gascon *et al.* 1999 and Tabarelli and Gascon, 2005). The difference in morphospecies composition between the ant assemblages in PC compared to CC appeared greater than the difference between the assemblages in PC compared to WC. Whilst this difference was not statistically verified, it may imply that the boundary between pasture/cropping is ‘harder’, and therefore less permeable (Stamps *et al.* 1987; Berggren *et al.* 2002), than the pasture/woodland interface. This appears to be feasible, as the physical delineation between PC & CC was far more abrupt than between PC & WC, where the boundary was visibly more diffuse, with elements of the ground cover being similar (grass tussocks in both woodland and pasture) and isolated paddock trees being present in the pasture in some cases.

It was also interesting to note that certain taxa (e.g. *Melophorus* 1a, *Paratrechina* 1a) were associated with edge habitats. Indeed, of the 571 specimens of *Paratrechina* 1a recorded, only four specimens were not found at the pasture/cropping edge. Such occurrences may be due to abiotic factors such as nutrient concentration at edge habitats, or biotic factors such as prey availability, or interspecific interactions such as competition (Fagan *et al.* 1999; Landis *et al.* 2000)

The frequent and intense nature of physical disturbances associated with crop management and chemical application (Thorbek and Bilde, 2004) combined with the greater clay content (and hence smaller aggregate size) of the soil in cropping land (Andersen, 2003) may render this land use unsuitable for nesting by many ant species. As well as species occurring in woodland but not the other land uses, eleven morphospecies occurred in pasture, but not woodland, indicating the potential value of agricultural matrix habitats. This may be due to competitive exclusion from less disturbed environments (Roxburgh *et al*. 2004), habitat association with particular resources such as grass seeds (Mott and McKeon, 1977), or a preference for areas with greater insolation due to lack of canopy cover (Vanderwoude *et al*. 2000). In addition, four taxa occurred in only CC and CE. However, this apparently specialised distribution may be due to insufficient sampling effort, as two of the four taxa were represented by single records of minute species. There were also a number of examples of closely related taxa displaying consistent and mutually exclusive habitat specificity. For instance *Notoncus* sp. 1 (*Notoncus capitatus* (Forel)) was found only in WC and WE sites, whereas *Notoncus* sp.2 (*Notoncus ectatommoides* (Forel)) was found only in PC, CE and WE sites. As discussed above, potential explanations for this could include a clear habitat preference, competitive exclusion or a combination of these factors. In this instance, it is likely to be preference, as Braby *et al*. (1999) indicates that *N. capitatus* prefers moister environments than *N. ectatommoides*, which prefers drier locations (also Alan Andersen pers. comm.). Furthermore, competitive exclusion appears unlikely, as another study found both species in the same patch of remnant woodland (House *et al*. 2006). Several other such associations were apparent in the CCA biplot, with representatives of the genera *Pheidole*, *Paratrechina* and *Meranoplus* displaying markedly different habitat preferences. Similarly sharply demarcated distributions have been reported in Portugal for the invasive ant *Linepithema humile* (Mayr), which may have been excluded from some areas by a suite of dominant native species (Way *et al*. 1997).

Ecological theory related to edge effects suggests that the assemblage composition at WE should be different to that at WC due to microclimatic differences, altered resource availability and other influential biotic changes (Baldiserra *et al*. 2004; Ries *et al*. 2004; Watson *et al*. 2004). However, in this study, no differences were evident between the two treatments. Whilst this may be due to treatment proximity (minimum of 50 m apart) and subsequent auto-correlative effects, it may also be due to the modified nature of the woodlands that are naturally of an open stand structure, have a long history of stock grazing, are highly fragmented and have been invaded by a range of exotic pasture plants and other weeds. Grazing, for instance, can lead to trampling and altered soil structure and loss of leaf litter and cryptogams, altered ground and shrub layer structure, altered botanical composition favouring less palatable species, nutrient enrichment and transport of weed propagules (Abensperg-Traun *et al.* 1996; Bromham *et al.* 1999). Weed invasion meanwhile can result in changes to hydrology, nutrient cycling, fire frequency and intensity and plant and animal community structure (Levine *et al.* 2003), in addition to altered ground cover structure and impacts upon animal behaviour (Maron and Lill, 2005). Such degradation of habitat quality may mean that much of the 'core' woodland habitat of the region is operating functionally as 'edge' habitat. This may indicate that a priority conservation strategy for the region is to remove threatening processes and use active management to improve the condition of a proportion of woodlands in the region.

3.4.2 Functional group response.

Numerous studies around the world have demonstrated that ants respond predictably to habitat disturbance and stress (Hoffmann and Andersen, 2003; Majer *et al.* 2004; van Hamburg *et al.* 2004; Ottonetti *et al.* 2006). Ant community responses have been simplified in numerous studies by compartmentalising taxa into functional groups based upon their response to disturbance. This is useful in allowing comparisons of ant assemblage responses to similar disturbance regimes that may consist of different species (e.g. in different biogeographical locations), but can be compartmentalised into the same functional groupings. The literature analysis of functional group responses indicated that there may be some globally predictable changes in ant functional group composition between native vegetation and agricultural land-use types. In the field study, there were relatively few statistically significant differences of functional group representation among land uses, although there were some interesting non-significant trends that may merit further investigation. For instance, Opportunistic taxa exhibited a near-significant proportional abundance increase with increasing land-use intensification in the field study and were more prevalent in agricultural than native land-uses types for the literature analysis. The morphospecies *Rhytidoponera* sp. 1 (*metallica* group) in particular was more abundant in intensive land uses such as cropping than the less-disturbed woodland in the field study, but again this was a non-significant trend, and accordingly should be treated with caution. Such trends broadly accord with the summation of disturbance response for this group compiled by Hoffmann and Andersen (2003) and its greater prevalence in habitats of low complexity (Lassau and Hochuli, 2004), and with the findings of Andersen (2003) that Opportunist ants were the most abundant on clay soils. The lack of significant results observed in the present study may be attributable to the fact that all land-use types in the study were subjected to disturbance, and it would be interesting to have compared the data from these sites with those from undisturbed native vegetation, if such sites could be found.

The observed greater mean abundance of Generalised Myrmicinae in PC, WE and WC compared to CC may be due to more favourable nesting conditions due to much-reduced soil disturbance, and to the availability of small seeds from the abundant grass cover in both pasture and woodland. Other groups that displayed a predicted response of declining abundance with increasing intensification were the Subordinate Camponotini and the Specialist Predator group. The former in particular was more prevalent in the woodland core treatment than any other land-use type. This accords with the literature analysis findings, in that both of these groups declined in abundance from native vegetation to agricultural systems.

However, much as Hoffmann and Andersen (2003) reported a mixture of positive and negative responses to disturbance for many genera and species groups, I also found contradictory responses among several taxa within functional groups and genera. For instance, *Pheidole* sp. 3 was more abundant in pasture than woodland, whereas *Pheidole* spp. 2 and 5(b) displayed the opposite habitat association. Similarly, several of the *Crematogaster* species displayed idiosyncratic habitat responses. This was further evidenced by the ANOSIM results reporting greater assemblage dissimilarity among land-use treatments for the morphospecies data than the functional group data. Whilst I did not include functional grouping in the canonical correspondence analysis, several taxa belonging to the climate specialist groups displayed interesting responses to habitat variables. For instance, at least three species of *Melophorus* (hot climate specialist) were associated with bare ground cover (particularly '*Melophorus* 1'), whilst '*Notoncus* 2' (cold climate specialist) was strongly associated with forb cover, perhaps indicating that although this species favours open habitats, it may require broad-leaved cover within such habitats to stabilise microclimatic conditions. Overall, the functional group analysis proved useful in finding some broad trends (i.e. the literature analysis), but was not as sensitive in determining between different land-use types as the morphospecies data. These findings are very much in accordance with those of Nakamura *et al*. (2007), and indicate that whilst very useful, the functional grouping approach (which often only requires identification to genus level), is best used to augment rather than replace finer scale taxonomic analysis.

3.4.3 Distributional complexities and conservation priorities

Whilst a small number of taxa were restricted to the native woodland patches (e.g. Fig. 3.11, b), the vast majority of taxa displayed individualistic responses that included presence in all habitats and populations restricted to, or peaking in, pasture sites. The study did not have a sufficiently exhaustive sampling regime to test the continuum model of faunal utilisation of human-modified landscapes (Fischer and Lindenmayer, 2006), (whereby each species has specific habitat requirements rather than adhering to human-defined concepts of what constitutes 'habitat'). However, the results of within- and between-land-use sampling indicate that the model appears to provide a realistic description of biological distribution in complex mosaic landscapes, and that 'habitat' is a species-specific concept (Fischer *et al.* 2004).

These field results also point to the underestimation of the conservation value of landscape components sometimes dismissed as an inhospitable matrix. For instance, many taxa found in woodlands were also found in pastures, whilst others were restricted to pastures. The pastures may operate as a surrogate habitat for species that inhabited the extensive swathes of native grassland that formerly occupied the more productive soils of the region (Fensham, 1997; Fensham and Fairfax, 1997). They may also provide important ephemeral and/or spatially scattered resources for a number of taxa, and they appear to increase ant richness at the landscape scale by providing habitat for species not present in woodlands (at least during the narrow sampling window). From a conservation perspective, this is important, as native grasslands (let alone mixed-native/exotic pastures) are often undervalued in terms of conservation value, particularly for fauna (Williams and Cary, 2001; Fischer *et al.* 2004; Sheahan, 2009). The value of the matrix for biodiversity has long been recognised in the semi-natural landscapes of Europe that have long been managed primarily for agricultural production (Sutherland, 2004), and is now beginning to receive attention in regions of the world where biodiversity conservation has generally been restricted to reserved areas and remnants of native vegetation in human-dominated landscapes (Hughes *et al.* 2002; Haslem and Bennett, 2008a). For instance, Fischer *et al.* (2005) state that the matrix is vitally important for wildlife and that by including the matrix in conservation management, one is able to include the most productive parts of the landscape. A ‘softening’ of the matrix (maintenance of a mosaic of land uses, use of native perennial pastures, retention and promotion of non-production components such as paddock trees, reduced-intensity cropping management, etc.) may help maintain resources for declining taxa (Manning *et al.* 2004; Maron, 2005) and increase landscape connectivity (Fischer *et al.* 2005; Attwood *et al.* 2009). Increased connectivity due to sympathetic matrix management may also aid the incremental relocation of assemblages due to climate change (Donald and Evans, 2006).

Despite the positive biological attributes of the pasture matrix, the areas in which ants were most diverse were woodlands. Several of these remnants were small (smallest was seven hectares), but still contained a wide range of taxa, thus supporting the argument of Fischer and Lindenmayer (2001) that small habitat patches are of considerable conservation value and may provide important habitat for less area-sensitive taxa such as invertebrates. However, Tscharntke *et al.* (2002) reported that whilst small habitat patches may be sufficient for polyphagous and generalist species, more specialist taxa are often lost.

Habitat condition is also a major determinant of taxonomic assemblage. For instance, Driscoll and Weir (2005) found that different beetle species responded differently to habitat condition. Bromham *et al.* (1999) found that ants of the genera *Camponotus* and *Iridomyrmex* were more abundant in grazed compared to ungrazed woodland, whilst spiders of the families *Amaurobiidae* and *Zordaridae* showed the opposite trend. The woodlands in that study exhibited greater species richness than the agricultural land uses and contained assemblages distinct from the other land-use types. This implies that even degraded remnants of native vegetation are a source of biological value in highly modified agricultural landscapes and hence are a priority for protection and sympathetic management.

Based on these findings, at least some components of ant (and possibly other arthropod) biodiversity can be retained in agricultural landscapes via a mixed land-use mosaic that incorporates woodland patches and areas of pasture. Loss of woodland remnants (as much through senescence and degradation as through land clearing) would probably lead to the loss of the many species restricted to, or predominantly present in, woodlands. A move to broadacre cropping (unlikely in this region, but common practice elsewhere) would probably result in enormous biodiversity loss due to the extirpation of both woodland-associated and grassland-associated species.

Chapter 4

Agricultural land-use type influences body size and morphology of arthropod assemblages

4.1 Introduction

Measures such as taxonomic richness, abundance and feeding guild representation are often used to investigate the impacts of land use and management on biotic assemblages. However, other potential complementary approaches for assessing the impacts of land-use disturbance and modification on arthropod assemblages include comparisons of body size (Braun *et al*. 2004) and morphology (Ribera *et al*. 2001). Body size patterns and comparisons of morphological features, both within species and within assemblages (i.e. across species), may be particularly useful indicators of system disturbance as they are correlated with various aspects of organism life history, such as reproduction rate, developmental rates and dispersal (Braun *et al*. 2004; Magura *et al*. 2006), which are in themselves related to taxon and assemblage abilities to recover from disturbances and recolonise areas after disturbance (Siemann *et al*. 1999). Body size and morphological patterns can also be related to ecological interactions relating to interspecific competition and resource use (Gotelli and Ellison, 2002; Magura *et al*. 2006), and may be useful as indicators of environmental stress or disturbance (McGeoch, 1998).

Numerous studies have focussed upon the across species changes in body size metrics of arthropod (often carabid beetle) assemblages along urban or rural/urban gradients (e.g. Niemalä *et al*. 2002; Alaruikka *et al*. 2002; Ishitani *et al*. 2003; Magura *et al*. 2006) and in landscapes of differing disturbance and composition (e.g. Burel *et al*. 2004). However, studies examining body size and morphological changes within agricultural landscapes consisting of land uses of differing levels of intensification, disturbance and modification are much scarcer, with a study by Ribera *et al*. (2001) being a notable exception. A potential advantage of studies of body size and morphological attributes is that they do not necessarily require taxonomic analysis beyond the level of order or family (although within-taxon analyses are relatively common in the literature), thus rendering such studies well within the capacity of the non-expert, or suitable for very rapid data processing.

An overarching conceptual premise of how environmental factors shape and influence biological characteristics is the habitat templet concept (Southwood, 1977; Ribera *et al*. 2001; Statzner *et al*. 2001). This states that habitat provides the templet upon which evolution forges species traits and characteristics (Ribera *et al*. 2001;

Statzner *et al.* 2001), whilst at the same time acting as a filter to sort species according to their current morphological characteristics and life history strategies. This latter process determines which taxa are able to occupy and persist in a particular habitat type (Ribera *et al.* 2001). Where habitats have remained relatively stable for a sufficient length of time for evolution to act, it may be that selection for traits that confer adaptation to the local environment are the dominant feature in shaping these species' traits and hence determining the composition of biotic assemblages. For instance, in deserts there are certain morphological and life history traits associated with water retention and coping with high diurnal temperature fluctuations that are common among many taxa and expressed in convergent evolution (for instance fused elytra that can reduce water loss in desert-dwelling ground beetles; Stantzer *et al.* 2001).

In habitats that have been altered relatively recently, however, the incumbent biological assemblages are far more likely to have been influenced by the 'filtration' process than the evolutionary one. Such is the case with agricultural landscapes, where frequently changing land uses, shifting land-use/habitat boundaries and fluctuating frequency and intensity of disturbance regimes are likely to lead to biological assemblages that are in a state of non-equilibrium (Wallington *et al.* 2005). Where this occurs in a mosaic of different land-use and land cover types, such as in mixed land-use farming landscapes, the array of land uses and differing disturbance regimes can lead to a correspondingly complex array of biotic assemblages. Such complexity is not only expressed taxonomically, but also in terms of common morphological features and life-history characteristics. Such morphological responses have been found by McIntyre (2008) for plant leaf traits in agricultural land-use types of differing intensity and modification, with observations including an increase in specific leaf area as land-use intensity (grazing, fertilisation and cultivation) increased.

When applied to arthropod assemblages, such a phenomenon may become particularly apparent in more disturbed environments, with arthropod assemblages displaying more similar morphological and life history traits (effectively trait homogenisation) in highly disturbed environments (Stantzer *et al.* 2001). In the context of an agricultural landscape, intensively managed cropping systems are highly modified from the native systems that originally occupied that land, are subject to rapid plant growth and biomass removal through harvesting, and are subjected to physical and chemical disturbance events such as tillage, harvest and agro-chemical application (Thorbek and Bilde, 2004). Consequently, one can reasonably expect that certain morphological traits may be more evident in the most intensively managed land-use types in a mosaic production landscape, such as cropping, compared to less intensively managed land uses. The habitat filtration processes that help shape community composition may be especially prevalent in agricultural landscapes in regions where agriculture is a relatively recent introduction, such as Australia. In such regions, evolutionary processes will have adapted biota to indigenous vegetation systems and environments with characteristically low or infrequent levels of disturbance, with agriculture very recently modifying or replacing these systems, forcing recent and rapid changes in assemblage composition (Attwood *et al.* 2008; see Chapter 2).

Other studies that have examined arthropod size and morphological responses to disturbance, habitat condition and habitat succession have found a range of trends. For instance, some studies (e.g. Siemann *et al.* 1999; Cunningham and Murray, 2007) have indicated greater abundance of small-bodied organisms in late successional compared to early successional habitats. Explanations for such patterns include shifts in feeding guild representation that are in turn related to body-size patterns (Cunningham and Murray, 2007).

Meanwhile, numerous other studies have reported a prevalence of species with smaller body size and a greater occurrence of more vagile taxa in more disturbed environments (e.g. Blake *et al.* 1994; Magura *et al.* 2006; Gobbi *et al.* 2007). Others have found more subtle patterns in the frequency of morphological traits in response to disturbance, such as trends in carabid trochanter and femora structure that in turn have indicated trends in feeding guild assemblage composition (Ribera *et al.* 2001) and locomotion (Ribera *et al.* 1999). Whilst many studies have focussed upon a particular group of arthropods (often beetles of the family Carabidae), others have examined more than one group and found different responses, such as carabid beetle body size declining along a disturbance gradient, but spider body size displaying no response (Alaruikka *et al.* 2002).

Due to increasingly frequent and intense disturbance events, mean organism body size and presence of apterous/brachypterous and large-bodied taxa often decrease as land use intensifies (although see Siemann *et al.* 1999; Braun *et al.* 2004 and Cunningham and Murray, 2007 for other patterns of response), and that abundance of small-bodied individuals and macropterous taxa can increase with increased land-use disturbance (Gray, 1989; Ribera *et al.* 1999 & 2001). However, the relative proximity of land uses of differing levels of disturbance in agricultural landscapes typical of southern Queensland may lead to a more diffuse and uniform distribution of morphological traits across the landscapes, as individuals move relatively freely between land-use types. Related to this is the fact that all components of the sampled landscapes in this study are subjected to production activities—for instance, the native woodland remnants are unfenced, grazed and frequented by cattle and hence are subjected to a similar disturbance regime as the pastures, despite having a different habitat structure. Therefore, this study sought to investigate if the mean of morphological traits observed across all individuals of a particular group (e.g. body size of all spiders, body size of all lycosids, wing morphology of all beetles) varied with habitat disturbance and modification in a complex fine-grained mosaic landscape consisting of different land-use types. Furthermore, given that various studies have found inconsistent patterns of morphological traits among different taxonomic groups in response to disturbance (e.g. Alaruikka *et al.* 2002), I sought to explore if observed morphological differences are consistent across three broad taxonomic groups (Araneae, Coleoptera and Formicidae) and within finer scale taxonomic groups (e.g. family and genera).

The specific research questions were:

1. Do mean arthropod body sizes decrease along a gradient of increasing land-use intensification?
2. Are more macropterous individuals and fewer apterous/brachypterous individuals present in more disturbed/modified habitats?
3. Are observed patterns in morphological traits among land-use types consistent among different taxonomic groups?

4.2 Method

4.2.1 Study area and study sites

The study was performed at the study sites detailed in Chapter 3, in the rural areas around Pittsworth, Felton, Cambooya and Mt Tyson, west and south-west of Toowoomba in south-east Queensland, Australia (420–560 m a.s.l., 27°26′–47′S, 151°33′–51′E). For details of regional climate, soil and vegetation associations, see Methods section (Section 3.2.2) of Chapter 3.

4.2.2 Experimental design

As with the sampling of ant morphospecies, arthropods were sampled in grazed remnants of native woodland, grazed pasture/grassland and cereal crops, during October and November 2005. No lower area size limit was set for the inclusion of woodland patches, as small, highly fragmented areas of native woodland are a dominant feature of the region. The size of woodland patches ranged from 7 ha to over 100 ha. Pasture/grassland sites were areas cleared of wooded native vegetation that had been converted to grassland or had undergone pasture improvement via reseeding and fertilisation. In most cases, the ground vegetation cover was a combination of both native and exotic species. All woodland remnants and pasture/grassland sites were grazed during or close to the time of sampling. Cropping sites were restricted to cereal cropping (oats, wheat or sorghum), but owing to prolonged drought (and therefore reduced cropping activity) this included both standing winter crops and stubble from the previous summer’s crop.

The sampling design was the same as described in detail for the ant morphospecies collection in Chapter 3 (Section 3.2.3). The spatial arrangement of the landscape mosaic in the region followed a consistent pattern: woodland remnants on higher, rockier ground, grassland/pastures on the mid-slopes, and cropping land on the lower slopes and deeper soils. This allowed a block design for the study, but because of the consistent landscape arrangement, this was non-randomised. A transect was established that represented a gradient of land-use intensification, incorporating the three land-use types. This transect was replicated a total of ten times across the region, spanning eight different properties (See Figures 3.3 and 3.4, Chapter 3). Due to trampling by cattle during sampling, all sampling points along one transect were destroyed, as well as the cropping core and cropping/pasture interface from another site. This resulted in nine replicates each of woodland core (WC), woodland/pasture edge (WPE) and pasture core (PC) and eight replicates of cropping core (CC) and pasture/cropping edge (PCE).

Sampling points were located at five positions along the transect: the core of each land-use type and the two interfaces (in order, WC, WPE, PC, PCE & CC). The sampling point in the core of each land-use type was randomly located along the transect, but with the criterion that it must be situated a minimum of 50 m from adjoining land uses. Therefore, each land-use core sampling point was at least 100 m from the next core sampling point. For the edges, a sampling point was randomly located along the land-use interface. For further details of the sampling design, see Methods, Chapter 3.

4.2.3 Arthropod sampling

Surface-dwelling arthropods were sampled using pitfall traps, consisting of plastic containers with an opening diameter of 115 mm and a depth of 80 mm. Five traps were placed 5 m apart from each other at each sampling point and allowed to settle with lids on for seven days to reduce digging-in effects (Greenslade, 1973). In order to capture a comprehensive picture of each edge, traps were placed either side of the line of land-use interface, but no more than 0.2 m into the adjacent land use. The interface of pasture and cropping was determined as the point where the pasture abutted the complex of crop plants and bare ground that constituted the outermost perimeter of the crop field (generally c.0.5 m in width). The interface of pasture and woodland was determined as the edge of the tree drip (extent of canopy projection) line. Traps were then half-filled with 30 % ethylene glycol solution and a few drops of household detergent. All traps were simultaneously opened for four days and nights in November 2005. Traps were then removed, and the contents transferred to 70 % ethanol.

4.2.4 Arthropod measurements

A range of measures and observations were used for the focal taxa (all measurements taken using callipers accurate to 0.05 mm):

Spiders

The maximum width of the carapace and the longitudinal length of the carapace of all spider specimens were measured. Spider data analyses were conducted for “all spiders” (all specimens included), “adult spiders” and members of the families Linyphiidae and Lycosidae. Adult spiders were defined as those that had obviously developed palps or epigyne.

Beetles

The maximum pronotum width, pronotum length, maximum elytra width, elytra length and total body length (pronotum + elytra) were measured for each beetle specimen.

All beetles were dissected (removal of elytra) to determine if wing morphology was macropterous (developed wing), brachypterous (small, rudimentary wings) or apterous (no wings).

Ants

Ants were measured using 'Weber's length' (Weber, 1946; Brown, 1953), the distance from the posterior-most border of the metapleural lobe, to the anterior-most border of the pronotum, excluding the neck. As the number of ants was an order of magnitude greater than that of spiders and beetles, a subset of measurements was taken for each identified morphospecies. The mean of 10 individuals (or, if fewer than 10 available, the number of available individuals of a particular taxon) were taken, and multiplied by the total number of individuals of that species in each pitfall trap and treatment. For dimorphic ants such as *Pheidole* spp., only the minor workers were included in the calculation.

4.2.5 Data treatment and analyses

4.2.5.1 Mean body size

The grand mean body size (for each individual for beetles and spiders, for each taxon for ants, see above) at each site was calculated as the average size measure of every individual per pitfall trap. This was then averaged across all pitfall traps at a site for each treatment. Finally the mean body size for each treatment was calculated.

4.2.5.2 Body size class

Taxa were categorised according to body size classes as in Table 4.1. The total number of individuals in each body size class was used to generate the mean values for this analysis.

Table 4.1. Body size measurement classifications for ants, beetles and spiders.

Body size measure	Size class 1	Size class 2	Size class 3	Size class 4
Spider carapace width	<1 mm	1–2 mm	2–4 mm	>4 mm
Beetle total body length	<2 mm	2–5 mm	5–10 mm	>10 mm
Ant pronotum length	<1 mm	1–2.5 mm	>2.5 mm	N/A

4.2.6 Statistical analysis

Prior to analysis, data were logN transformed and tested for normality of distribution. Repeated measures ANOVA was used to test for differences in mean body size, body size class and wing morphology, with land-use type as the repeated measure. This followed the methods used by Magura *et al.* (2006), who used this approach in order to ensure independence of treatments in relatively close proximity along a gradient of increasing anthropogenic disturbance. Where Mauchly's assumption of sphericity was violated, a re-calculation of the F-ratio was conducted using new degrees of freedom, calculated using the Huynh-Feldt epsilon. Where a significant within-subject effect was detected, differences between each treatment were tested using paired t-tests. In order to explore the asymmetry of data for spiders and beetles among land-use types, I also calculated the skewness and Kurtosis of the data across land-use category. All analyses were performed using SPSS 14.0 for Windows (SPSS for Windows, 2005).

4.3 Results

4.3.1 Araneae

4.3.1.1 Mean body size

A total of 1052 spiders were trapped across the five land-use categories (159 in WC, 190 in WPE, 178 in PC, 244 in PCE and 281 in CC). Grand mean carapace width and carapace length differed among land-use types for both 'all spiders' (adults and immatures) and adult spiders only (Fig. 4.1 & 4.2; Table 4.2). Both carapace width and length declined with increasing land-use intensification/modification, with very similar results for both size measures and for all spiders combined and adult spiders only.

4.3.1.2 Body size class

The high abundance of size class 1 spiders (<1 mm) in the pasture/cropping interface (PCE) and the cropping core (CC) (Fig. 4.3 & Table 4.2) appeared to be driving the decline in mean spider body size observed in Figs. 4.1 & 4.2. Significantly more very small spiders were found in PCE and CC than the pasture or woodland treatments, whilst no differences were found in the abundance of other size classes among land-use categories.

Fig. 4.1

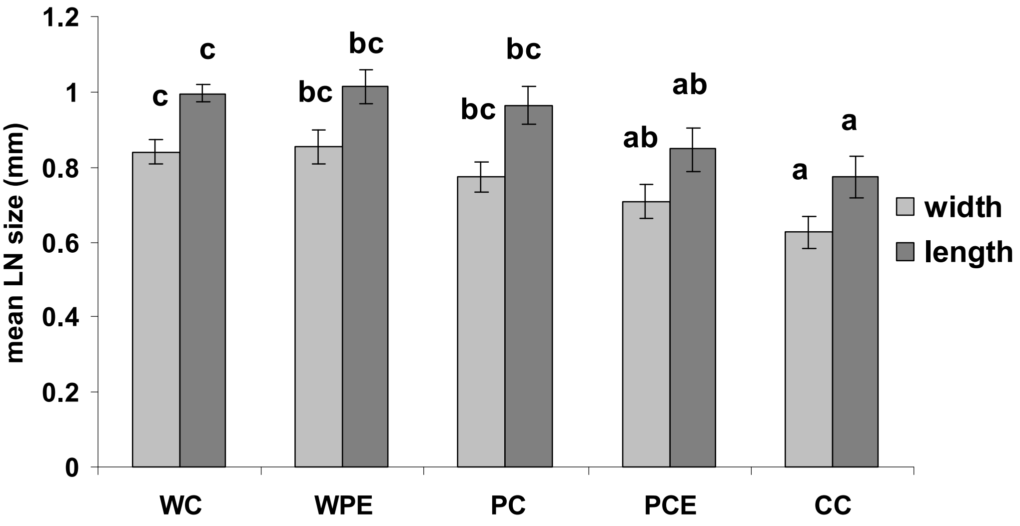

Fig. 4.2

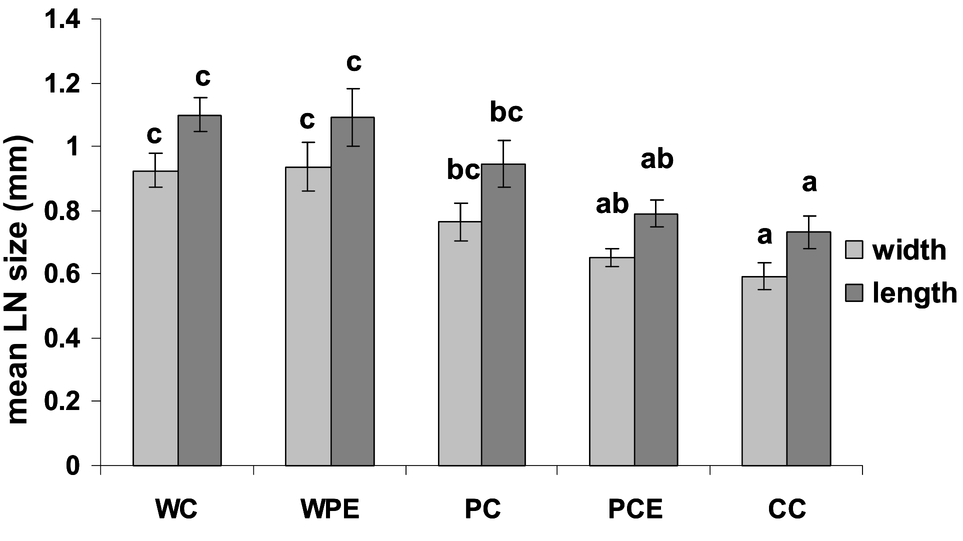

Fig. 4.1 and 4.2. Grand mean LN spider carapace width and length for all spiders (4.1) and adult spiders (4.2) across land-use types. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC. Error bars are S.E. of mean and different letter denotes significant difference for paired t-tests among treatments at $\alpha = 0.05$

Table 4.2. Repeated-measures ANOVA results for grand mean Araneae body-size statistics among different land-use treatments. D.f. = 4,28 in all cases.

Measure	**F**	**P**
mean spider carapace width among land uses (all spiders)	5.088	0.003
mean spider carapace length among land uses (all spiders)	4.554	0.006
mean spider carapace width among land uses (adult spiders)	10.702	<0.001
mean spider carapace length among land uses (adult spiders)	8.957	<0.001
mean abundance of spiders in size class 1 (<1mm) among land uses	7.749	<0.001
mean abundance of spiders in size class 2 (1–2 mm) among land uses	2.329	0.081
mean abundance of spiders in size class 3 (2–4 mm) among land uses	0.512	0.728
mean abundance of spiders in size class 4 (>4 mm) among land uses	1.031	0.411

4.3.1.3 Within-family

Within-family mean body size (carapace width and length) for Lycosidae and Linyphiidae was similar among land-use categories, although the frequent absence of individuals of these families from numerous sampling sites prohibited further analysis (i.e. Linyphiidae frequently absent from some woodland sites and Lycosidae frequently absent from all treatments at some sites). However, the similar mean body sizes and overlapping error bars in Fig. 4.4 & 4.5 indicate little difference among treatments for either family.

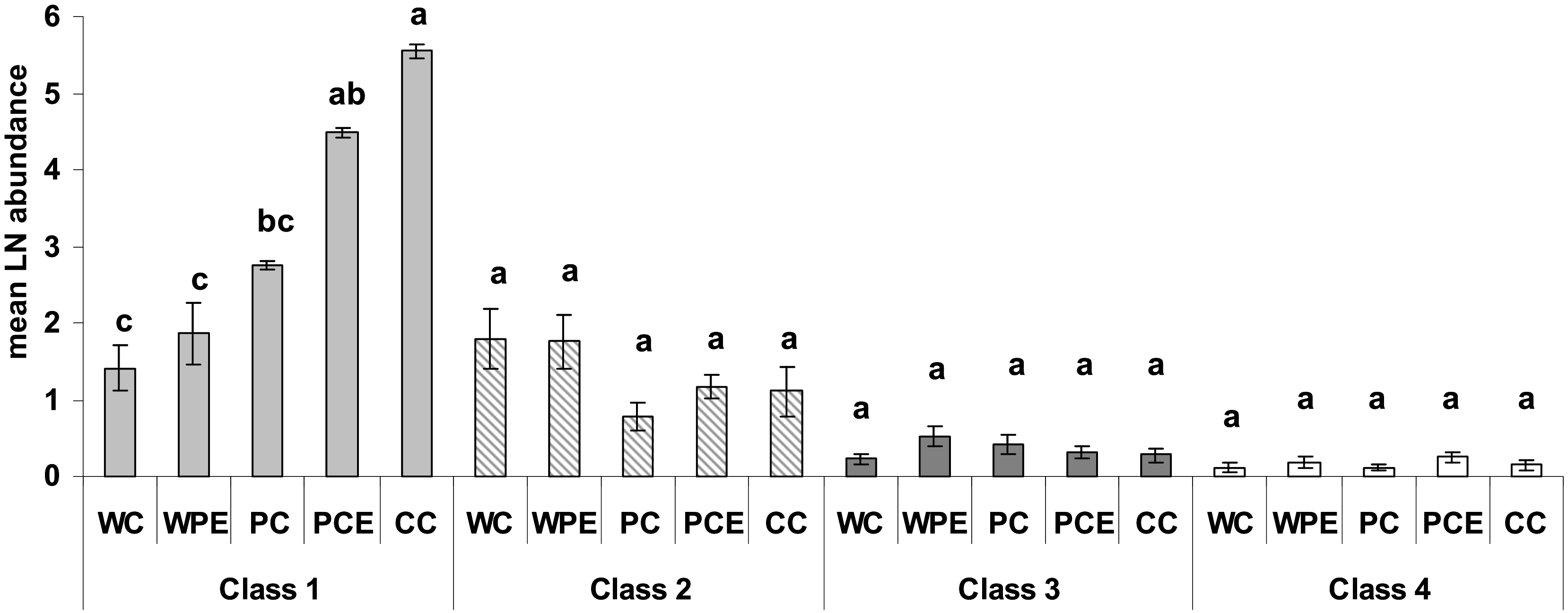

Fig. 4.3. Grand mean LN abundance of spiders in four size classes (based upon carapace width for all spiders) across land-use types. Size class attributions are Class 1 – <1 mm; Class 2 – 1–2 mm; Class 3 – 2–4 mm; Class 4 – >4 mm. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC. Error bars are S.E. of mean and different letter denotes significant difference for paired t-tests among treatments at $\alpha = 0.05$.

Fig. 4.4

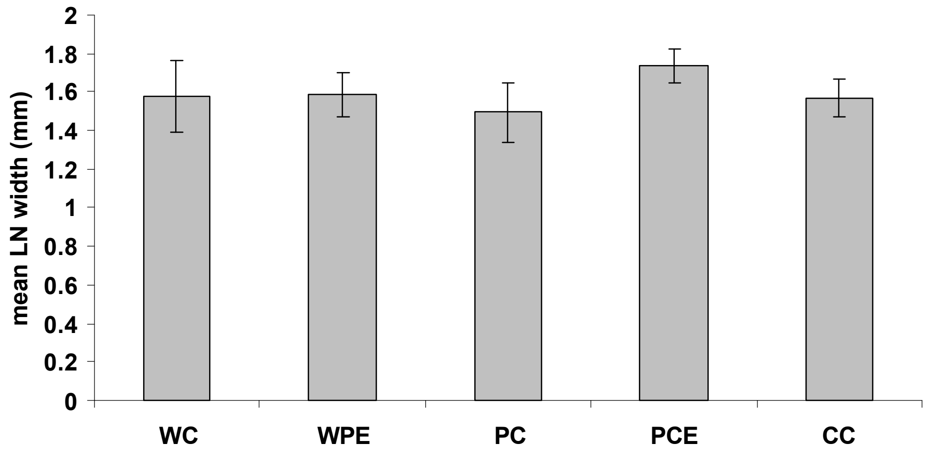

Fig. 4.4 Grand mean LN carapace width of a) Lycosidae spiders among land-use categories. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC. Error bars are S.E. of mean.

Fig. 4.5

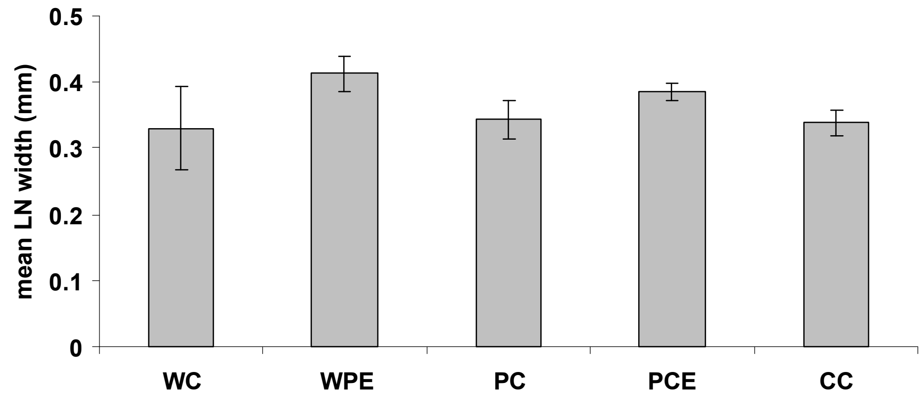

Fig. 4.5 Grand mean LN carapace width of Linyphiidae spiders among land-use categories. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC. Error bars are S.E. of mean.

4.3.1.4 Skewness and Kurtosis

Measures of spider carapace width/length data skewness and Kurtosis indicated the asymmetry of distribution of body size data in each land-use category (Figs. 4.6-4.9). The trend for high abundance of smaller spiders in the more highly disturbed and modified land-use types detected in the previous analyses are particularly evident in Fig. 4.8 and 4.9, where the higher skewness and Kurtosis values in PCE and CC indicate that more small individual adult spiders were present in these land-use types. The relatively low skewness and Kurtosis values observed in the WC and WPE treatments (see Fig.4.8 and 4.9) indicate fewer small spiders and/or more large spiders in these less disturbed/modified environments.

Fig. 4.6

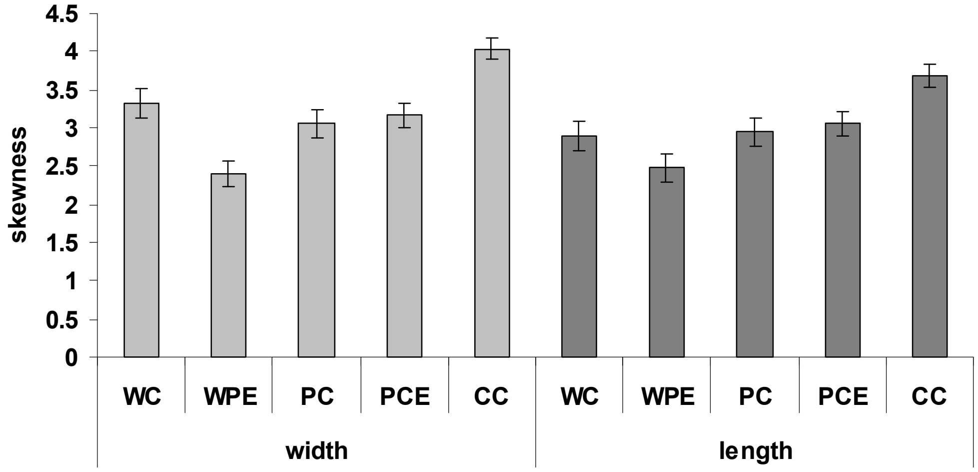

Fig. 4.6. Skewness values for ‘all spider’ carapace width and length measurements. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC.

Fig. 4.7

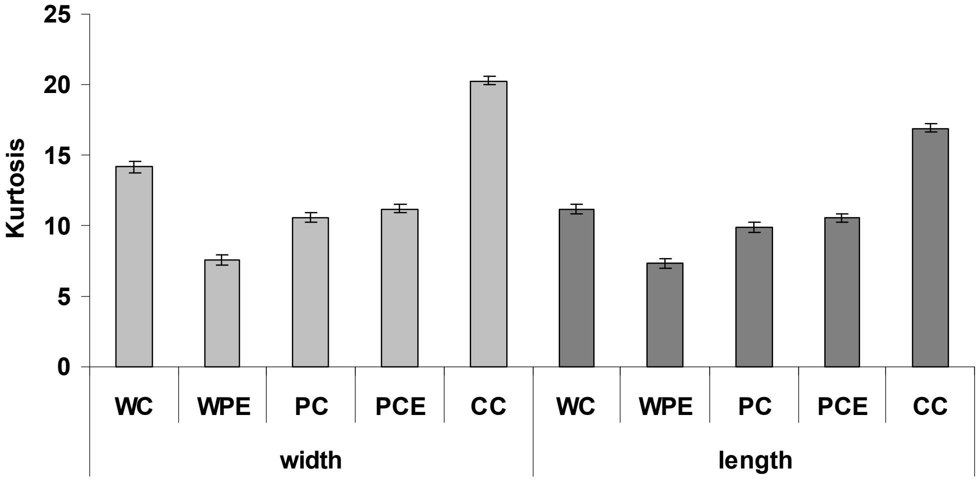

Fig. 4.7. Kurtosis values for ‘all spider’ carapace width and length measurements. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC.

Fig. 4.8

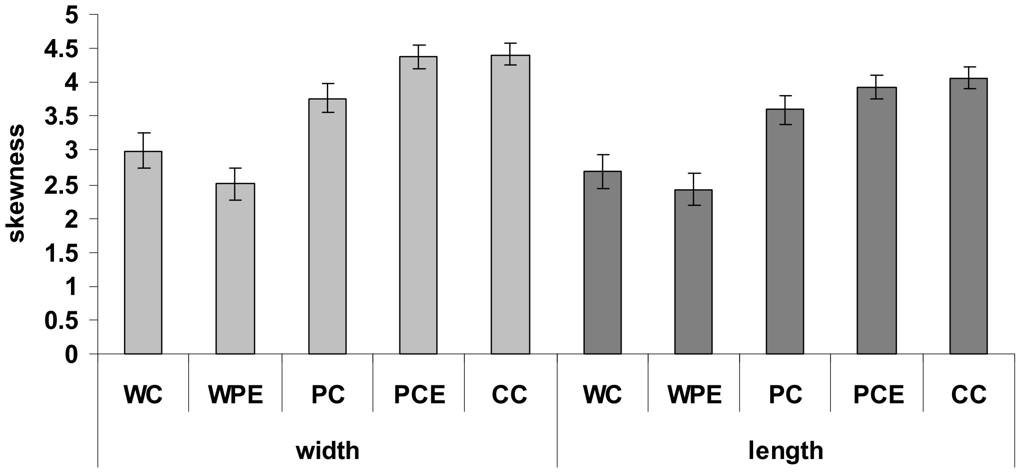

Fig. 4.8. Skewness of adult spider width and length measurements. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC.

Fig. 4.9

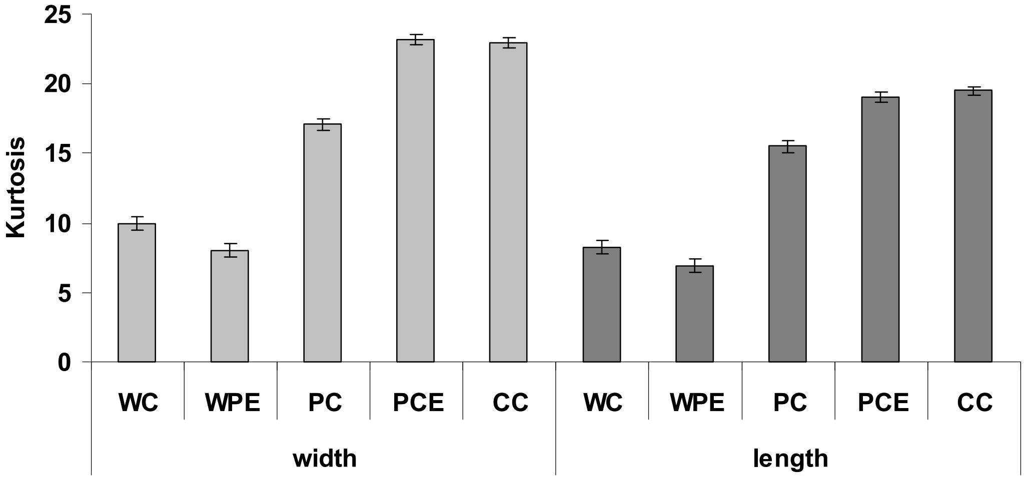

Fig. 4.9 Kurtosis of adult spider width and length measurements. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC.

4.3.2 Coleoptera

4.3.2.1 Mean body size

A total of 751 beetles were collected across the five land-use categories (91 in WC, 117 in WPE, 109 in PC, 228 in PCE and 206 in CC)..Despite an apparent trend for decreasing mean beetle body size with increasing land-use intensification/modification for several body size measures (Fig. 4.10), only mean pronotum length differed significantly (Table 4.3). Subsequent paired t-tests did not find any differences for mean pronotum length among individual land-use pairs, however. No other significant differences were found for mean body size among land uses, which may be due to the high within-treatment variability that was found for all body-size measures. This is in contrast to the observed significant decline in body size of spiders along the land-use intensification gradient (Fig. 4.1 & 4.2; Table 4.2).

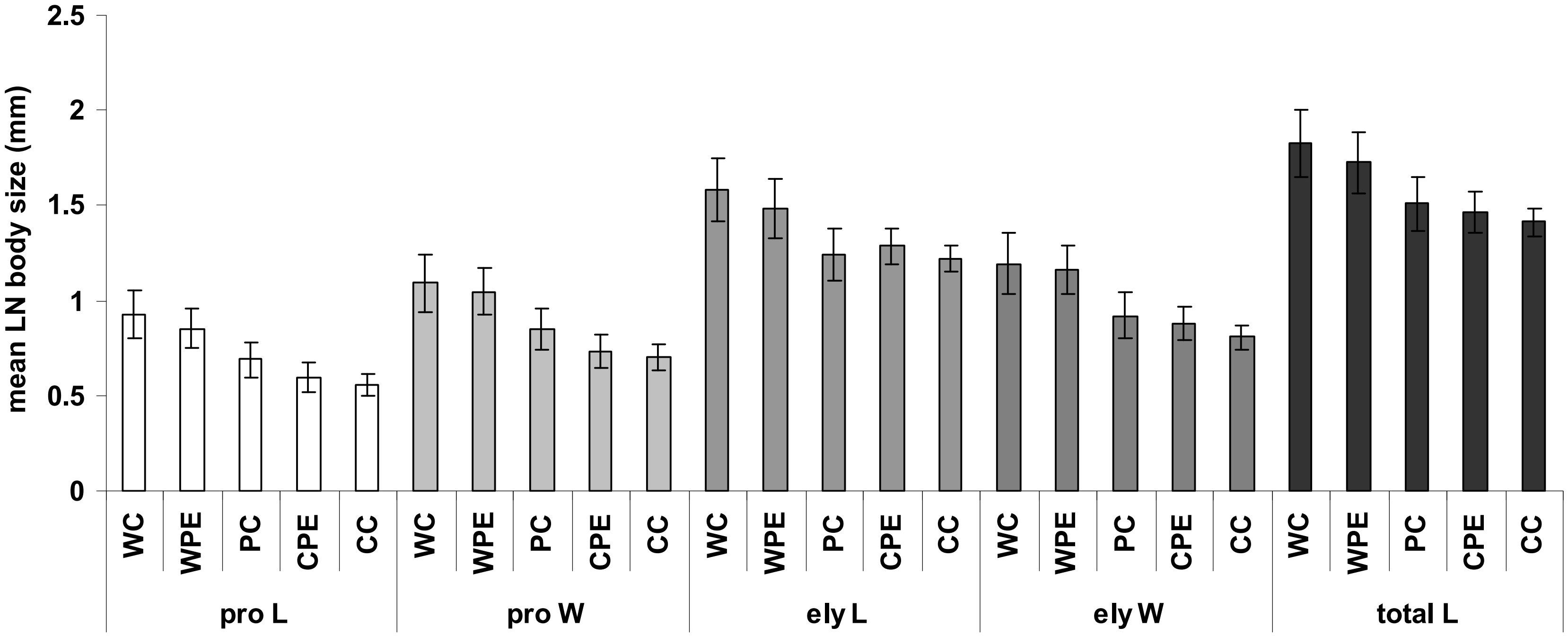

Fig. 4.10. Grand mean LN beetle pronotum length, pronotum width, elytra length, elytra width and total body length (pronotum length + elytra length) across land-use types. Measurement abbreviations: 'pro L' – pronotum length; 'pro W' – pronotum width; 'ely L' – elytra length; 'ely W' – elytra width; 'total L' – total body length. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; CPE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC. Error bars are S.E. of mean. There were no significant pair-wise differences.

Table 4.3. Repeated-measures ANOVA results for grand mean Coleoptera body-size statistics among different land-use treatments. d.f. = 4,28 in all cases.

Measure	**F**	**P**
mean beetle pronotum length among land uses	2.747	0.048
mean beetle pronotum width among land uses	2.402	0.074
mean beetle elytra length among land uses	1.381	0.266
mean beetle elytra width among land uses	1.947	0.13
mean beetle total body length among land uses	1.46	0.241
mean abundance of beetles in size class 1 (<2mm) for total body length, among land uses	3.408	0.022
mean abundance of beetles in size class 2 (2–5mm) for total body length, among land uses	4.556	0.006
mean abundance of beetles in size class 3 (5–10mm) for total body length, among land uses	0.078	0.989
mean abundance of beetles in size class 4 (>10mm) for total body length, among land uses	2.926	0.039
mean abundance of winged (macropterous) beetles among land use types	5.726	0.002
mean abundance of apterous and brachypterous beetles among land use types	2.033	0.117

4.3.2.2 Body size class

Whilst there were few differences reported among land uses for mean beetle body size, mean abundance in three of four size classes indicated significant differences (Fig. 4.11 & Table 4.3). These tended to show increased abundance of small individuals (size classes 1 & 2) in the more disturbed and modified land-use types than the less disturbed/modified land-use types. Significantly more beetles of size classes 1 (<2 mm body length) and 2 (2–5 mm) were present in the cropping core (CC) and cropping/pasture edge (PCE) than the woodland core (WC). Larger beetles showed less clear responses to land-use type, although beetles in size class 4 (>10 mm) were significantly more abundant in woodland/pasture edge (WPE) than pasture (PC) or cropping (CC).

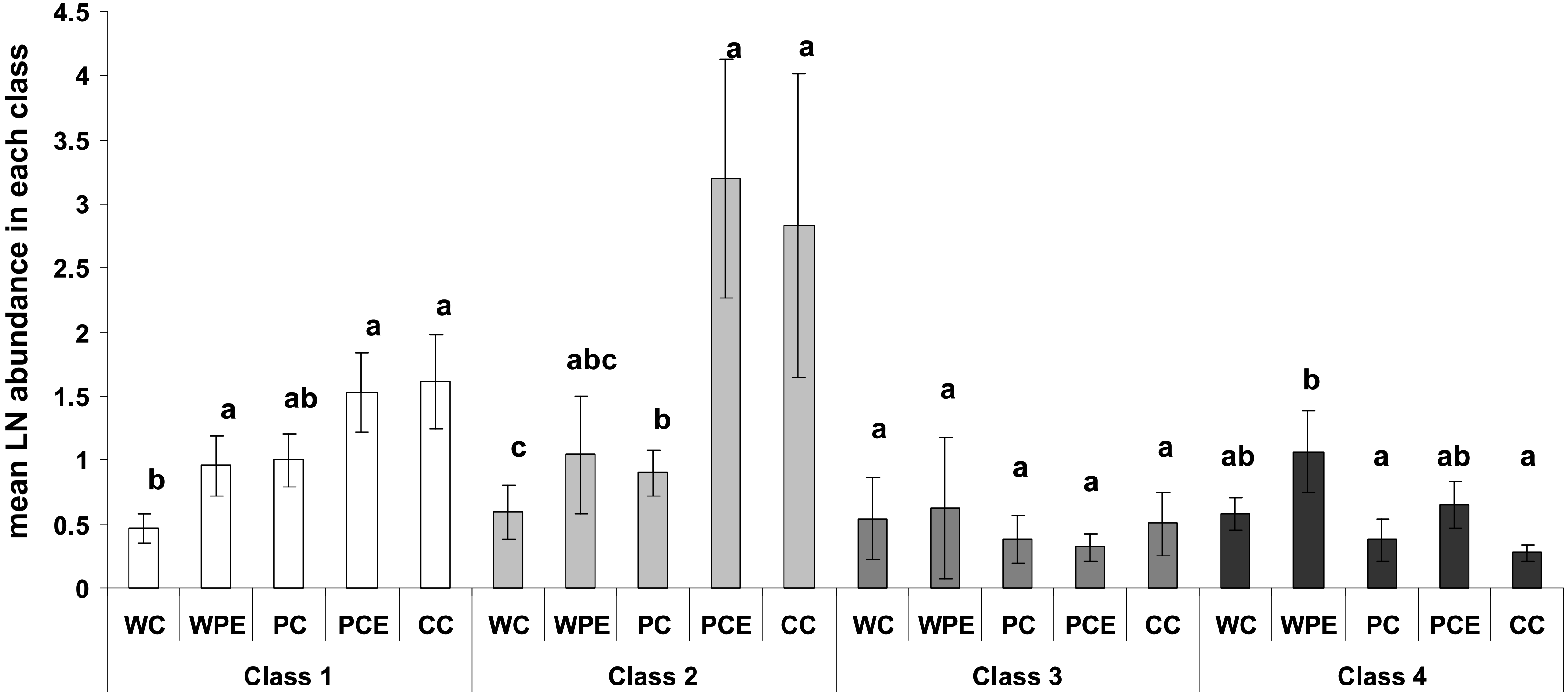

Fig. 4.11. Grand mean LN abundance of beetles in four size classes (based upon body length) across land-use types. Size class attributions are Class 1 – <2 mm; Class 2 – 2–5 mm; Class 3 – 5–10 mm; Class 4 – >10 mm. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC. Error bars are S.E. of mean and different letter denotes significant difference for paired t-tests among treatments at $\alpha = 0.05$.

4.3.2.3 Wing morphology

The abundance of macropterous beetles increased significantly with increasing land-use modification, with abundance of macropterous individuals following the pattern CC>PCE>PC>WPE>WC (Fig. 4.12 and Table 4.3). However, no significant differences were found in the abundance of apterous/brachypterous individuals among land-use types.

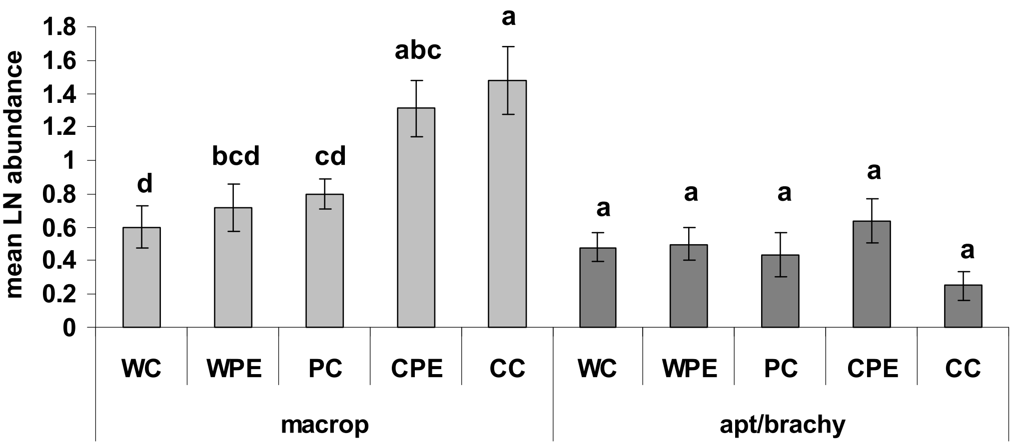

Fig. 4.12. Grand mean abundance of macropterous (winged) and apterous/brachypterous (no-wings/short-wings) beetles among land-use types. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; CPE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC. Error bars are S.E. of mean and different letter denotes significant difference for paired t-tests among treatments at α = 0.05.

4.3.2.4 Skewness and Kurtosis

The beetle data displayed similar responses to the spider data—increased skewness and Kurtosis in more disturbed/modified land uses, indicating a greater number of small-bodied individuals in those land-use types. However, the results appeared even more pronounced for beetles than for spiders (Fig. 4.13 & 4.14).

Fig. 4.13.

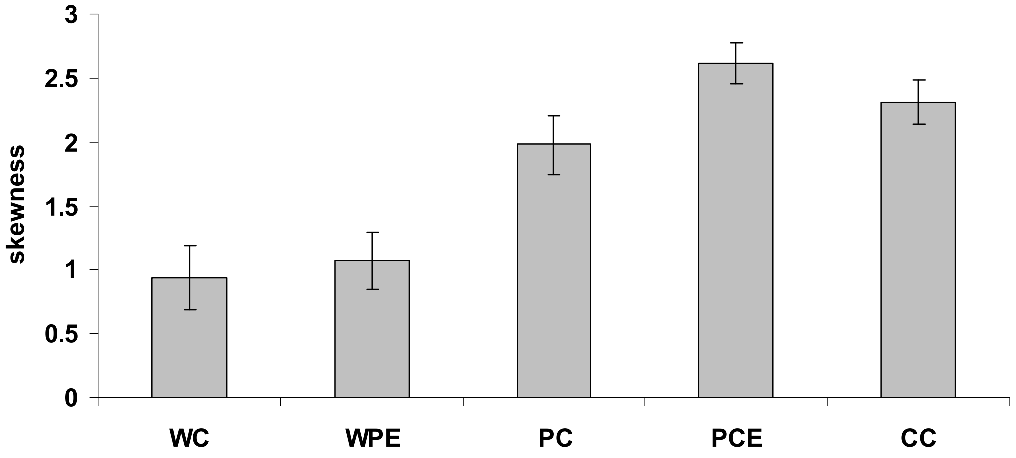

Fig. 4.13. Skewness values for beetle total body length measurements. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC.

Fig. 4.14.

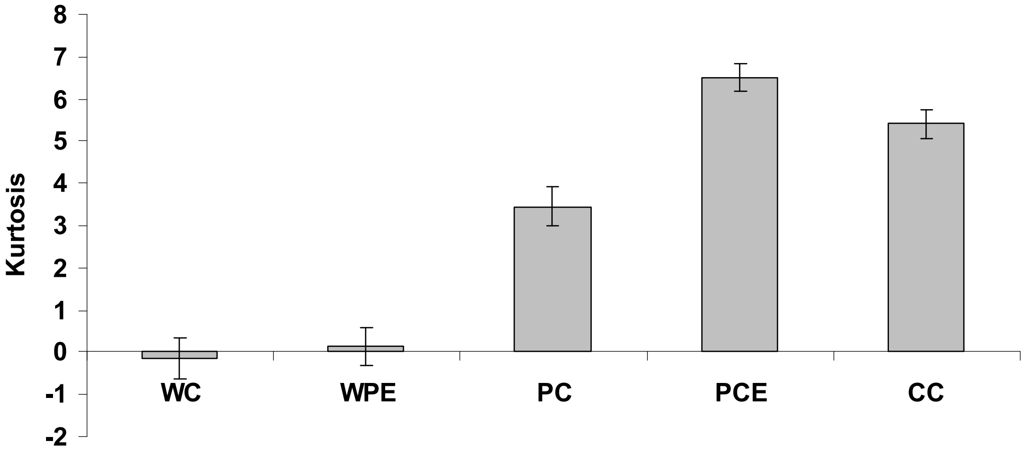

Fig. 4.14. Kurtosis values for beetle total body length measurements. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC.

4.3.3 Formicidae

4.3.3.1 Mean body size

No differences were found in mean ant body size among land-use types (Fig. 4.15; Table 4.4).

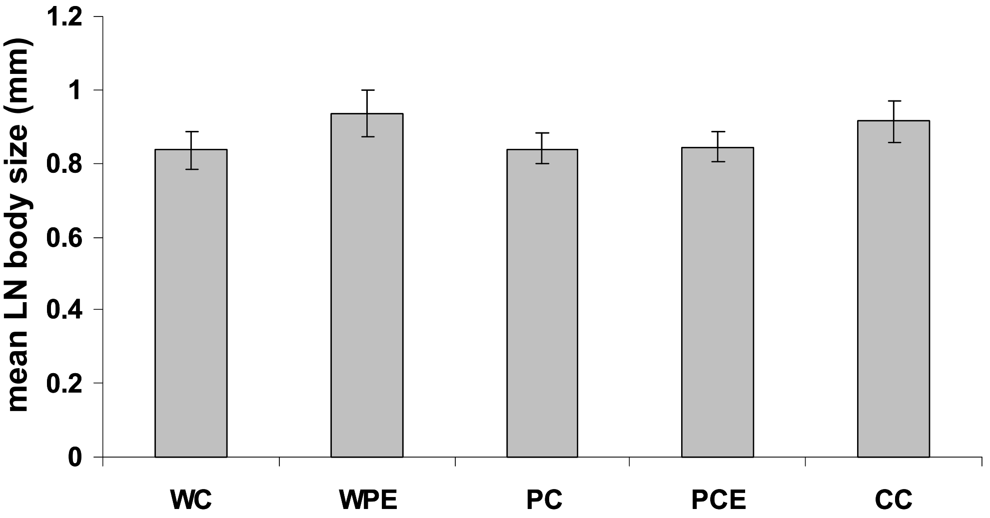

Fig. 4.15. Grand mean LN ant body size across land-use types. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC. Error bars are S.E. of mean.

Table 4.4. Repeated-measures ANOVA results for Formicidae grand mean body-size statistics among different land-use treatments.

Measure	**F**	**d.f.**	**P**
mean ant body size among land uses	0.674	4,28	0.615
mean abundance of ants in size class 1 (<1 mm) among land uses	5.121	4,28	0.003
mean abundance of ants in size class 2 (1–2.5 mm) among land uses	1.273	4,28	0.304
mean abundance of ants in size class 3 (>2.5 mm) among land uses	7.226	2.193,15.353†	0.005

† denotes Huynh-Feldt adjusted degrees of freedom.

4.3.3.2 Body size class

Significantly fewer ants in body size class 1 (small: <1 mm) and class 3 (large: >2.5 mm) were present in the cropping core (CC) treatment than the other land-use types (Fig. 4.16; Table 4.4). However, this may have been a function of significantly lower overall ant abundance in CC (see Chapter 3) than the other land-use types, rather than a specific body-size response. No other differences in body size class were apparent among other land-use types.

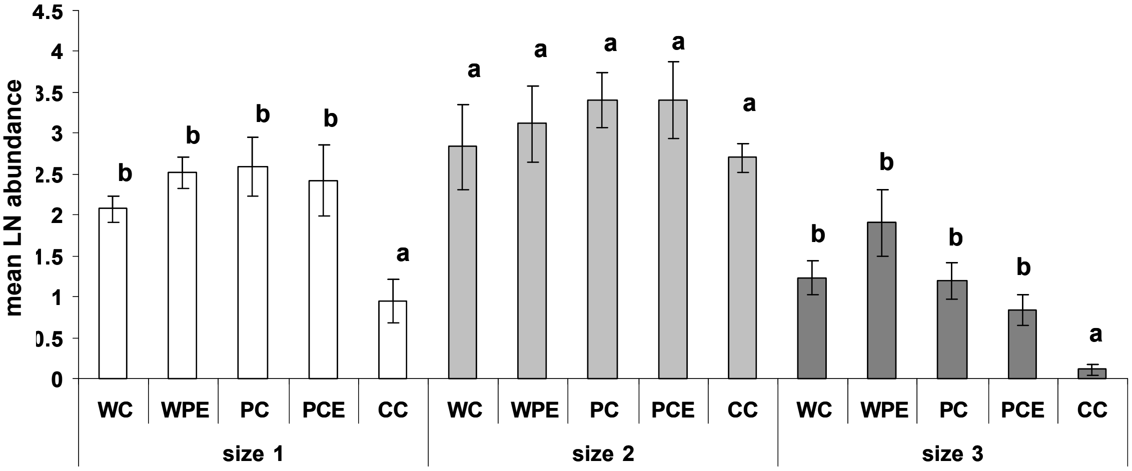

Fig. 4.16. Grand mean LN abundance of ants in three size classes (based upon meta-pleural length) across land-use types. Size class attributions are Class 1 – <1 mm; Class 2 – 1–2.5 mm; Class 3 – >2.5 mm. Land-use type abbreviations: WC = woodland core; WPE = woodland/pasture edge; PC = pasture core; PCE = cropping/pasture edge; CC = cropping core. Replicates are 9 each for WC, WPE & PC and 8 each for PCE & CC. Error bars are S.E. of mean and different letter denotes significant difference for paired t-tests among treatments at $\alpha = 0.05$.

4.4 Discussion

In general, smaller spiders and beetles were more abundant in more disturbed habitats, and highly mobile, winged beetles were more abundant in highly disturbed cropping compared to relatively undisturbed woodland. There were fewer small and large ants in the most disturbed land use (cropping) compared to other land-use types, but this may be due to far lower overall ant abundance in cropping compared to other the land uses. In general, the patterns in morphology showed concordance with expectations that habitat type and degree of modification may act as an environmental filter in terms of trait representation among taxa, but there were a number of responses that appeared to differ across taxonomic groups.

Spider carapace size (width and length) decreased significantly along the land-use modification gradient for all spiders combined (adults and immatures) and adult spiders only, with significantly greater numbers of very small spiders in more intensive land uses. However, there was no difference in the numbers of large spiders in the less-disturbed habitat types compared to the more disturbed areas. Therefore, it appears that the decline in assemblage average body size with intensifying land use was predominantly due to very large numbers of small spiders in the more highly disturbed habitats.

Although not tested statistically (due to absences of these families from some treatments at some sites), there appeared to be little difference in within-family body size for either Lycosidae or Linyphiidae spiders. Linyphiids were far more abundant overall in the cropping (CC) and cropping pasture interface (PCE) than in woodland habitats (not statistically tested due to being absent from most replicates of woodland treatments), which may have been further driving the high numbers of very small spiders in disturbed land uses. This finding was supported by the relatively high values of skewness and Kurtosis for body size data from CC and PCE, indicating that the assemblages in those land uses were dominated by small-bodied individuals. Only mean pronotum length of beetles changed significantly along the land-use gradient. However, all other body-size measures (pronotum width, etc.) displayed a non-significant declining trend along the gradient. By contrast, significant differences in abundance were found among land-use types for three of the four size classes, with more small beetles tending to occur in the intensive land uses. These patterns were strongly supported by the skewness and Kurtosis data, indicating that assemblages in more disturbed/modified land-use types are dominated by small-bodied individuals. Significantly more macropterous beetles were found in the most disturbed/modified habitat (CC) than the less disturbed/modified WC, WPE and PC, but there were no equivalent patterns for apterous or brachypterous taxa.

Finally, ants showed little response other than to confirm that far fewer ants were present in the CC treatment compared to the other treatments (see Ch. 3), except for size class 2, which incorporated specimens of the *Rhytidoponera metallica* (Smith) group, one of the few taxa to proliferate in the cropping core treatment.

4.4.1 Declining spider body size with increasing land-use intensification

The observed decline in spider body size in the more modified land-use types was mainly due to the high abundance of very small spiders in highly modified areas. This was evident in the significantly greater abundance of size class 1 (<1 mm) spiders in the more disturbed areas and the observed high levels of skewness and Kurtosis for spider assemblages in these land-use types, further indicating high abundance of small spiders. It is feasible that greater small-spider representation in highly modified land uses may have been due to higher numbers of immature spiders (from within-field breeding or spillover from adjacent, less-disturbed habitats). However, the difference for 'adult spiders only' was greater than for adult and immature spiders combined, indicating that other factors related to body size may be driving the observed differences. Whilst not statistically tested (due to infrequent occurrence in less modified land-use types), the overall abundance of linyphiid spiders was much greater in the cropping (CC) and cropping/pasture interface (PCE) areas than other treatments, indicating that the results for decreasing spider body size along the modification gradient may have been largely driven by high Linyphiidae abundance in cropping and cropping-edge treatments. This is consistent with the findings of Pearce *et al.* (2005), who reported that linyphiid spiders in south-east Queensland were the most abundant in samples of ballooning spiders in cropping and adjacent field margin and roadside verge sites, and Fitzgerald (2007) who reported high abundances of linyphiids in cropping areas, with very few in woodland remnants. The high numbers of small species may also reflect the ability of spiders, and linyphiids in particular, to colonise agroecosystems by ballooning, following disturbances such as cultivation (Nyffeler and Sunderland, 2003; Thorbek and Bilde, 2004). Whilst the greater abundance of small spiders in cropping may reflect their ability to colonise frequently disturbed environments rapidly (Halley *et al.* 1996), it may also reflect a response to the distribution of preferred, small-bodied prey (Harwood *et al.* 2001). For instance, potential prey for small spiders, such as aphids, are often found in greater abundance in cropping than other less-disturbed land uses (e.g. Favret and Voegtlin, 2001). There are instances of generalist predatory arthropods aggregating according to prey density (e.g. Pearce *et al.* 2006), and this may well be reflected at the individual habitat patch scale (i.e. field or paddock as in this study). Meanwhile, a rather homogenous distribution was reported for lynyphiids in wheat (Holland *et al.* 1999). A further factor potentially influencing spider distribution is that small species and individuals may be occupying cropping areas to avoid predation pressure, possibly from other spider taxa (Wise, 1993) or ants (Schmidt *et al.* 2008). Certainly, the treatment with the highest occurrence of small spiders (cropping) also had the lowest abundance of ants; it is feasible that high ant abundances may mediate numbers of small spiders through predation (Polis and Myers, 1989; Sanders and Platner, 2007) and this may be a potential relationship worth testing in the future.

The quality of habitat and resources have also been proposed as influential determinants of both within- and among-taxon body size (Peters, 1983; Steffan-

Dewenter and Tscharntke, 1997; Cunningham and Murray, 2007), and given that the cropping paddocks contained plants in generally poor health (due to drought), this may indicate that poor habitat quality was influential. Finally, avoidance of competition has been suggested as a reason for non-random body-size patterns in arthropod assemblages, particularly ants (Sanders *et al.* 2007). On this basis, there may be more than one factor influencing the high abundance of very small spiders in cropping areas, but it is likely that rapid colonisation of disturbed areas is a contributory factor.

Larger taxa, being more vulnerable to fragmentation (Gaston and Blackburn, 1996; although see Henle *et al.* 2004), were expected to be less abundant in highly disturbed areas such as cropping. However, this was not the case, with no difference in the abundance of the largest body size class (generally from the families Lycosidae and Oxyopidae) among land-use types. This may be due to the complex spatial arrangement and proximity of land-use types. Given the likelihood that woodland remnants in Australian agricultural landscapes may support lycosid assemblages containing generalist species that have a broad tolerance of different habitat types (Major *et al.* 2006), the spatial arrangement/proximity of other land-use types may permit movement among these land uses. This would enable large generalist predatory hunting spiders to persist, at least temporarily, in other land-use types.

4.4.2 Declining beetle body size with increasing land-use intensification

Whilst differences in mean beetle body size among land uses were less marked than for spiders, there were significantly greater numbers of the two smaller size classes of beetles (<2 mm and 2–5 mm respectively for total body length) in the more intensively disturbed and modified land-use types than the less disturbed land uses. The reasons for this may be related to small-bodied taxa suffering less mortality due to disturbance (Magura *et al.* 2006) and the faster development of smaller taxa and ability to subsist on fewer resources (Peters, 1983). However, when the body-size trends are considered in tandem with the trend for significantly more macropterous beetles in more disturbed/modified land-use types, it indicates that vagility, especially when coupled with an ability to rapidly colonise ephemeral and disturbed habitats such as cropping, may be a major determinant of beetle morphological distribution among land-use types (Ishitani *et al.* 2003; Magura *et al.* 2006). The presence of metathoracic wings has been identified as a morphological feature related to tolerance of disturbed agricultural habitats in carabid beetles (Gobbi and Fontaneto, 2008) and the colonisation of streams following disturbance is related in part to the vagility and dispersal capabilities of organisms (Wallace, 1990).

Conversely, there were no differences in the abundance of apterous or brachypterous taxa among the treatments, indicating that the proximity and complexity of spatial arrangement of landscape components may be sufficient to enable taxa of relatively low dispersal capability to negotiate the landscape.

Whilst there was far more evidence for trends involving small and highly mobile taxa, large beetles (>10 mm body length) were significantly more abundant in the woodland/pasture interface than in pasture or cropping. The majority of these beetles were large, flightless, predatory members of the family Carabidae. It may be that these individuals are using the woodland/pasture boundary as a navigable feature of the landscape (Ferguson, 2000) or are taking advantage of potentially higher densities of prey (Rand *et al*. 2006) that themselves are exploiting a habitat interface.

The results seem to give an indication that dispersal may be a major factor in the morphological traits of beetles in highly disturbed land uses. However, the manner in which I included abundance of all individuals in both mean body size calculations and size class representation within a land-use type, means that the results may be greatly influenced by a few species that occur at very high abundances. If this is the case, it implies that reproductive strategy may be an important determinant of observed body size distribution patterns, with *r*-selected species (*sensu* MacArthur and Wilson, 1967) reproducing rapidly and profusely in highly disturbed, but ephemerally suitable, habitats.

4.4.3 Ant body size and increasing land-use intensification

Although significantly fewer small (size class 1) and large (size class 3) ants were present in the most modified land use (CC) than the other land uses, it appears that this was largely a function of their far lower overall abundance in the cropping core (CC) than the other land-use types, and is discussed at length in chapter 3. However, ants from the *Rhytidoponera metallica* group were rather abundant in the cropping areas (see Fig. 3.11 g). This accounted in part for similar abundances of size class 2 ants (*R. metallica* being in this class) in all treatments. The high abundance of *R. metallica* in a highly modified environment from which many other taxa were absent is consistent with their reputation as a highly disturbance-tolerant organism

(Hoffmann and Andersen, 2003). The lack of differences in body size patterns for mean body size or size class for the woodland pasture and edge land-use types may be, in part, a function of the noisy data that can be associated with social insects and the influence on the results of potentially confounding variables such as distance of trapping points from nests and spatial array of foraging trails.

4.4.4 Alternative body-size/land-use intensification responses

The trend for decreasing body size with increased land-use intensification and modification are in accordance with some of the literature that have studied similar arthropod responses to disturbance/modification gradients (e.g. Blake *et al*. 1994; Ribera *et al*. 2001; Alaruikka *et al*. 2002; Magura *et al*. 2006). However, there is a body of work that has found an opposite relationship, indicating that average body size of arthropods can be greater in early successional habitats (e.g. Siemann *et al*. 1999; Cunningham and Murray, 2007). There are two broad explanatory approaches to this phenomenon: i) reduced body size due to poor-quality resources in late-successional habitats, with small-bodied, specialised herbivorous species advantaged (Cunningham and Murray, 2007) and ii) for some taxa (e.g. wasps) large-bodied species may be better dispersers (Gathmann *et al*. 1994, in Cunningham and Murray, 2007).

The instances in this study where mean body size across a taxonomic group did not decline with increasing land-use disturbance (e.g. ants) are similar to that recently reported by Ulrich *et al*. (2008). They found that the decreasing body size hypothesis (mean body size of an assemblage will decrease with increased environmental disturbance/modification), developed for predatory carabids, could not be generalised to necrophagous staphylinids that displayed no decline along an intensification gradient. It is also possible that many small ants (e.g. many individuals from the genera *Monomorium* and *Pheidole*) were found in the woodland areas because these areas are still subjected to disturbance (cattle grazing) and modification (weed invasion), that may favour small ant taxa. Ants may be sufficiently responsive to environmental stimuli (Andersen and Majer, 2004) for even moderate levels of disturbance to affect assemblage body-size patterns. Also, many small species of ant are specialised for living in leaf litter systems, sometimes specialised predators of collembola, and therefore are likely to be restricted to the woodland areas (Shattuck, 1999; see also Sanders and Platner, 2007).

In several instances, however, this study found a trend for decreasing mean body size of assemblages with increasing disturbance. Therefore, any influence of poor-quality resources in late-successional habitats that may have been driving mean body size down in woodland (*sensu* Siemann *et al*. 1999 and Cunningham and Murray, 2007) may have been overwhelmed by the considerable structural differences between the studied land-use types (i.e. mature trees, shrubs and litter/grass ground structure for woodland, more uniform grass cover and no trees for pasture, uniform vegetative structure, monoculture and bare-ground for cropping). More subtle factors such as resource quality may therefore have been far less of a determinant of arthropod distribution than land-use type in this study.

A further confounding factor that resulted in inconsistent body size trends across taxonomic groups may have been that the approach I used to examine trends was at a very broad taxonomic level (i.e. order for spiders and beetles and sub-family for ants). However, whilst I could not perform statistical analyses at a finer scale taxonomic resolution due to higher taxa distributions being very land use specific (leading to many zero scores for some treatments), no patterns were apparent at the level of family for Lycosidae and Linyphiidae. Further investigation at the taxonomic level of species or morphospecies may have yielded interesting within-taxon patterns, but were outside the scope of a study intended to look for broad across-taxon patterns. Such investigations may be particularly insightful for ‘disturbance specialists’ such as *Rhytidoponera metallica* ants, in order to see if a species that proliferates in disturbed environments displays a within-taxon body size trend consistent with that observed across many taxa.

4.5 Conclusion

There are many possible determinants of patterns in arthropod body sizes among land-use and habitat types. These include organism dispersal capability, habitat quality, habitat disturbance regimes and ecological interactions such as predation and competition. Although numerous other studies have examined single or closely related taxonomic groups (particularly carabid beetles) and found relationships between body size and habitat disturbance and/or modification, fewer studies have compared responses for unrelated taxa. In this study, I often found broadly similar results for beetles and spiders, but not for ants. The difference in body-size trends for beetles and spiders may reflect the stark structural differences in the habitat types, compared to studies which examined similar habitat types in differing landscape contexts (Alaruikka *et al*. 2002). Furthermore, it has been suggested that body-size differences in some arthropod communities may only be detectable for large environmental differences; for instance, body-size differences were apparent between beetle communities between rainforest and pasture, but no body-size patterns were reported, for more subtle environmental changes such as fragmentation or aridity (Grimbacher *et al*. 2008). This study indicates that for some arthropod groups, habitat type exerts a strong influence on the body size and morphological features of taxa comprising the assemblage, and that these changes are discernable even in landscapes where land uses are arrayed in relatively close spatial proximity. Whilst these findings are of ecological interest in how land-use type can shape trait representation in arthropod assemblages, there may also be implications beyond purely ecological circles. For instance, given that morphological traits are closely related to life-history, arthropod provision of essential ecosystem services may be influenced by body-size representation in assemblages. For example, the pest control potential of a spider assemblage that consists largely of very small taxa and/or individuals may be very different from one that contains a more even spread of body-size representation.

Chapter 5

Adjacent habitat influences arthropod assemblages and predation rates in cereal crops

5.1 Introduction

Agriculture is the dominant terrestrial land use globally (McNeely and Scheer, 2003) and, as the previous chapters have shown, exerts a considerable influence on biological diversity and ecosystems (McLaughlin and Mineau, 1995). In many regions of the world, the area of agriculture continues to expand. This, combined with projected future world population and food demand increases (UN, 2006), increased meat consumption in many developing nations (Delgado *et al.* 1998; 1999; IAASTD, 2008), the redirection of crop production for biofuel production (IAASTD, 2008) and the demand for unseasonal fruit and vegetables in developed countries (Stutchbury, 2007) ensure that the impacts of agriculture on the environment and biodiversity continue to be well-documented global issues (Benton *et al.* 2002; Gaston *et al.* 2003; Gallant *et al.* 2007).

The structure, composition and disturbance profiles of many agricultural systems and land-use types are highly ephemeral, with land-use change, changing management regimes and production outputs driven by a number of influences, ranging from variable market demands, government policy changes, physico-chemical limitations of the land and climatic changes and variability (Lambin *et al.* 2001; 2003). This ephemerality, coupled with the inherent spatial and temporal complexity of a patchwork of land uses, often leads to highly dynamic ecological systems (Levin and Paine, 1974; Topping and Sunderland, 1998). For instance, in many tropical systems, the expansion of both large-scale, industrial agriculture and subsistence farming leads to the clearing, fragmentation and degradation of native vegetation systems (Bradshaw and Marquet, 2003; Lambin and Geist, 2003), with concomitant changes to biological assemblages. Alternatively, in systems that have a long association with agriculture, two principal trajectories can have dramatic impacts on the ecology of agricultural landscapes: (i) the change from traditional farming practices in favour of intensification of management, with the aim of increasing productivity (Tilman, 2001) and (ii) the abandonment of farming in marginal areas, leading to succession and land-use change (MacDonald *et al.* 2000; Poyatos *et al.* 2003). Such changes amount to a 'shifting mosaic' (*sensu* Bormann and Likens, 1979). This can be expressed at a range of scales, from the continental to the paddock scale, and may result in highly complex and transitional abiotic/biotic and interspecific interactions that are rarely in a state of equilibrium (see Wallington *et al.* 2005 and references therein).

One well-known symptom of this combination of frequently-changing disturbance regimes and complex land-use arrangements is the ubiquity of edge and interface habitats in agricultural systems (Ries *et al.* 2004; Rand *et al.* 2006). As habitat loss and fragmentation continue, edge habitats are likely to remain a prevalent landscape feature, with an increase in edge to interior habitat ratios and increased spatial juxtaposition of native vegetation and production land-use interfaces (Rand *et al.* 2006). Accordingly, it is anticipated that there will be an increase in the influence of edge or edge-mediated effects on abiotic conditions and ecological processes both at habitat interfaces and in the adjacent habitat patches (Saunders *et al.* 1991; Burke and Goulet, 1998). Whilst the term 'edge effect' was originally intended to refer to observed increases in species abundance and richness at habitat edges (e.g. Leopold, 1933), the term has expanded to encompass a wide range of physical and biological changes in factors ranging from nutrient transport and assemblage interactions (Fagan *et al.* 1999; Hartley and Hunter, 2005; Taylor *et al.* 2008) to trans-boundary soil organic carbon (Collard and Zammit, 2006).

The influence of habitat edges on biota in agricultural landscapes is of particular interest to a range of stakeholders, from conservation biologists to land managers and farmers. From a conservation perspective, edges can be both advantageous and disadvantageous for biota. For instance, both abundance and richness of small passerines have been observed to be lower at woodland edges and in highly fragmented woodlands due to the presence of the noisy miner *Manorina melanocephala* (Latham) (Piper and Catterall, 2003; Taylor *et al.* 2008). This hyper-aggressive bird species has been advantaged by increases in edge habitat in eastern Australia associated with habitat loss, fragmentation and land-use change (Piper and Catterall, 2003; Taylor *et al.* 2008). Furthermore, species dependent on the ecological conditions associated with relatively unmodified and undisturbed 'core' habitat are often unable to persist in edge habitat. As edge effects can occur considerable distances into a patch of natural habitat (Murcia, 1995), such species can become locally extinct in highly fragmented landscapes containing only small and/or linear patches of habitat (Ewers and Didham, 2006).

In a European context, edge habitats also encompass linear habitat features such as hedgerows and field margins. An extensive review of the functions and interactions of field margins with agriculture in northern Europe has been undertaken by Marshall and Moonen (2002), which details their structure and 'anatomy'. These include i) *the boundary*, the barrier between fields or different land uses, ii) *the margin strip*, a strip of vegetation that is established between the field and boundary, and iii) *the crop edge*, the outermost extent of the crop. Such edge and boundary habitats in extensively-managed European agricultural landscapes are of vital importance for a wide range of 'farmland specialist' taxa. Hedgerows, a familiar boundary vegetation feature in many European agricultural landscapes, provide valuable habitat and resources for birds such as the yellowhammer *Emberiza citrinella* (L.) and butterflies such as the brown hairstreak *Thecla betulae* (L.) which have undergone recent declines, due in part to a loss and degradation of edge habitat features (Dover and Sparks 2000; Hinsley and Bellamy, 2000). Such features are also of considerable cultural significance, with hedges often marking historically important parish boundaries in the UK (Rackham, 1986; Oreszczyn and Lane, 2000).

From a more utilitarian and agrarian perspective, edges, margins and boundaries are often valuable habitats for predatory and parasitic arthropods (Rand et *al.* 2006). Many margin strips, especially if they have a complex vegetation structure and composition, can provide such natural enemies with a range of pollen and nectar resources, alternative prey and hosts, shelter and microclimate stability (Landis *et al.* 2000; Koji *et al.* 2006; Rand *et al.* 2006; Knight and Gurr, 2007), thus providing refuge from deleterious cropping activities and periodic resource depletion in cultivated systems (Thorbek and Bilde, 2004; Landis *et al.* 2000; Gavish-Redev *et al.* 2007). Structurally and/or compositionally complex edge and margin habitat (e.g. such as botanically diverse field margins) may also be influential at a range of scales, with the diversity and abundance of arthropod natural enemies increasing with the area or diversity of non-cropped habitat in the landscape surrounding cropped fields (Elliot *et al.* 1998; Rand *et al.* 2006). This maintenance of natural enemy populations can have potentially beneficial implications for agricultural production, such as suppressing populations of phytophagous arthropods before they reach problematic densities, or reacting to and reducing populations of arthropods that do reach pest proportions (Weidenmann and Smith, 1997).

Therefore, a potential beneficial effect of edge and margin habitats (be they linear habitat features or the outer edge of an adjacent habitat block) is their potential role as natural enemy sources, which, through the movement of beneficial arthropods from the adjacent habitat into the adjoining crop, may help reduce numbers of pest arthropods (Landis *et al*. 2000).There are several possible explanations for this: such movements may be prompted by the difference in productivity between natural and semi-natural habitats and adjacent cultivated systems that are periodically more productive. Predator and parasite movement into crops may be in response to temporarily high pest/prey densities (Rand *et al*. 2006). Such inter-habitat movements are related to the concepts of resource mapping (where an organism's distribution matches that of its resources) and access to spatially separated resources (i.e. an organism's required resources are situated in more than one habitat type, and therefore presence at edges optimises access to these disjunct resources) highlighted by Ries *et al*. (2004) that explain the concentration of organisms at habitat edges.

Movements of mobile taxa between habitats may also be influenced by the permeability of the interface. In describing interface permeability, edges and boundaries are often classified as 'hard' (difficult to cross, often found between structurally different habitat patches) and 'soft' (more 'porous' to organisms, often found between structurally similar habitats) (Duelli *et al*. 1990; Ries *et al*. 2004). Whilst compositional, structural and disturbance-related factors may determine whether an edge or boundary is hard or soft, the height and density of vegetation in each adjoining habitat is thought to be particularly influential (Ries *et al*. 2004). Biotic changes at edges may also have secondary impacts on edge permeability for other taxa by advantaging aggressive competitor or predatory species (Dauber and Wolters, 2004).

In intensively managed landscapes, areas of relatively low disturbance and high heterogeneity can be vital refuges for arthropod natural enemies (Langellotto and Denno, 2004). Furthermore, higher trophic taxa such as predators are likely to be particularly heavily impacted by intensified land use, as their resources are easily fragmented (Tscharntke *et al*. 2007). Consequently, relatively undisturbed and complex edge habitats in intensive systems are an important source of habitat, refuge and food for such organisms.

Two such low-disturbance/high heterogeneity potential sources of mobile beneficial arthropods in agricultural landscapes are i) natural habitat patches that border production land, and ii) linear habitat features that form the boundaries (margins) between agricultural fields. Whilst the edges of natural habitat patches are likely to be remnants of the previous indigenous vegetation type, linear habitats are increasingly established by land managers partly for the purpose of encouraging and harbouring arthropod natural enemies (MacLeod *et al*. 2004).

In general, native vegetation patches are likely to have greater structural and compositional complexity, experience less frequent and intensive disturbance and have more niche opportunities than cropping systems. Such factors are likely to lead to higher species richness and abundance of natural enemies in native vegetation. Factors such as greater structural complexity may also offer more refugia from antagonistic processes such as intra-guild predation leading to greater predatory arthropod abundance (Finke and Denno, 2002; Langellotto and Denno, 2004; Langellotto and Denno, 2006). For instance, a meta-analysis of arthropod responses to a range of agricultural land use types found greater richness and abundance of predatory taxa in native systems compared to agricultural land uses across a wide range of countries, vegetation types and land-use categories (Attwood *et al*. 2008; see Chapter 2 of thesis).

Although linear edge and boundary habitats occur in agricultural regions around the world, European examples of such habitats have received the overwhelming majority of management, policy, on-ground funding and research attention. Despite the emphasis on European crop edge, boundary and margin habitats, and the lack of studies in regions that have a more recent history of agricultural introduction and development, there has recently been considerable interest in the role that anthropogenic landscape features, or ‘countryside elements’, may play in biodiversity conservation in relatively recently established agricultural systems (Hughes *et al*. 2002; Haslem and Bennett, 2008a).

Australian agricultural landscapes often consist of a mosaic of land-use types ranging from cropping of various degrees of intensity, to improved and native pastures, to remnants of various woody native vegetation types. Such systems often contain linear strips of vegetation (often consisting of a mix of native and introduced grasses, forbs and woody vegetation) situated between fields or paddocks of crops. However, many parts of eastern and southern Australia are undergoing a process of agricultural intensification (Walcott *et al*. 2001) involving an increase in irrigated cropping (Maron and Fitzsimons, 2007) and a loss of low intensity agricultural land uses and semi-natural habitats such as native pastures (Attwood *et al*. 2009; Sheahan, 2009). Such changes in land use and field size are likely to lead to a simplification of the agricultural landscapes of the region (*sensu* Benton *et al*. 2003). Furthermore, these changes are likely to result in a reduction in edge habitats formed by a) low intensity land uses abutting cropping (due to loss of low intensity habitats such as native pastures) and b) linear vegetation strips and margins bordering cropping fields (Wilson *et al*. 1999). Given that these more complex habitats are likely to support relatively high arthropod biodiversity, which may in turn provide ecosystem service benefits to agriculture (Altieri, 1999; Landis *et al*. 2000; Langellotto and Denno, 2004; Attwood *et al*. 2008; Letourneau *et al*. 2009), the loss of such edge habitats may potentially lead to a loss of both biological diversity and associated system function.

In order to investigate the possible implications of edge habitat change, I conducted a field study in mixed farmland in eastern Australia. Specifically, I aimed to examine the arthropod biodiversity value and pest-control potential of a linear crop boundary or margin (referred to in text as 'linear-edge') compared to a native remnant woodland/crop boundary ('woodland edge' or 'wood-edge').

A primary research focus was whether linear-edge habitats such as grassy margins, generally viewed as a quintessentially European habitat component, could fulfill similar conservation and ecosystem service roles (e.g. relatively high biodiversity compared to the dominant cropping land use) in the context of a region where agriculture was a relatively recent arrival. Furthermore, it is important to discover if the biodiversity benefits of native habitats and relatively low intensity land uses extend into the cropping systems, as this could multiply the potential benefits of relatively undisturbed habitats situated adjacent to crops.

In addition to examining arthropods in general for this study, I focussed on ants in particular as they are sensitive to environmental gradients (Dauber and Wolters, 2004), are known to be important generalist predators of agricultural pests (Way *et al*. 2002; Atlegrim, 2005; Argawal *et al*. 2007), and influence predator assemblages through intraguild predation (Mansfield *et al*. 2003). Two practical considerations also favoured ants—they are readily caught in pitfall traps and are one of the few taxa to remain highly abundant during persistent drought (see Method, Chapter 3 and Fig. 5.3). In addition, I examined the responses of other arthropods (at order level) and spiders, themselves considered to be generalist predators in cropping systems (Sunderland and Samu, 2000). In order to try and gauge the extent to which different edge habitat types may influence ecosystem service delivery, I also examined the predation rates of *Heliothis* eggs at the two different edge types. Finally, I examined whether mean spider body size differed among the two edge habitat types and adjacent crops. This was done to determine if any morphological assemblage patterns were evident in a predatory group known to be important in both shaping ecological processes and delivering ecosystem service benefits (Sunderland and Samu, 2000).

The primary research questions were therefore:

1. Does the frequency and direction of movement of arthropods between the crop interior and the crop boundary differ among edge habitat types?
2. Do arthropod abundance, ant morphospecies richness, ant morphospecies/functional group assemblage composition, or spider body size differ between cropping edges adjacent to remnant woodland and linear grassy margins?
3. Do arthropod abundance, richness and composition differ between crop edges and crop interiors?
4. Do arthropod assemblages of within-crop areas differ from each other depending upon their nearest adjacent habitat type?
5. Does adjacent habitat type and distance into crop influence predation rates of a common agricultural pest, *Heliothis armigera*?

5.2 Methods

5.2.1 Study area and study sites

The study was conducted on four farms in the Cambooya and Felton districts in south-east Queensland, Australia (27º41’–50’ S; 151º48’–49’ E; see Fig. 5.1). The mean maximum summer (Dec–Feb) temperature is 29.8ºC; the mean minimum winter (June–August) temperature is 2.6ºC (Bureau of Meteorology, 2008). The mean summer (Dec–Feb) rainfall is 279 mm and mean winter (June–August) rainfall is 112 mm, with a mean total annual rainfall of 720 mm (BOM, 2008). The landscape is highly heterogeneous, consisting of cereal, legume, vegetable and fodder crops, cattle-grazed native, mixed and improved pastures and cattle-grazed remnants of *Eucalyptus orgadophila* (Maiden and Blakely) and *E. crebra* (F. Muell.) woodland. The landscape also contains a range of semi-natural habitat components such as grassy field margins and headlands, isolated paddock trees and cropping paddocks that are no longer cultivated and are in the process of reverting to native or exotic grassland with sporadic tree and shrub regeneration.

Fig. 5.1. Map of Queensland and sampling locations. Polygons represent paddock/woodland site where sampling took place. The photo on the far right depicts one field bordered by woodland and other fields, and depicts the woodland edge and linear edge sampling points. Please see following Figure 5.2 for depiction of sampling points in one field.

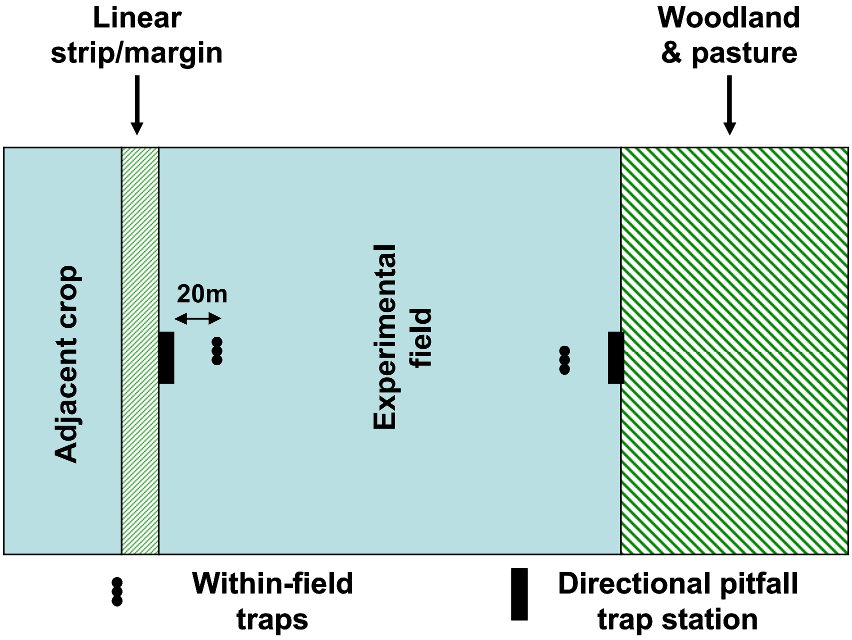

Fig. 5.2. Schematic of sampling locations in and around a selected sorghum field. Please compare to Figure 5.1.

5.2.2 Experimental design and sampling

I selected two commonly-occurring edge habitat types adjacent to crops of sorghum (*Sorghum* sp.): i) cropping abutting the edge of woodland and pasture elements (‘woodland-edge’) and ii) cropping abutting a grassy margin or other linear vegetation strip that separated the experimental field from another cropping field ('linear-edge') (Fig. 5.2). Due to the severity of ongoing drought (see Fig. 5.3), only four crops of sorghum that adhered to this design could be located. All cropping sites were subjected to minimum or no-till management, and sampling was conducted when approximately half the sorghum plants were flowering (Vanderlip & Reeves, 1972).

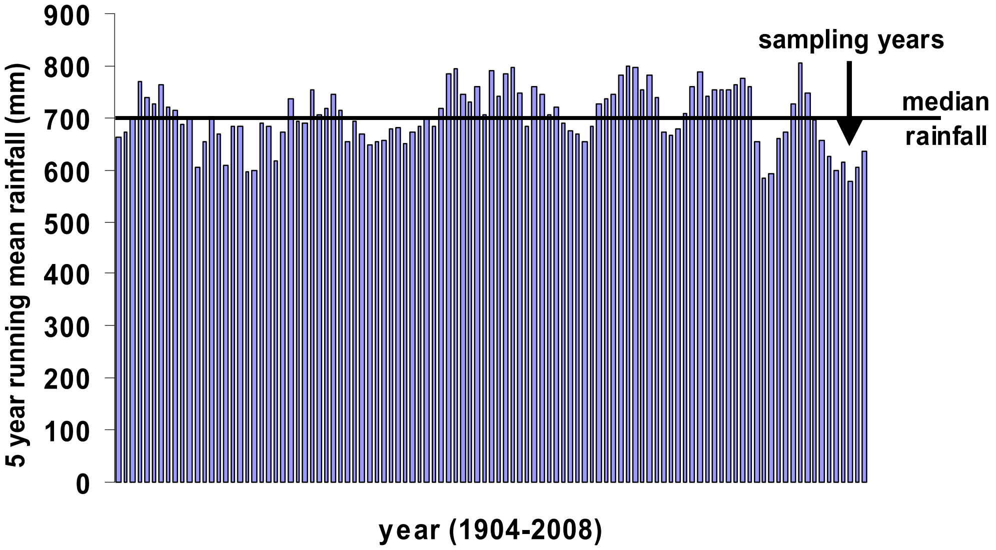

Fig. 5.3. Five year running average total annual rainfall for southern Queensland study area (data 1900–2008), with sampling years and median rainfall value indicated. Data from Bureau of Meteorology (2009).

5.2.2.1 Arthropod sampling

Three pitfall trapping sampling stations were placed along each edge type, with each sampling point consisting of an 'ingoing' trapping point on the edge-side and an 'outgoing' trapping point on the crop-side. Therefore, sampling was conducted at the 'woodland edge' (where woodland interfaces with crop field), the 'linear strip edge' (where linear vegetation strip interfaces with crop field), 'woodland crop' (cropping field proximate to woodland edge), and 'linear edge crop' (cropping field proximate to woodland edge) (see Fig. 5.2). The placement was determined using a random numbers table but with points at least 100 m apart in order to retain independence of sampling points. To sample edge arthropods at each sampling point, I erected a directional pitfall trap frame at the boundary between the crop and the edge of the adjacent vegetation (Fig. 5.4). Whilst directional pitfall trapping is not as frequently used as other pitfall trapping approaches, several authors have found that it is a useful method for identifying the movements of ground-dwelling arthropods between adjoining habitat types (e.g. Duelli *et al*. 1990; Collinge and Palmer, 2002). I dug the frames into the ground and secured them with tent pegs in order to reduce the likelihood of ‘incoming’ arthropods falling into ‘outgoing’ pitfall traps. Three pitfall traps, consisting of plastic containers with an opening diameter of 115 mm and a depth of 80 mm, were placed in the ground on each side of the frame’s central barrier (Fig. 5.4). To sample within-crop arthropods, I placed a further three pitfall traps 20 m into the crop from each sampling station. These pitfall traps had covers similar to the covering of the edge traps, in order to simulate conditions under the directional pitfall trap covers and protect the traps from any rain events. Each sampling point was replicated 12 times across the four farms, with sampling points at least 100 m apart and farms separated by at least 1.5 km. This resulted in a total of 12 each of edge side traps and crop-side traps at the woodland-edge and 12 each of edge side traps and crop-side traps at the linear-edge (see Fig. 5.4 for example of one trap set).

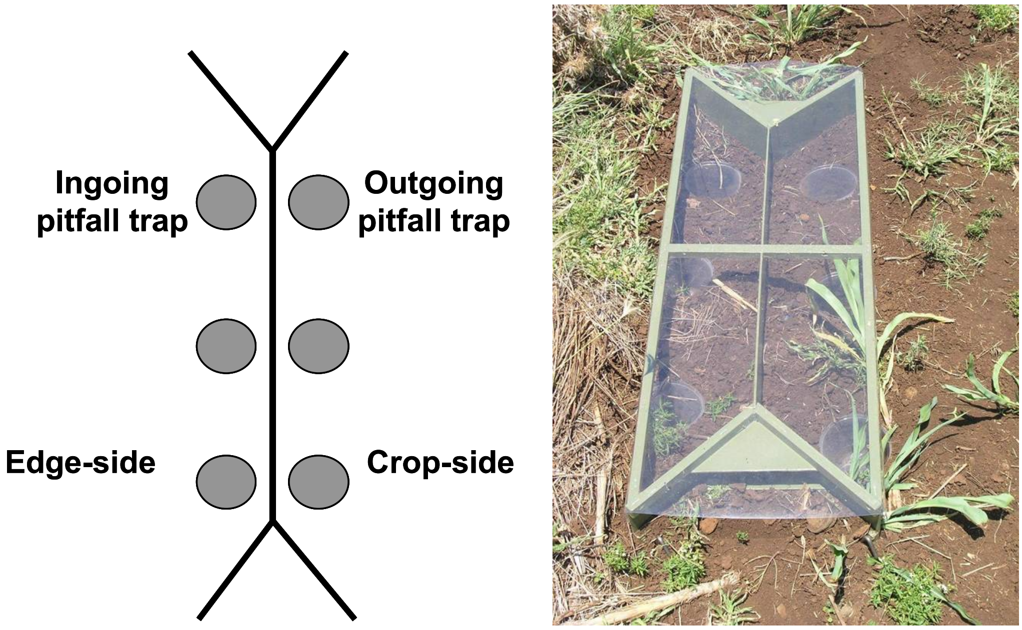

Fig. 5.4. Directional pitfall trapping frame and trap placement. Each trapping frame was placed parallel to the boundary of the cropping paddock.

After the pitfall traps were placed in the ground, they remained closed for one week to allow settling-in. After this period, I then half-filled all traps with 30% ethylene glycol solution and a few drops of household detergent. Traps were left open for seven days and nights, with all sampling conducted within a four-week period in November 2006. After the seven-day sampling period all traps were taken to the laboratory and the contents stored in 70% ethanol solution. I identified all ant specimens to genus and morphospecies using a stereomicroscope and standard reference works (Shattuck 1999; Andersen, 2000; Shattuck and Barnett, 2001) and specimens were attributed to functional groupings after Hoffmann and Andersen (2003) and Andersen and Majer (2004). I also identified all arthropods to Order level, and body length of all spiders from chelicerae to the tip of the spinnerets was measured.

In addition to collecting arthropods using pitfall traps, I also sampled in the crop canopy using a Stihl leaf blower with a vacuum attachment. Only six replicates of each treatment across the landscape were sampled using the leaf blower, in order to avoid disturbance of cattle in some crops at the time of sampling (at property owner's request). The treatments sampled were 1 m into the crop at the woodland-edge, 20 m into crop at the woodland-edge, 1 m into the crop at the linear-edge and 20 m into the crop at the linear-edge. The sampling locations were adjacent the pitfall sampling points (hence three per treatment at each site). I performed five suction samples at each of the three sampling points, each of ten seconds duration within a 1m radius and all five samples subsequently pooled.

5.2.2.2 Heliothis egg predation

Heliothis armigera (Hübner) eggs (laid on paper towel), obtained from the Queensland Department of Primary Industries and Fisheries, were attached to pieces of card measuring approximately 2 × 2 cm. The number of eggs per card varied, and removing eggs from cards to have equal numbers on each would have destroyed the eggs. Therefore, I arranged them into sets of five cards with approximately equal total numbers of eggs (mean of 326 eggs per card set, +/- SD of 21, a variability of 6% in total egg numbers averaged across a set of cards) for the field trial. Whilst not as ideal as having exactly equal numbers of eggs for the five cards at each point, I felt that 6% variability in egg numbers across cards was unlikely to affect predation rates due to unequal prey availability and predator satiety. Sampling was conducted commencing at approximately 1700 hrs during three consecutive days in November 2006. I stapled five egg cards to plant stems at a height of approximately 2 cm, at points 1 m and 20 m into the crop at each sampling point on the four farms. I recorded the number of eggs on each egg card at the time of placement. Twelve hours later, I collected the cards and sealed them in polythene bags, and placed these on ice for their return to the laboratory for counting.

5.2.2.3 Habitat Structure

The habitat types to be sampled differed to some extent in their habitat structure. In a qualitative sense, it was evident that woodland edges differed from linear strip edges, in that the former contained habitat elements such as coarse woody debris and leaf litter, and were sometimes overhung by the edge of the tree drip line. Meanwhile, crops abutting linear strip edges lacked the leaf litter often evident in crops abutting woodland edges. In order to capture some of these apparent differences, I recorded quantitative measures of habitat structure at the following six locations for each sampling point: Woodland-edge (the outermost margin of the crop where it abutted the adjacent woodland patch—Fig. 5.5, sampling point 5), woodland crop (20 m into the crop from the woodland/crop interface—Fig. 5.5, sampling point 4), woodland patch (20 m into the adjacent woodland patch—Fig. 5.5, sampling point 6), linear-edge (the outermost margin of the crop where it abutted the adjacent linear grass strip—Fig. 5.5, sampling point 2), linear-crop (20 m into the crop from the linear grass strip/crop interface—Fig. 5.5, sampling point 3), next cropping field (20 m into the adjacent cropping field beyond the linear grass strip—Fig. 5.5, sampling point 1). The measures consisted of percentage cover of the following variables: tree cover, shrub cover, forb cover, tussock grass cover, mat-forming grass cover, coarse woody debris cover, leaf litter cover, rock cover, bare ground cover, crop cover and crop residue cover, and measurements for litter depth, grass height and grass density. Methods of measurement followed those described in Chapter 3 for habitat structure variables. The habitat measures were divided into local habitat (sampling points 2, 3, 4 and 5) and adjacent habitat (1 & 6) types when used for analysis (see section *5.2.3.4*).

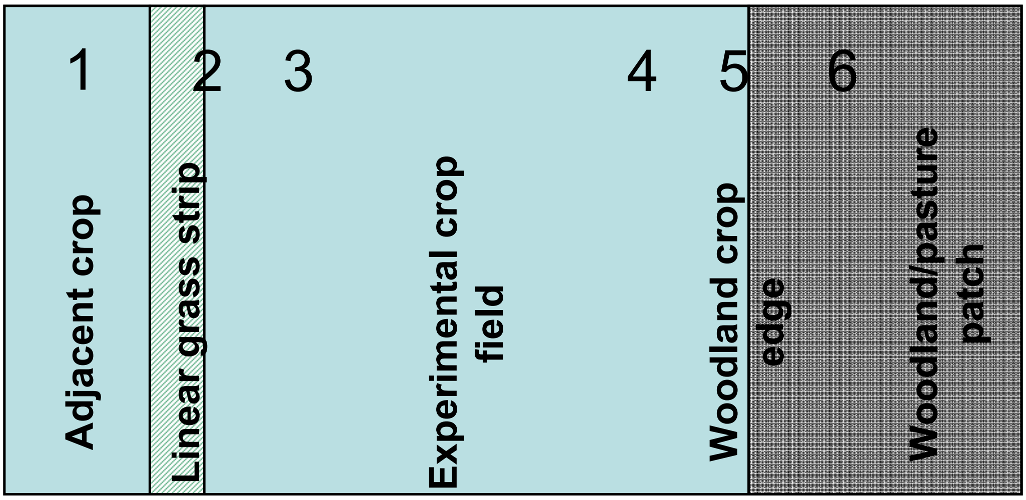

Fig. 5.5 Habitat structure measurement sampling points (see text in 5.2.2.3)

5.2.3 Data Analysis

The abundances for Formicidae and Araneae and all arthropods combined were determined by calculating the mean abundance for the three pitfall traps at each sampling point. Formicidae morphospecies richness and Order-level richness was calculated as the total number of morphospecies summed from the three pitfall traps at each sampling point.

I classified all spiders into one of three size classes depending upon their body length: Class 1: <2.5 mm; Class 2: >2.5–5 mm; Class 3: >5 mm (Alaruikka *et al.*, 2002). From this I calculated the mean abundance of each size class for the three pitfall traps in each sampling point. For each egg card, the proportion of eggs taken was calculated and from this I determined the mean proportion taken for each sampling point. All analyses were based upon a total of twelve replicates of each treatment. Prior to analysis, I tested data for normality and transformed them accordingly. All proportional data were arcsine square root transformed.

5.2.3.1 Univariate

In order to first determine if there were differences in arthropod measures between the ingoing and outgoing pitfall traps in the directional trap setup, I performed paired t-tests. As no significant differences were found, the mean richness, abundance, etc., of the ingoing and outgoing traps at each sampling point was derived and subsequently termed 'woodland-edge' (i.e. the mean of the ingoing and outgoing traps at the woodland boundary) or 'linear-edge' (i.e. the mean of the ingoing and outgoing traps at the linear grass strip edge).

I then used a series of linear mixed effects model analyses to test for differences in arthropod abundance, richness and (for spiders) body size class and egg card predation rates among the following habitat types: woodland-edge, linear-edge, woodland-crop and linear-crop. Distance (edge compared to 20 m into adjacent crop) and edge type (woodland or linear strip habitat for both distance classes) were included as fixed factors in the analysis, and farm was included as a random factor. Where a significant distance and/or edge habitat type treatment effect was found ($P = <0.05$), I used paired t-tests to test for differences between individual habitats (wood-edge, woodland-crop, linear-edge, etc.). All univariate analyses were performed using SPSS 14.0 for Windows (SPSS for Windows, 2005).

5.2.3.2 Assemblage composition

To examine if patterns of ant assemblage composition and relative abundance differed with edge habitat type and distance into crop (i.e. crop edge compared to crop interior), I first calculated a Bray-Curtis similarity matrix from the fourth root-transformed morphospecies data for each sampling point and performed ordinations using non-metric multidimensional scaling. This transformation was used to reduce the influence of very high abundances of some ant taxa in some samples. The differences among ant assemblages for both treatment and farm were tested using ANOSIM, with 9999 permutations. A similar procedure was used for the functional group data. In order to reduce data 'noise', I omitted all taxa from the assemblage analysis that occurred at only one trapping station. Finally, I identified the morphospecies that made the greatest percentage contribution to treatment dissimilarity using SIMPER. All multivariate analyses were undertaken using PRIMER® (Clarke and Gorley, 2001).

5.2.3.4 Influence of environmental variables on ant assemblage composition

Analysis of which environmental variables were most influential in shaping the ant assemblages at habitat-crop edges and crop interiors was performed in PRIMER® (Clarke and Gorley, 2001), using the BEST analysis. Ant data were combined for edges (i.e. woodland-edge and linear-edge data combined) and for crop interiors (woodland-edge 20 m into crop combined with linear-edge 20 m into crop). Habitat data (see section 5.2.2.3, above) were categorised as local environmental variables (those recorded at the point where the ants were sampled) and adjacent habitat environmental variables. The habitat variables were coded as ‘local’ or ‘next’ on this basis. BioEnv procedures were conducted for both edge (woodland-edge and linear-edge combined) ant and habitat data and crop interior (woodland-edge 20 m into crop combined with linear-edge 20 m into crop), in order to examine if ‘local’ or ‘next’ habitat features were most influential in shaping ant assemblage composition both at crop edges and interiors. Consideration was given to excluding some correlated habitat variables, but as variables that showed a relatively high incidence of correlation (e.g. tree cover and leaf litter cover) may operate in ecologically distinct ways for arthropods, all variables were included in the analysis. The analysis was run using 99 permutations, using Spearman’s Rho.

5.3 Results

5.3.1 Arthropod richness and abundance

5.3.1.1 Directional pitfall trapping

A total of 26,098 arthropods (excluding Collembola) were trapped, which included 20,275 ants and 807 spiders. There were 43 ant morphospecies from 17 genera with the most abundant genera being *Iridomyrmex* (12,182 individuals), *Paratrechina* (5,173 individuals), *Pheidole* (2,224 individuals) and *Rhytidoponera* (415 individuals). Paired t-tests revealed there were no significant differences in abundance or richness between ingoing and outgoing traps for any taxa (see Fig. 5.6 for ant data), and therefore I used the mean of the ingoing and outgoing traps to calculate ‘wood-edge’ and ‘linear-edge’ for all statistical analyses.

Table 5.1 Linear mixed-model results for arthropod directional pitfall trapping among distance from edge and edge and crop types. Distance refers to the comparison between the edge (wood or linear) and 20 m into the adjacent crop; edge type refers to the comparison between the two adjacent habitat types (wood or linear for both the edge and the adjacent crop). Size class 3 = (>5 mm body length), Size class 2 = (2.5-5 mm body length), Size class 1 = < 2.5 mm body length. d.f. = 1,42 in all cases

Taxon	Measure	treatment	F	P
Order level	**Order richness**	distance	1.493	0.229
		edge type	3.073	0.087
	Abundance	distance	0.016	0.9
		edge type	2.85	0.099
Formicidae	**Morphospecies richness**	distance	6.676	0.013
		edge type	24.047	0.001
	Abundance	distance	12.519	0.001
		edge type	8.693	0.005
Araneae	**Abundance of individuals**	distance	0.452	0.505
		edge type	1.452	0.235
	Mean body length	distance	0.028	0.869
		edge type	1.732	0.195
	Mean abundance of size class 3	distance	0.706	0.405
		edge type	4.144	0.048
	Mean abundance of size class 2	distance	0.487	0.489
		edge type	0.836	0.365
	Mean abundance of size class 1	distance	0.35	0.852
		edge type	0.418	0.521

Mean ant morphospecies richness differed with distance into the crop (edge compared to crop) and adjacent habitat type (woodland or linear grassy strip) (Fig. 5.7 & Table 5.1). Richness in the woodland-edge was significantly greater than that of the other three treatment combinations (Fig. 5.7 & Table 5.1). Richness was also greater in the crop adjacent to the woodland-edge than the crop adjacent to the linear-edge (Fig. 5.7 & Table 5.1). LogN grand mean ant abundance also differed significantly among treatments (Fig. 5.8 & Table 5.1) with significantly greater abundance at the woodland-edge than other land uses and significantly lower abundance in the crop adjacent to the linear-edge than the other land uses (Fig. 5.8 & Table 5.1).

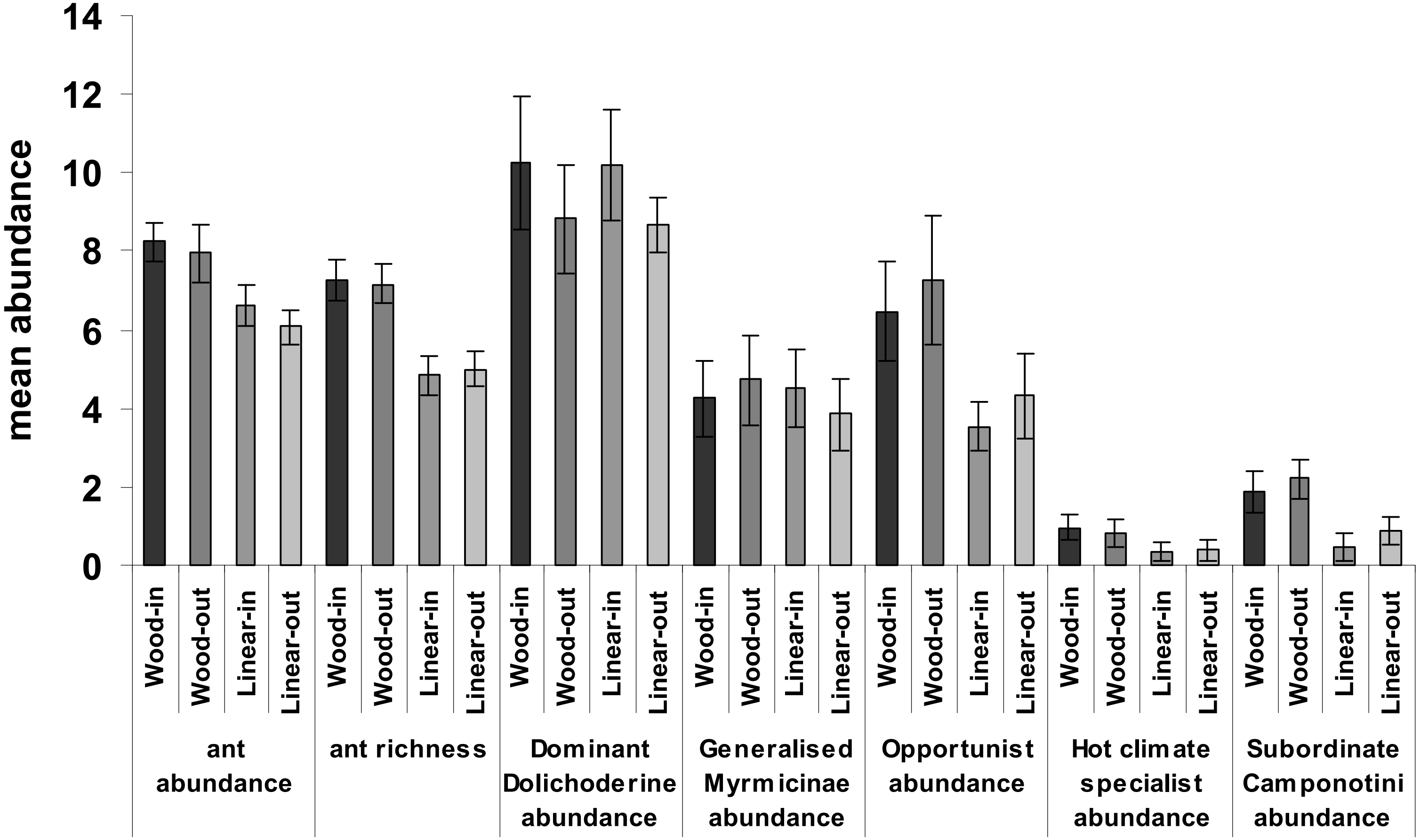

Fig. 5.6 Mean ant abundance (LogN transformed), mean ant richness and mean abundance of selected ant functional groups (LogN transformed) for ingoing and outgoing directional pitfall traps at both woodland and linear strip edges.

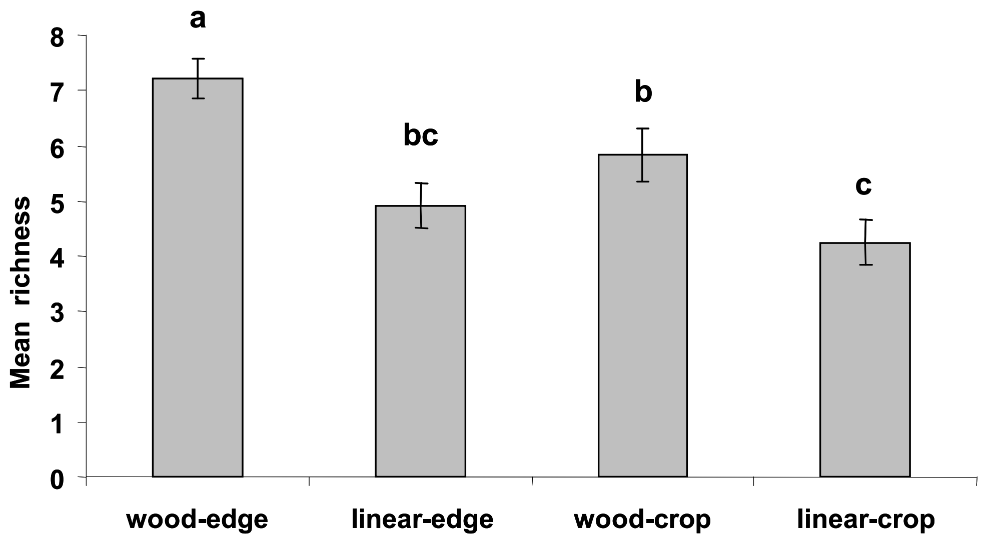

Fig. 5.7 Mean ant morphospecies richness in woodland and linear-edge habitats and 20m into crop from each edge type. N = 12 replicates for all treatments, error bars are S.E. of mean and different letter denotes significant difference for paired t-tests among treatments at $\alpha = 0.05$

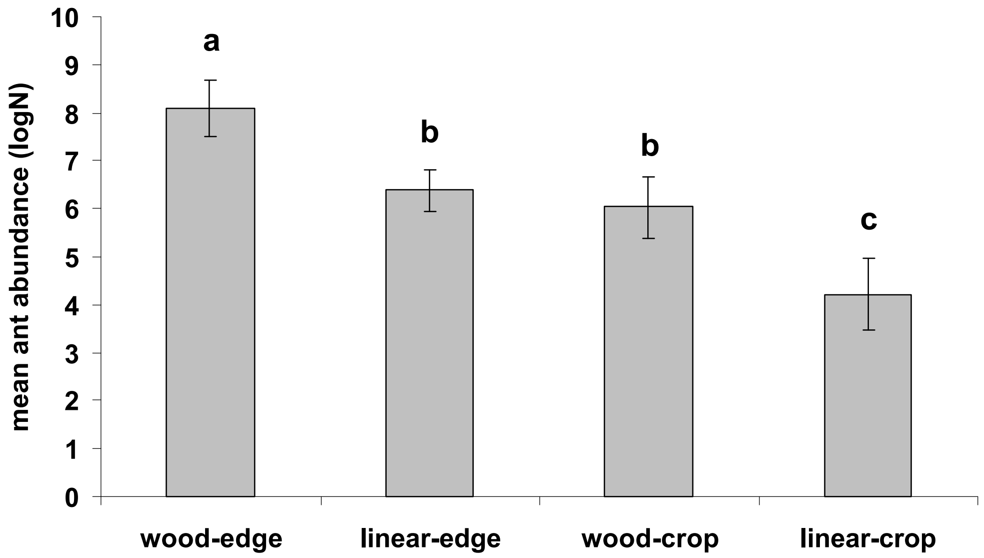

Fig. 5.8 LogN grand mean ant abundance in woodland and linear-edge and 20m into crop from each edge type. N = number of replicates, error bars are S.E. of mean and different letter denotes significant difference for paired t-tests among treatments at $\alpha = 0.05$

In contrast, no difference was found among treatments for either arthropod (excluding Formicidae) abundance or order/class level richness (Fig. 5.9 & Table 5.1). Nor was there any significant difference in spider abundance among edge or crop treatments (Figs. 5.10; Table 5.1). However, adjacent habitat/edge type did appear to influence the abundance of spiders in the largest size class (>5 mm), with significantly more of these spiders occurring in the linear-edge habitat than in the wood-edge or wood-crop habitats (Fig. 5.11).

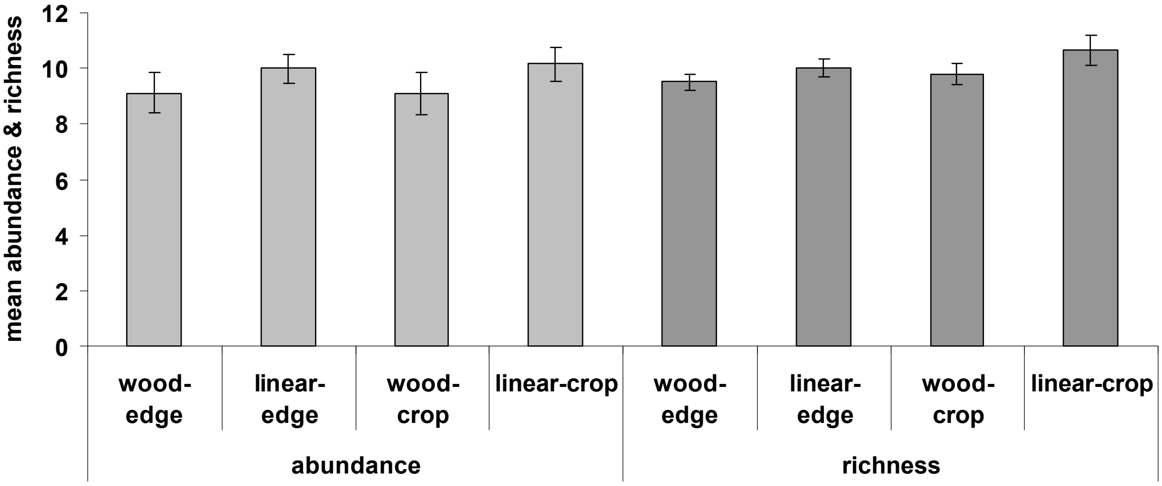

Fig. 5.9 LogN grand mean arthropod abundance and order/class level richness in woodland and linear-edge habitats and 20m into crop from each edge type. N = 12 replicates in all cases, error bars are S.E. of mean.

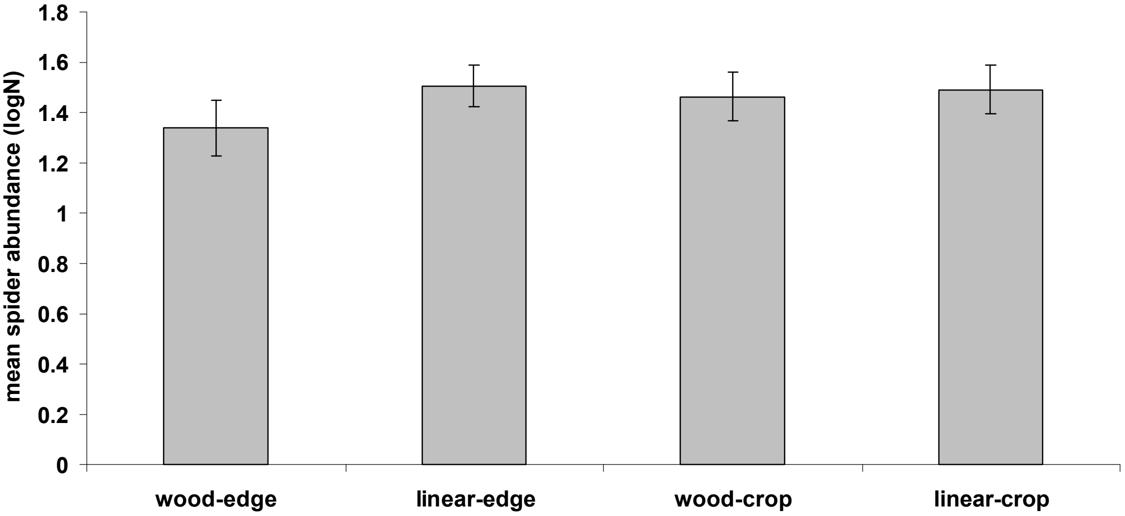

Fig. 5.10 LogN grand mean spider abundance in woodland and linear-edge habitats and 20m into crop from each edge type. N = 12 replicates in all cases, error bars are S.E. of mean.

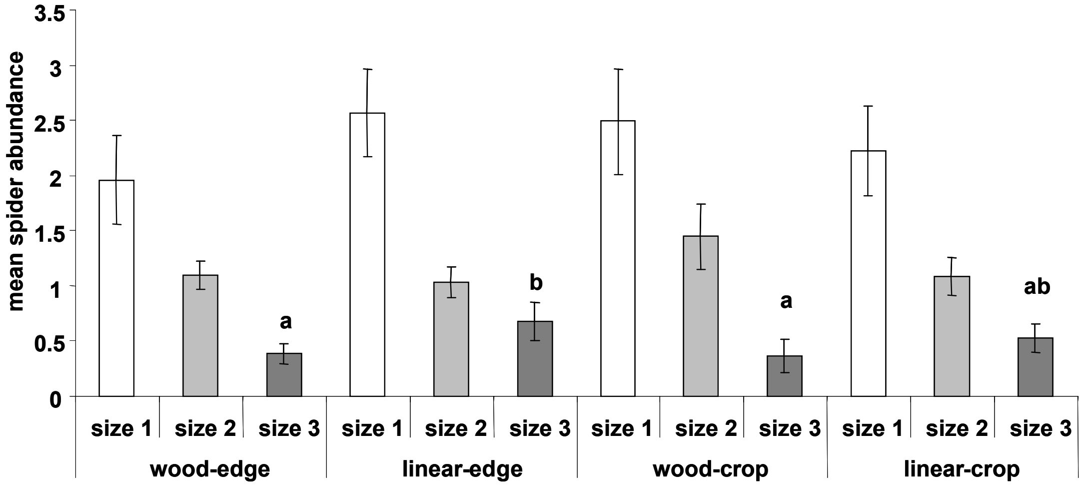

Fig. 5.11 grand mean spider size class abundance in woodland and linear-edge habitats and 20m into crop from each boundary type. N = 12 replicates in all cases, error bars are S.E. of mean. Paired t-tests only performed on size class 3. Different letter denotes significant difference at α = 0.05

5.3.1.2 Suction sampling

Only one significant difference was found for all comparisons of data from suction sampling, with greater abundance of predatory arthropods (spiders and coccinellid beetles) at 20 m than 1 m into the crop (Table 5.2). No differences were found in predatory arthropod abundance between the woodland and linear-edges and no differences in Thysanoptera or Homoptera abundance were apparent among the edge types or with distance into the crop (Table 5.2).

Table 5.2 Linear mixed-model results for LN transformed abundance of Thysanoptera, Homoptera and predatory arthropods (spiders and coccinellid beetles) from reverse-leaf blower suction samples. Comparisons are between crop edge and crop interior (1 m and 20 m distances into crop) (data from both edge types combined) and between woodland and linear-edge type (data from both cropping distances combined). d.f. = 1, 20 in all cases.

Arthropod group	**Mean ab (± S.D) crop edge (1 m)**	**Mean ab (± S.D) crop interior (20 m)**	**F**	**P**
Thysanoptera	3.14 (2.15)	3.81 (1.43)	1.78	0.19
Homoptera	3.03 (1.00)	2.65 (0.67)	1.41	0.25
Predatory arthropods	1.44 (0.5)	1.97 (0.56)	8.22	0.01*
Arthropod group	**Mean ab (± S.D) woodland edge**	**Mean ab (± S.D) linear-edge**	**F**	**P**
Thysanoptera	3.6 (1.52)	3.34 (2.14)	0.28	0.60
Homoptera	2.69 (0.88)	2.99 (0.85)	0.84	0.37
Predatory arthropods	1.65 (0.55)	1.76 (0.64)	0.42	0.53

5.3.1.3 Egg card predation

The mean proportion of *Heliothis armigera* eggs taken was significantly greater 1 m into the crop than 20 m into the crop ($F_{1,42} = 6.66$; $P = 0.014$) (Fig. 5.12). When the proportion of eggs taken at different edge habitat types were compared using combined 1 m and 20 m samples, there were no significant differences ($F_{1,42} = 1.61$; $P = 0.21$).

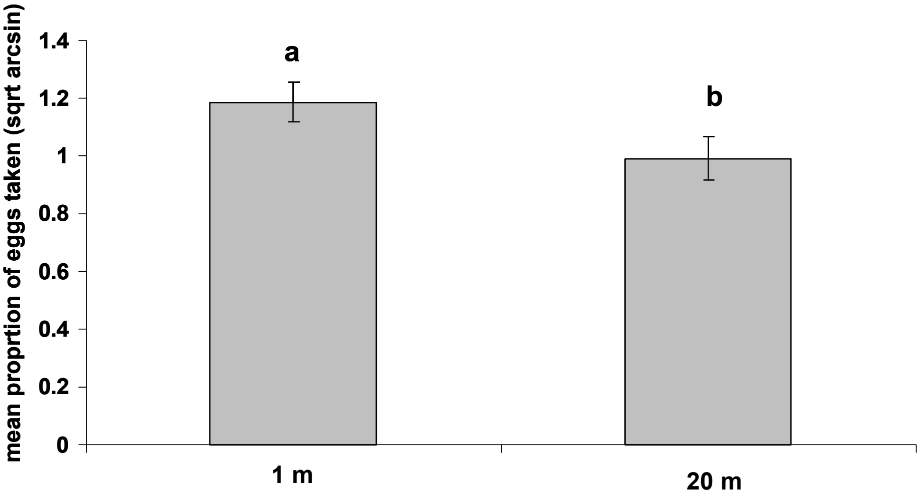

Fig. 5.12 Mean arcsine square root transformed proportion of *Heliothis* eggs taken 1 m and 20 m into crop (edge habitat types combined). Error bars are S.E. of mean and different letter denotes significant difference for linear mixed-model analysis at $\alpha = 0.05$

5.3.1.4 Ant morphospecies and functional group assemblage composition

The nMDS ordination and ANOSIM results indicated that the ant morphospecies assemblage at woodland/crop edges and the adjacent crops was different to that at linear strip edges and the adjacent crops (Fig. 5.13a; R = 0.186, P = <0.01). Similarly, the assemblage composition at crop boundaries (woodland and linear strip treatments combined) was also significantly different from the assemblage in the crop itself (woodland and linear strip combined) (Fig. 5.13b; R = 0.128, P = 0.01). Where boundary and crop types were not combined (i.e. analysed as woodland-edge, linear-edge, woodland-crop and linear-crop), significant differences in assemblage composition were found between: wood-edge and linear-edge, wood-edge and linear-crop, wood-crop and linear-edge, wood-crop and linear-crop and linear-edge, and linear-crop (Fig. 5.13c; Table 5.3).

Table 5.3 ANOSIM results for ant morphospecies assemblage composition.

Global test comparison	Global R	P	Pairwise test comparison	R	P
Comparison of all treatments	0.195	<0.01	Wood-edge vs wood-crop	0.071	0.085
			Wood-edge vs linear-edge	0.164	0.010
			Wood-edge vs linear-crop	0.343	0.001
			Wood-crop vs linear-edge	0.288	0.001
			Wood-crop vs linear-crop	0.173	0.008*
			Linear-edge vs linear-crop	0.15	0.011

Table 5.4 ANOSIM results for ant functional group assemblage composition. * denotes statistically significant difference in assemblage between/among treatments ($\alpha = 0.05$).

Global test comparison	Global R	P	Pairwise test comparison	R	P
Comparison of all treatments	0.125	0.01	Wood-edge vs wood-crop	0.092	0.051
			Wood-edge vs linear-edge	0.045	0.172
			Wood-edge vs linear-crop	0.342	0.001
			Wood-crop vs linear-edge	0.067	0.098
			Wood-crop vs linear-crop	0.097	0.063
			Linear-edge vs linear-crop	0.103	0.034

Fifty-one percent of the dissimilarity between the woodland treatments (edge and crop combined) and the linear strip treatments (edge and crop combined) was accounted for by four taxa: ‘*Iridomyrmex* 1’ (more abundant in linear strip areas), ‘*Paratrechina* 1a’ (more abundant in woodland areas), ‘*Pheidole* 3’ (more abundant in woodland areas) and ‘*Camponotus* 1a’ (more abundant in woodland areas) (Table 5.5). The same four morphospecies, together with ‘*Rhytidoponera* 1’, accounted for 59% of the dissimilarity between the edge and crop areas (Table 5.6). These five taxa also accounted for much of the dissimilarity between the more detailed treatment comparisons (e.g. woodland-edge compared to woodland-crop).

Table 5.5 Morphospecies percentage contribution to dissimilarity derived from SIMPER analysis between edge and crop treatments proximate to woodland, and edge and crop treatments adjacent to linear grass strip

Morphosp.	**Wood edge Av. abundance**	**Linear edge Av. abundance**	**Av. Dissim.**	**Dissim. /S.D.**	**% Dissim.**	**Cumulative % Dissim.**
Iridomyrmex 1	110.7	213.8	9.6	1.3	17	17
Paratrechina 1a	39.5	9.7	6.9	1.1	12	29
Pheidole 3	44.4	25.8	6.8	1.3	12	41
Camponotus 1a	2.7	0.04	5.6	1.4	10	51
Rhytidoponera 1	6.5	4.2	4.5	1.2	8	59
Iridomyrmex 7	5.46	0.2	4.1	0.9	7	66

Table 5.6 Morphospecies percentage contribution to dissimilarity derived from SIMPER analysis between edges (woodland edge and linear grass strip edge combined) and the adjacent crops.

Morphosp.	**Edge Av. abundance**	**Crop Av. abundance**	**Av. Dissim.**	**Dissim. /S.D.**	**% Dissim.**	**Cumulative % Dissim.**
Iridomyrmex 1	282.3	42.1	11.2	1.3	20	20
Pheidole 3	17.8	52	7	1.3	13	33
Paratrechina 1a	44	5	6.5	1	12	45
Rhytidoponera 1	5.1	5.6	4.8	1.2	9	54
Camponotus 1a	1.3	1.5	3.7	1	7	61
Iridomyrmex 7	1.2	4.5	3.6	0.8	6	67

To some extent, the functional group results mirrored the morphospecies results, although treatment effects were less distinct (Fig. 5.14 a–c; Table 5.4). For instance, whereas the morphospecies assemblage was significantly different between the woodland and linear grass strip sites (Fig. 5.13a; Table 5.3), the difference between the same treatments using the functional group data was not significant (R = 0.09; P = 0.051; see Fig. 5.14a), but showed a trend for a similar relationship as the morphospecies data. However, for functional group assemblage composition between the crop edge and crop interior, there was a significant difference, similar to that for the morphospecies data (R = 0.115, P = 0.01; Fig. 5.14b). Also, the morphospecies data indicated different assemblages between the wood-crop and the linear-edge, and between the wood-crop and the linear-crop (Fig. 5.13c; Table 5.3), whilst the difference in functional group data was not significant for these comparisons (Fig. 5.14c, Table 5.4).

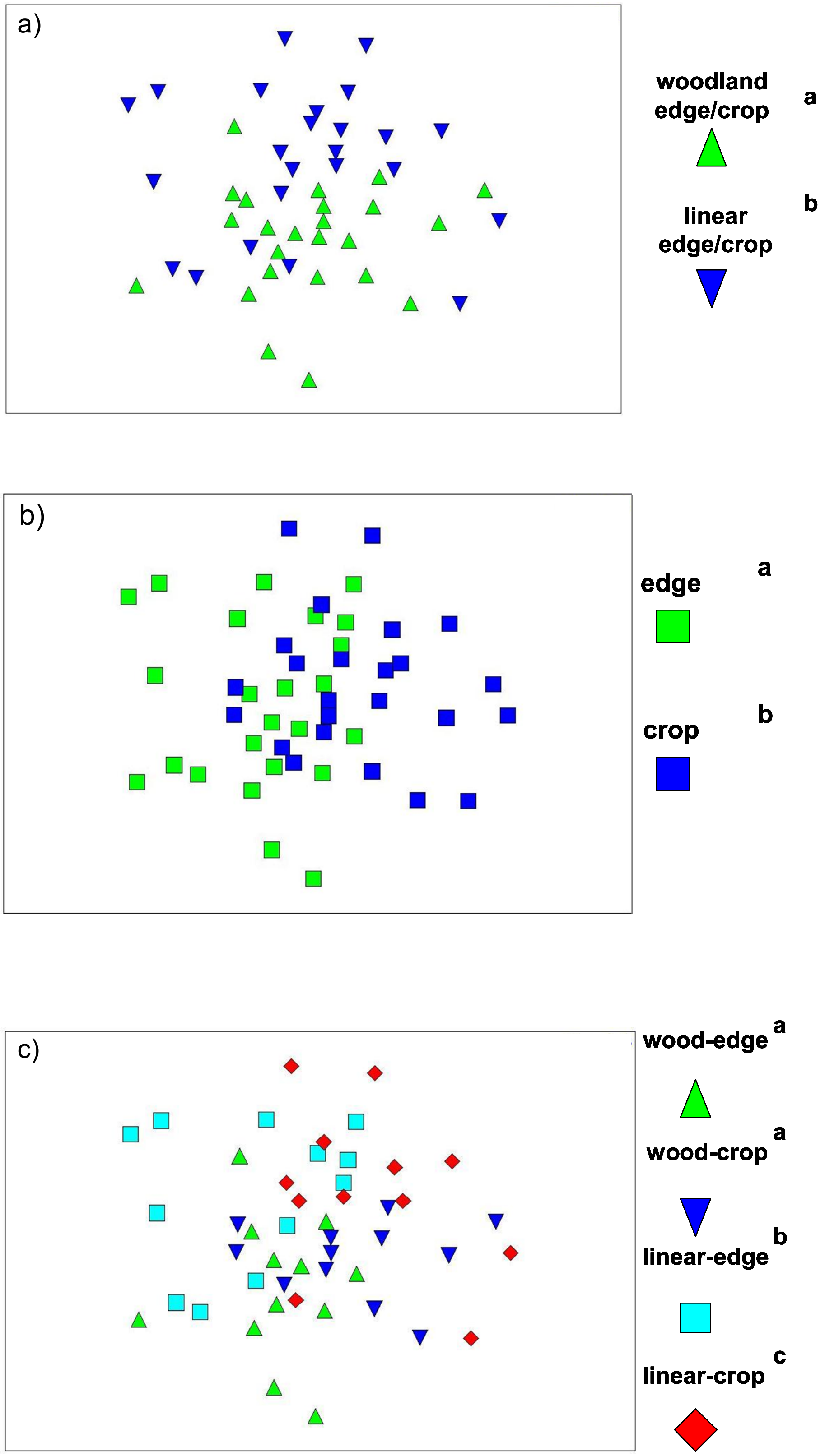

Fig. 5.13 nMDS ordination of 4th rt transformed ant morphospecies data, Bray-Curtis similarity matrix for a) woodland-edge and crop compared to linear-edge and crop; b) woodland and linear edge compared to woodland and linear-crop; c) each edge and crop type compared. Stress in all cases = 0.23. Different letter denotes statistically significant difference between treatments for ANOSIM tests ($\alpha = 0.05$).

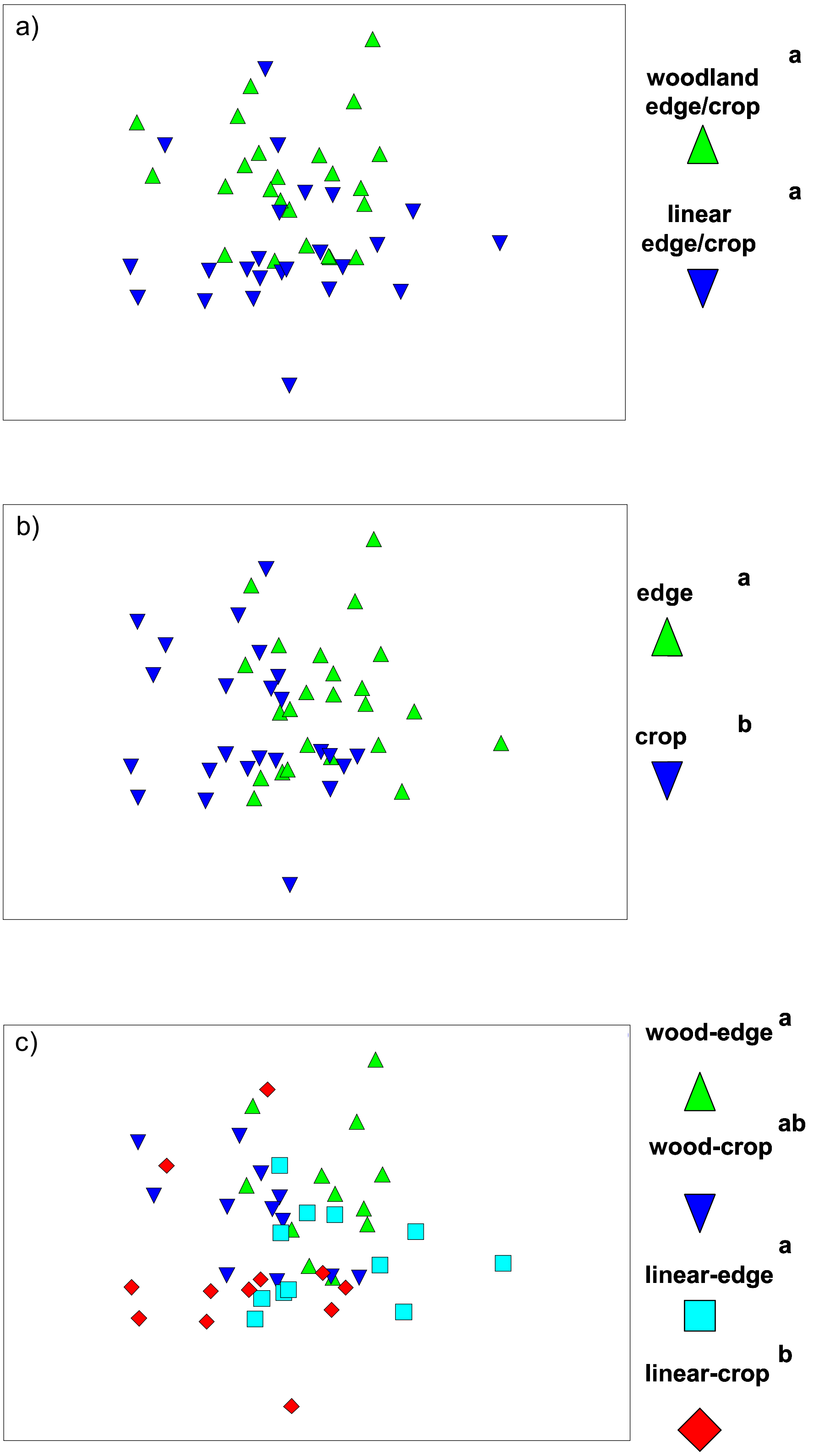

Fig. 5.14 nMDS ordination of 4th rt transformed ant functional group data, Bray-Curtis similarity matrix for a) woodland-edge and crop compared to linear-edge and crop; b) woodland and linear-edge compared to woodland and linear-crop; c) each edge and crop type compared. Stress in all cases = 0.19. Different letter denotes statistically significant difference between treatments for ANOSIM tests ($\alpha = 0.05$).

The proportional abundances of Dominant Dolichoderines appeared to be more prevalent on average in woodland edge and woodland crop than linear treatments, Generalised Myrmicinae were more prevalent in cropping than edge treatments, and both Hot Climate Specialists and Subordinate Camponotini were more prevalent in woodland than linear treatments) (Fig. 5.15).

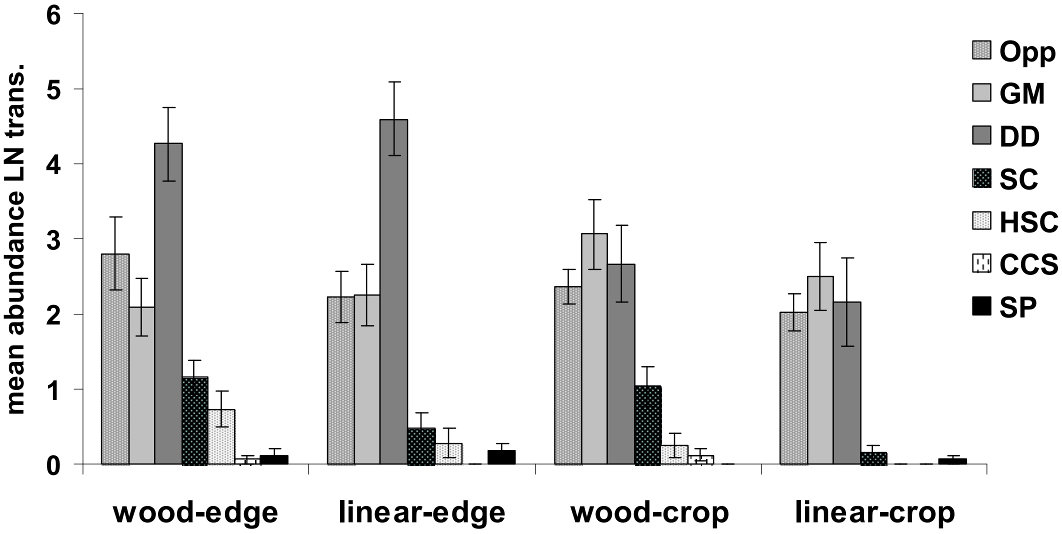

Fig. 5.15 Mean LN transformed abundance of ants by functional group in the four edge and cropping treatments. Functional group abbreviations are: SP – Specialist predator; CCS – Cold climate specialist; HSC – Hot climate specialist; SC – Subordinate Camponotini; DD – Dominant Dolichoderinae; GM – Generalised Myrmicinae; Opp – Opportunists. Error bars are standard error of the mean (N = 12 for each treatment).

5.3.1.5 Influence of habitat variables on ant morphospecies assemblage composition

The measured habitat variables significantly influenced both the edge (Global R = 0.702, P = 0.007) and the crop interior (Global R = 0.918, P = 0.001) ant morphospecies assemblages. The five most influential variables shaping edge assemblages were local coarse woody debris cover, local rock cover, the density of mat-forming grasses in the adjacent habitat, coarse woody debris cover in the adjacent habitat, and the density of crop residue in the adjacent habitat. Ant morphospecies assemblages in the crop interior, meanwhile, were most influenced by three local environmental variables—mean graminoid height, graminoid density and crop cover, and two variables from the adjacent habitat—coarse woody debris cover and bare ground cover.

5.4 Discussion

The ecological literature provides many examples of the complex roles that edges play in shaping ecological assemblages, interactions and processes (Ries *et al.* 2004). The range of responses to edge type and distance from edge in this study supports this view. For instance, ant richness and abundance differed with both distance from edge and edge type, whereas spider abundance did not. Meanwhile, there were no arthropod richness or abundance differences of any kind observed between arthropods entering and arthropods leaving crop fields. Ant assemblages on the other hand were distinct between different edge habitat types and distance into the field when examined at a taxonomic level, but edge habitat type made little impression on functional group assemblage composition. Finally, predation rates of *Heliothis* eggs were greater at crop edges than 20 metres into the crop. There are several potential reasons and contributory factors for these findings.

5.4.1 No difference between ingoing and outgoing arthropod assemblages

The lack of difference between ingoing and outgoing assemblages caught in the directional pitfall traps may be attributable to both ecological and experimental design factors. For instance, some arthropods may have a tendency to move parallel to a visible edge (Pratt, *et al.* 2001) and predators may use habitat edges to navigate the landscape (Ferguson, 2000). Therefore, many organisms in this study, rather than crossing the boundary, may have travelled parallel to the field edge and therefore had a roughly equal chance of being caught in either the ingoing or outgoing traps. Optimal directional pitfall trapping would be achieved if all taxa crossed the field boundary in a straight, perpendicular trajectory. However, some arthropods are known to utilise a random walk movement and foraging pattern (Wallin and Ekbom, 1988) that consists of straight line movements interspersed with turning angles, which can be influenced by the immediate environment (Challet *et al.* 2005). Consequently, individuals entering the crop from the neighbouring habitat may have fallen into the outgoing pitfall traps due to convoluted routes, and vice versa. This behavioural trait may have been exacerbated by an aspect of the experimental design that could have biased results. For instance, the length of the partition between the ingoing edge-side and outgoing crop-side traps may have been insufficient to successfully segregate arthropods leaving or entering the crop. Another possible effect of the sampling approach could have been attraction of arthropods from all directions to the trapping station, which may have provided desirable conditions (e.g. high humidity, microclimate stability) for certain taxa. Finally, sampling was only conducted during one stage of crop development (approx. 50 % of heads flowering)—it is possible that differences in immigrating and emigrating assemblages may have been detectable had sampling been conducted during other periods of crop development.

5.4.2 The influence of edge type on arthropod assemblage composition

My results indicate that edge type (i.e. type of habitat adjacent to the crop) was highly influential in shaping certain aspects of arthropod assemblages both at the crop edge immediately adjacent to the edge habitat and some distance into the crop itself. For instance, ant richness, abundance and morphospecies assemblage composition differed by edge habitat type, with both local habitat variables and adjacent land use habitat attributes found to influence assemblage composition. It appears that both edges and adjacent habitats may potentially influence arthropod assemblages through a variety of mechanisms.

5.4.2.1 Effect of edge habitat type—composition and structure

Numerous studies have indicated that the structure and composition of edge habitat may affect the arthropod assemblages inhabiting it, with habitat structural and compositional complexity playing important roles. The effects of adjacent habitat structure and composition may provide potential explanations as to the greater ant richness and abundance observed at the woodland-edges compared to the linear-edges. For instance, Lagerlöf and Wallin (1993) found that a floristically diverse crop margin supported greater arthropod abundance and diversity than a margin dominated by couch grass *Elytrigia repens* (L.), and Meek *et al.* (2002) reported that richness and abundance of butterflies and abundance of bumblebees (*Bombus* spp.) were greater in floristically diverse six-metre field margins than other, less diverse, field margin types. These results indicate that the diverse vegetation associated with complex margins and linear field edge vegetation may provide a greater diversity of resources for a wide range of taxa. Furthermore, the structural complexity of a margin can also greatly influence arthropod assemblages. For example, Baines *et al.* (1998) found greater spider abundance and richness in long-established margins than newly established ones. Arthropods can also be affected by the management of margins and boundaries, particularly where such management alters habitat complexity. For instance, Bell *et al*. (2002) found that cutting of grass margins and glyphosate application decreased the abundance of the spider *Lepthyphantes tenuis* (Blackwall).

There are relatively few studies that have compared arthropod assemblages in a woodland habitat/crop boundary and a linear habitat/crop boundary, but Kells and Goulson (2003) reported bumblebee assemblage differences between margins associated with a woodland/crop boundary and a field/crop boundary. The responses to habitat varied among species; for instance, *Bombus lapidarius* (L.) was far more prevalent in the field/crop boundaries than in the woodland/crop association, whereas *B. pascuorum* (Scopoli) displayed the opposite trend. The adjacent habitats (woodland and a crop field/paddock) that comprised the edges in this study were very different structurally and compositionally and appeared to exert a considerable influence over observed differences in biological assemblages occurring at the respective habitat/crop edges.

5.4.2.2 Effect of edge habitat type—Habitat extent

There are a number of factors beyond the immediate vicinity of the crop/adjacent habitat interfaces that could potentially influence arthropod community composition in these edge habitat zones, including the area of adjoining habitat. The woodland patches in this study were far greater in area than the linear grass strips. This is one possible reason why ant richness was higher in the crop edge that bordered the relatively large blocks of woodland and grassland compared to the linear habitat/crop edge—there was simply a larger pool of species in the woodland habitat that could then potentially occur at its interface with the crop. For instance, if a cropping field with sides of 500 m in length is bordered on one side by a linear grassy margin or strip of 1.5 m width, the area of that adjacent habitat would be 750 m^2. If the same field is bordered by a block of remnant native vegetation with a width of 400 m, then the area of adjacent habitat would be 200,000 m^2. Species-area relationships, where larger patches of habitat harbour more species, suggest there would be more species (and more individuals) in the block than the linear strip.

Whilst arthropods may not necessarily require large areas of suitable habitat (Fischer and Lindenmayer, 2002b), it may be that for some species (e.g.

'*Camponotus* 1a' which was commonly found at the woodland edge but very rarely in the linear edge) a linear grass strip provides insufficient habitat to support viable populations. It is also likely that larger patches of habitat may contain a greater diversity of niches (Mason *et al*. 2008), capable of supporting a greater diversity of taxa. Furthermore, native remnant patches are more likely to contain critical habitat resources for certain ant taxa, such as abundant quantities of coarse woody debris (Kirby, 1992; Lafleur *et al*. 2006). Consequently, there are likely to be concentrations of taxa dependent upon such resources for nesting, but which may be capable of foraging over large areas in less concentrated numbers. It is telling that some of the morphospecies restricted to the woodland treatments in this study were those found only in woodlands and pastures in the study in Chapter 3, and therefore may be able to easily move into crop edges.

5.4.2.3 Effect of edge habitat type—adjacent habitat disturbance

It may be that the differences in ant assemblages observed at the different edge types abutting the cropping, may be attributable, in part, to differences in disturbance regimes impacting on the two adjacent habitat types. In this study, the woodland and linear grass strip habitat types that border the crops are subjected to different management regimes. For instance, both the woodland edge abutting the crop and the linear strip are exposed to the management activities occurring in the crop (for instance, pesticide and herbicide application), which can result in both direct and indirect mortality of both target and non-target arthropods (Freemark and Boutin, 1995; Thorbek and Bilde, 2003). However, the majority of the woodland patch will be far less affected by the adjacent cropping activities than the narrow strip which is bordered on both sides by intensive cropping. The main disturbance process impacting upon the woodlands and associated grassland areas is grazing by cattle. This difference in management may translate into the woodland patches having a different (and arguably less intensive) disturbance profile than the linear strip habitat, and consequently able to support species other than those restricted to highly disturbed habitats. These organisms may, in turn, be able to repopulate the more highly disturbed woodland/crop interface from the woodland patch interior.

This is particularly likely to be the case for the relatively high number of ants belonging to the genus *Camponotus* being present in the woodland edge samples. In particular, '*Camponotus* 1a', a taxon found in Chapter 3 to be largely restricted to woodland (see Appendix C.1), was abundant in the woodland edge samples, but largely absent from the linear edge samples. This appears to indicate that the woodland itself is a source of certain taxa that are sufficiently dispersive and/or tolerant of disturbed habitats to frequent the woodland/crop edge, but insufficiently dispersive/tolerant to occur in the linear strip areas.

Whilst ant morphospecies richness and abundance was greater in the woodland edge than the linear edge, the latter still supported a total of 23 morphospecies, compared to 35 in the woodland edge and a total in all treatments at all sites of 43 morphospecies. This indicates that linear strips of grassy vegetation are able to provide habitat for over half the morphospecies recorded in the study. Although ant richness did not differ between the linear edge and its adjacent crop, there was greater abundance in the linear edge than the crop, and the assemblage composition at morphospecies and functional group levels also differed between the two treatments. The increased abundance in the edge habitat in particular indicates that it is biologically less depauparate than the adjacent crop lands.

5.4.3 The influence of edge and adjacent habitat type on arthropod assemblages in crops

This study found that edge habitat type exerted an influence some distance into the crop. Both ant abundance and richness were significantly greater in the crops adjacent to the woodland edge than those bordered by the linear strip. Furthermore, both morphospecies and functional group assemblage composition differed significantly between the two crop treatments. Both local habitat and adjacent habitat were found to exert an influence on the ant assemblages in crops, with grass height and density and crop cover at the local scale, and dead-wood and bare ground cover in the adjacent habitat influencing within-crop assemblages.

Given the influence that arthropods can have in cropping systems (as predators, pests, parasites, ‘ecosystem-engineers’, etc), it is perhaps surprising how few studies have focussed on the impact of edge habitat type and adjacent habitats on arthropod assemblages in the crop adjacent to that edge habitat, and how ‘spill-over’ from an adjacent habitat may influence within-crop arthropod assemblages. I found only four published studies (Varchola and Dunn, 1999; Lee *et al*. 2001; Varchola and Dunn, 2001; Marshall *et al*. 2006) that compared arthropod richness in crops with different edge habitat or field margin types, with none reporting significantly greater richness in the crop with the more complex edge habitat, as has been found in this study. I also found few studies that examined the effects of edge habitat or field margin type on arthropod abundance and density in adjacent crops, with results varying among studies.

Of those that did examine these areas of research, Marshall *et al*. (2006) reported greater abundance of bumblebees and in particular *Bombus lapidarius* (L.) in crops with 6 m margins, and significantly more non-Lyniphiidae spiders in crops with no margins in fields of intermediate size. Varchola and Dunn (2001) compared the abundance of carabid beetles between cereal fields bordered by complex hedges and simple grass margins, finding that carabid densities were greater in crops bordered by hedges than those adjacent to grass margins early in the crop growth season. However, this pattern changed as corn development progressed to canopy closure, with density became greater in the fields bordered by grass margins.

There are at least three possible explanations for the increased richness and abundance of ants adjacent to native habitat observed in my study findings. Firstly, ants are known to be highly responsive to a wide range of environmental variables, ranging from soil structure to vegetation structure and composition, disturbance, land management, interspecific interactions and landscape composition and configuration (Andersen, 1995; Andersen, 2003; Hoffmann and Andersen, 2003; Underwood and Fisher, 2006; Debuse *et al*. 2007; Spiesman and Cumming, 2008). Several studies have concluded that ant assemblage composition is highly influenced by within-patch habitat characteristics (e.g. Debuse *et al*. 2007). It may be that the habitat and biological assemblage characteristics of the edges and adjacent habitats also exert an influence on the assemblage some distance into the adjacent crop, through organism spill-over and movement.

Secondly, the crop sampling points were only 20 m into the crop from the edge of the adjacent habitat. It may be fruitful to examine how far that influence extends into the crop by locating trapping stations at different distances into the crop. Several studies that have examined the influence of edge habitats at increasing distances into an adjacent crop have found that biological assemblages can change with increased distance from the edge. For instance, groups of spiders in Israel, termed field 'residents', were more abundant in the field than the adjacent arid natural habitat and increased in abundance with distance from the field edge (Gavish-Regev *et al*. 2008). Conversely, this study found that cursorily dispersing spiders from the family

Gnaphosidae were more abundant closer to the natural habitat edge. Meanwhile, Bowie *et al.* (1999) reported that the number of Syrphidae (hoverfly) adults decreased with increasing distance from canola patches into wheat fields, whilst the number of adult aphids greatly increased with distance. Other studies have found that arthropod distributions in crops may be more complex than merely being a function of distance from edge. For instance, Holland *et al.* (1999) reported that arthropod distribution and abundance in crops displayed considerable temporal variation, but with marked intertaxon variation, with spiders of the family Linyphiidae being reasonably uniformly distributed throughout crop, whereas carabid beetles and lycosid spiders were found predominantly within 60 m of the field edge. Similarly, Pearce and Zalucki (2006) found considerable spatial and temporal variation of arthropod distribution in apparently uniform soybean fields, with lycosids again displaying a preference for areas close to complex adjacent habitats, in this study lucerne *Medicago sativa* (L.). Considering the very depauparate ant fauna found in crops (> 50 m from edge) in Chapter 3, it is likely that a decline in observed ant richness from crop edge to more distant crop interiors would be observed.

Thirdly, the two adjacent habitat variables that exerted the greatest influence on within-crop ant morphospecies assemblage composition were coarse woody debris cover and bare ground cover. Dead wood is known to be an important component of some ant species' life cycles (Shattuck, 1999) and invertebrate ecology generally (Kirby, 1992), and the amount of bare ground in woodland can greatly influence ant assemblages through processes such as insolation regulation (Bestelmeyer and Wiens, 1996). Consequently, it appears that the effects of adjacent habitat characteristics may be felt some distance into areas of crops.

5.4.4 Mixed results for other arthropod measures

There were no statistical differences among the other treatments for non-Formicidae arthropod abundance, order/class level richness or spider abundance. These findings are possibly attributable to the low taxonomic resolution used for identification. Had I identified other arthropod groups to genus or morphospecies level, then perhaps differences among treatment assemblages would have become apparent. However, some studies focussing on the issue of taxonomic resolution for invertebrates have concluded otherwise. Bowman and Bailey (1997) generated Bray-Curtis similarity matrices for a dataset of macroinvertebrates stratified at a range of taxonomic levels (e.g. genus, family, order); they concluded that the degree of similarity (or difference) among treatments based upon analysis at coarse taxonomic levels (e.g. order) were similar to that evident at finer taxonomic levels (e.g. genus). Similarly, Nakamura *et al.* (2007) discovered that differences between rainforest and pasture sites were evident in ants at the level of genus, species and functional groups, and coarse arthropod data at the level of order and class. Meanwhile, Andersen *et al.* (2002), found that by using large ant morphospecies (>4 mm body length) only, they were able to replicate the findings of a comprehensive ant survey in relation to responses to SO_2 outputs from a metal smelter.

The results of the ant functional group data were also mixed. Whilst the functional group assemblage composition displayed broadly similar patterns among treatments as the morphospecies data, the differences were not as pronounced. This is testament to the usefulness of the approach in making some broad generalisations that concur with finer scale taxonomic approaches, but also indicates the limitations of the approach in discerning differences among subtly different treatments. For instance, ant morphospecies assemblage composition differed significantly between the woodland edge treatment and the linear strip edge treatment, whereas there was no significant difference between the functional group assemblage composition for these two treatments. Some individual functional groups appeared to respond to habitat as may be anticipated. For instance, the Generalised Myrmicinae group was generally more abundant in the crop than the edge habitats. This functional group was largely represented in this study by the genus Pheidole, a group that, according to Hoffmann and Andersen (2003), usually respond positively to disturbed environments. On the other hand, the Opportunist group did not appear to differ among treatments, despite also responding positively to highly disturbed, early successional environments. This may be because the responses of this group may be determined by disturbance at a larger spatial scale (e.g. encompassing both crop field and crop edge habitats) than that represented by the treatments in this study.

It is interesting that significantly more large (>5 mm) spiders were found in the linear edge habitat than in the woodland edge habitat, particularly given that numerous studies have reported that increased arthropod body size can be related to reduced disturbance or other aspects of increased habitat quality (e.g. Blake *et al.* 1994; Miyashita *et al.* 1998). One possible explanation for my finding could be that reduced interspecific competition and/or intraguild predation may have enabled greater numbers of large spiders to forage in areas of reduced ant abundance. For instance, Sanders and Platner (2007) have shown that complex intraguild relationships between ants and spiders may greatly influence community structure, through competition or intraguild predation. However, several other studies that have investigated ant/spider co-occurrence have not reported ant presence and abundance having a negative impact upon spider abundance (e.g. Van Der Aart and De Wit, 1970; Lenoir *et al*. 2003).

5.4.5 Edge habitats and predation rates

A significantly greater proportion of *Heliothis armigera* eggs was taken from the edge of the crop than 20 m into the crop, but edge habitat type had no effect on the proportion of eggs taken at either crop edge or crop interior. This appears to indicate that predation pressure is greater at the interface of the crop and the neighbouring habitat than in the crop itself (at least at the time when sampling was conducted), but that the adjacent habitat or edge type itself has little bearing upon rates of egg predation. From this one could surmise that boundary habitats are likely to be a source of predators (Dennis *et al*. 2000 (in Ekbom *et al*. 2000); Landis *et al*. 2000) and that linear grass strips perform an ecosystem service (pest predation) at crop edges, comparable to that provided by the boundaries of more extensive and natural habitat types. The only potentially predatory group for which I found a higher abundance at edges compared to crop interiors was ants, and there are many examples of them acting as generalist predators in agricultural systems (e.g. Way *et al*. 2002). Furthermore, there were occasional instances (although not frequent enough to influence egg removal results) where, upon counting the egg removal rates in the laboratory, I had inadvertently removed individual ants from the field, which were found to be feeding on the eggs. Ants belonging to two different genera were observed in this behaviour (*Iridomyrmex* and *Paratrechina*). Also, ants that could have been either of these two genera were observed on egg cards in the field during collection. However, if ant abundance was the main driver of the egg card predation, then one would expect to see greater predation at the woodland-edge treatments than the linear-edge treatments, as significantly greater ant richness and abundance (including the two genera mentioned above) was observed in the woodland treatments. Perhaps one reason why I did not observe any such predation trend is the length of time that the cards were left in situ (twelve hours). This may have been too long, as in many woodland and linear strip edges, many cards were entirely depleted of eggs by the time I collected them, thus potentially masking any difference in egg removal rate. One way to overcome this would be to check cards more frequently to establish the relative removal rate of eggs at each edge type.

5.5 Conclusions

This study found that habitat edges formed by the juxtaposition of crops with both remnant native vegetation and linear grass strips are capable of supporting a wealth of arthropod biodiversity. Furthermore, linear strips of vegetation between cropping fields contained a reasonable proportion of the ant taxa encountered in field trials (>50 %), and predation rates of *Heliothis* eggs appeared to be similar at both edge types. This indicates that linear vegetation strips may perform some of the same functions (biodiversity conservation, pest control potential) in regions where agriculture is a relatively recent source of landscape modification (‘frontier’ regions—see Chapter 1), as they do in regions with an ancient history of agriculture, and in which they represent more of a traditional landscape element (Marshall and Moonen, 2002). The loss of such features in intensifying Australian agricultural landscapes may therefore result in reduced local arthropod biodiversity and abundance, with concomitant impacts on ecosystem function. In terms of management, these findings imply that where there is an opportunity to partition agricultural production fields with linear vegetation features (similar to ‘beetle banks’, see Thomas *et al*. 2002; MacLeod *et al*. 2004) in ‘frontier’ agricultural landscapes, the biodiversity and predator source-habitat potential of such features should be a consideration. These findings further indicate that the conservation of such features in ‘frontier’ agricultural systems may be an important management and research issue.

However, the woodland remnant edges in this study provided the greatest biodiversity benefit, and I would argue from these findings that their loss would lead to a considerable reduction in landscape-scale (gamma) diversity of ants, and possibly of other groups. Therefore, the maintenance and sympathetic management of small patches of remnant vegetation in otherwise intensively managed landscapes should remain a high priority.

Furthermore, all linear grass strip edge sampling points, although considerable distances from the woodland patches (between 750 m and 2000 m), were spatially connected to the woodland patches via other grass strips and roadside verges. Such physical connectivity could allow colonisation of distant linear strips by species unable to move through the cropping areas from the more species rich remnant vegetation areas. The landscape in which I conducted this study consisted of numerous land-use types, and landscape heterogeneity and the proportion of natural habitat components in mosaic landscapes can greatly influence abundance and diversity of taxa (Benton *et al*. 2003; Tscharntke *et al*. 2005b). Consequently, the habitat value of a linear strip in a mosaic landscape containing habitat components of relatively low disturbance and high complexity may be significantly greater than the value of a similar strip in a monocropped landscape. Numerous studies have concluded that arthropod diversity is greater in intensively managed agricultural units embedded in complex than in simple landscapes for a wide range of taxa (e.g. Araneae, Schmidt *et al*. 2005; Syrphidae, Burgio and Sommaggio, 2007). Consequently, further research is required into the habitat value of semi-natural features such as linear grass strips in predominantly cropped systems. This could potentially be done by examining the biodiversity value of linear strips in ‘frontier’ agricultural landscapes that include both mixed land-use landscapes and landscapes that are largely devoid of native remnants.

Chapter 6

Conclusions, implications and limitations

6.1 Summary of Thesis

This thesis provides insights into the ways in which arthropod biodiversity responds to commonly-occurring agricultural land-use types, through local case studies and global meta-analyses. Chapter 2 used various meta-analytical techniques to identify general global patterns of arthropod richness and abundance among different land uses, and whether those patterns are evident for different feeding guilds and taxonomic groups. A general decline in taxonomic richness with intensified land use was found, with the rate of decline differing between different land-use types. The majority of taxa are lost in the transformation from native vegetation (woodland, forest, native grassland) to an agricultural land use (improved/introduced pasture, cropping). Losses among different agricultural land uses (from pasture to cropping and from reduced-input/intensity cropping to conventional cropping) were consistent, but of a much smaller magnitude. This pattern held across two analytical techniques and two feeding guilds (predators and decomposers) and the majority of taxa, but was not evident for the herbivorous feeding guild or several herbivorous taxa.

These results, coupled with those that found a general global difference in predator and decomposer abundance between native vegetation and agricultural land uses and between non-intensive and intensive cropping, are useful for predicting or modelling the likely changes in arthropod abundance, richness and feeding guild representation due to agricultural land-use change or management adjustment. However, as revealing as such broad-scale analysis is in developing generalisations, local environmental features will inevitably influence patterns in individual cases.

Chapter 3 examined the field responses of ant (Formicidae) assemblages to the intensity of agricultural land use in a mixed farming landscape in southern Queensland, and compared the findings to those of the meta-analysis for that taxonomic group as well as an additional global meta-analysis of ant functional group responses to land-use change. The global meta-analysis for ants indicated that ant richness generally declines with intensified land use, with moderately greater richness in pasture than cropping. However, in the field study, pasture had far greater richness than cropping and an assemblage composition that differed significantly from that of both woodland and cropping, as well as several taxa that were unique to pasture. This suggests that a comparatively low-intensity agricultural land use (such as pasture for livestock grazing) may have benefits for biodiversity, and potentially for associated ecological processes. The value of low-intensity agricultural land for wildlife is well recognised in parts of the world where biodiversity and agriculture have co-existed for millennia (e.g. Europe). However, the notion that this phenomenon may also be relevant to regions of the world (e.g. Australasia, Central America) where modern agriculture is a relatively recent introduction is consistent with recent insights from a range of authors (e.g. Hughes *et al*. 2002; Fischer *et al*. 2005; Sekerkioglu, *et al*. 2007; Haslem and Bennett, 2008a; 2008b) who suggest that the agricultural matrix may be of greater biodiversity value in such regions than has generally been recognised. For instance, it is feasible that pastures used for production purposes may provide surrogate habitat for some biodiversity that was previously dependent upon native grassland. The pastures in this study may provide resources, microclimates and habitat structure sought by ants that were formerly associated with the native grasslands which once covered much of the Darling Downs region (Fensham and Fairfax, 1997).

Chapter 3 also attested to other changes that occur among agricultural land uses of differing modification and management intensity. For instance, ant functional group assemblage composition differed among land uses, with proportionally more ruderal ‘opportunist’ taxa present in highly intensive land uses such as cropping. Such patterns of functional group response were found to be consistent for both the global meta-analysis and the local field study.

Chapter 4 dealt with changes to arthropod assemblage morphological representation among different land-use types. Morphological patterns were evident for a range of taxa, with both beetle and spider communities skewed towards a high abundance of small-bodied taxa in more intensive land-use types, and a greater presence of vagile, macropterous beetles in cropping than the other land uses. The potential reasons for such patterns include the greater dispersive abilities of small and winged taxa to colonise frequently disturbed environments (Gobbi and Fontaneto, 2008), and the generally rapid reproductive capacity of small taxa, thus allowing populations to recover quickly from a disturbance event (Peters, 1983; Magura *et al*. 2006).

The field study findings discussed in Chapters 3 and 4, covering patterns in richness, abundance, taxonomic and functional group composition and morphology, are all testimony to the power of agricultural land use and management to shape the communities of arthropods, with responses to fine-grained and sharply defined patterns of land use evident. Given the functional importance of arthropods in driving ecosystem processes (Tscharntke *et al*. 2005a), it is likely that such changes, driven by agriculture, may have important implications for aspects of agricultural production dependent upon biodiversity-driven ecosystem services (Altieri, 1999).

Chapter 5 explored the relationship between habitat components of mosaic agricultural landscapes and the ecosystem service delivery of arthropods. As anticipated, the edges of crops abutting native habitats supported greater richness of ants and a different assemblage composition than the edges of crops bordered by linear grass strips. However, abundance of ants and other important groups (e.g. spiders) did not differ between crop edges bordered by different adjacent habitat types. Predation rates of *Helicoverpa* eggs did not differ at the margins of crops with different adjacent habitat types, but were reduced in the crop interior compared to the crop edge. This indicates that the boundary habitat influences the community composition at the edges of crops, with differences still evident some distance into the crop. However, the rates of predation appear to be unaffected by the assemblage composition and may be more dependent on absolute numbers of predators. This appears to support the idea of edge habitats being a focus for predators that are able to take advantage of prey in both adjacent habitats as well as being able to utilise specific structural or compositional features of the edge itself (Landis *et al*. 2000). The observations of this study indicate that relatively simple linear grass strips, features more commonly associated with, and valued in, European agricultural systems, may have some ecosystem service properties for cropping comparable to those of native habitat components. This further emphasises the potential biodiversity and ecosystem service values of non-indigenous habitat components of the agricultural matrix. Such utilitarian aspects of modified habitat components add to the arguments that these features may also have biodiversity conservation value in highly altered landscapes (e.g. Haslem and Bennett, 2008b), and highlights potential risks associated with the loss of such landscape features due to agricultural intensification and landscape homogenisation (Benton *et al*. 2003).

6.2 Limitations

One of the inherent difficulties of studying arthropods is the limited knowledge of the taxonomy, life-history traits and ecological requirements of various taxa (Redak, 2000). Consequently, it is difficult to infer the precise ecological implications of the compositional patterns and trends detected without considerable further study. Whilst such fine-scale taxonomic and autecological work was beyond the scope of this study, it is hoped that it will serve as a basis for further research in similar systems. Whilst it would have been ideal to compare responses of ants with those of other taxa in the field, the arthropods are a vast group and as such only ants could be subjected to finer-level taxonomic study given the time available. However, this potential limitation was, in part, offset by the use of meta-analytical techniques which allowed comparison of a comprehensive range of arthropod group responses to altered land use.

The findings also represent a snapshot of a particular time, and hence offer no indication of how different habitat components are utilised at different times of year by various taxa. Numerous studies attest to the changes in arthropod populations over time (e.g. Pearson and Derr, 1986; Wiwatwitaya and Takeda, 2005; Chauvat *et al.* 2007), and ideally sampling would have been repeated at other times of year. Unfortunately, the practicalities of sampling several replicate sites, ongoing issues with drought (and therefore crop availability) and the large amount of arthropods to be processed precluded repeat sampling. Repeated sampling, whilst desirable, would have necessitated reduced sampling effort at each site or a reduced number of replicates. This is likely to be less of a problem for the land-use type sampling in Chapter 3, where the results were sufficiently similar to those of the meta-analysis in Chapter 2 to indicate that one sampling round may have been adequate to capture an accurate estimate of land-use impacts on ant assemblages. The directional pitfall trapping and predation-rate testing in Chapter 5 would probably have been enhanced by repeated sampling, particularly as the crop developed. This latter example represents a potentially useful option for future research, particularly in the area of temporally shifting predator/prey assemblage composition.

Another potential limitation of one-off sampling is that it is likely that absolute species richness (i.e. all species occurring in the patch were successfully sampled) for each land use was not attained. Greater sampling through time may well have yielded greater richness for all land-use types. However, in terms of relative richness (which was the aim of the study), equal sampling efforts in each different land-use type yielded markedly different levels of species richness that were largely consistent with the meta-analytical studies.

Pitfall trapping is widely recognised as standard technique for estimating relative abundance, richness, assemblage composition, etc., of a range of taxa from mammals (Umetsu *et al*. 2006), reptiles (Crosswhite *et al*. 1999), and in particular arthropods (e.g. Uetz and Unzicker, 1975). However, whilst the technique is popular and widely practiced, it is also considered to have limitations and carry the risk of bias in results (Topping and Sunderland, 1992)—such limitations may have influenced the results of this study in some way, and therefore merit discussion. For instance, pitfall trap samples compared to estimations with ground photoeclectors for epigeal arthropods indicated that abundance of Carabidae and Lycosidae was over-estimated with pitfall traps, whilst the abundance of Staphylinidae and Linyphiidae was underestimated (Land, 2000). The trend in disparity between the two techniques was greater in the more complex habitat type sampled (set-aside land in the Lang study). The implication of this for my work is that greater habitat complexity in pasture and woodland areas may have underestimated Linyphiid spider (and therefore small spider) densities in pasture and woodland habitats to some extent. However, given the enormous differences in Linyphiid abundance found in my study between crops and pastures/woodlands, it seems unlikely that the sampling technique alone was the cause of the observed differences. Lang (2000) also observes that there is a tendency for larger organisms to be caught in pitfall traps. This does not appear to have influenced my results unduly, as small taxa were caught in high numbers (e.g. ants of the genus Pheidole, caught in all habitat types and measuring approximately 2.0–3.5 mm in length). Another potentially confounding factor in the use of pitfall traps is that of predator satiation. The argument follows that hungrier individuals are likely to be more active (foraging), and hence more likely to be caught in pitfall traps (Chiverton, 1984). Therefore, pitfall trapping results may inadvertently be influenced by resource availability and trophic structure in a particular habitat type. In this study I found mixed results for predator abundance in different land use types (e.g. no difference in spider abundance between habitat types in Chapter 5, but ant abundance lower in crops than other land uses in Chapter 3), and therefore it is difficult to draw a conclusion as to how satiation and resource availability may have influenced predatory taxa activity in each land-use type.

All the woodland sites, despite representing the least disturbed and modified land-use type, were grazed by stock, either during or immediately prior to sampling. Consequently, they were somewhat modified, through soil compaction, increased nutrient loads, weed invasion and suppressed regeneration of native vegetation. This may account for the negligible difference between ant communities in the woodland core compared to the woodland edge, as all the woodland remnants are effectively highly disturbed and potentially operating as 'edge' habitat. Ideally, some reference sites of unmodified native vegetation would have been included, as several authors have indicated the differences in arthropod assemblages between grazed and ungrazed woodland (e.g. Abensperg-Traun *et al.* 1996; Bromham *et al.* 1999). Unfortunately, all accessible examples of this woodland type had been heavily grazed, and no reserved examples could be found.

Many studies have indicated the importance of habitat structure in determining arthropod assemblages (e.g. Rypstra, *et al.* 1999; Lassau and Hochuli, 2004). Although habitat structure was recorded at each sampling point, surveys of vegetation composition were not conducted. The botanical composition of sites may have helped explain some of the variation in arthropod assemblage structure, which was not explained by land-use type or landscape-scale variables.

Finally, the directional pitfall trap design may have benefited from an additional length of physical barrier separating the incoming from outgoing arthropod populations. Whilst the design was similar in scale to that used by Duelli *et al.* (1990), an additional barrier either side of the trapping frame (see Ch. 5) may have helped to differentiate further between the two treatments.

6.3 Management and policy implications

Collectively, the research outlined in this thesis demonstrates that agriculture can cause considerable biodiversity loss not only when native systems are cleared for farming, but when agricultural management is intensified. As Chapter 2 demonstrates, the greatest proportion of taxonomic richness is lost when one moves from native vegetation to agricultural land. However, there is also evidence that relatively low-intensity agricultural land uses may have some benefits for components of biodiversity, particularly when compared to high-intensity management systems. For instance, Chapter 2 indicates that compared to intensive cropping, pastures and reduced-input cropping systems can be expected to support more arthropod taxa as well as greater numbers of predators and decomposers, thus having potentially beneficial impacts on agricultural production. Both the loss of richness from native to agricultural systems and the potential biodiversity value of relatively low intensity agricultural land-use types were apparent in Chapter 3. In this study, richness was greater in the woodland (native vegetation) remnants than the agricultural land-use types, but grazed pastures contributed to greater gamma diversity in agricultural landscapes, and exhibited significantly greater richness than the more modified and intensively managed cropping areas. The potential of specific land-use components associated with intensive land use to maintain at least some proportion of arthropod biodiversity and deliver some potential ecosystem service benefits in the form of predation were also illustrated. For instance, in Chapter 5, linear strips abutting fields of crops contained similar abundances of arthropods as the boundaries of native vegetation adjoining crops.

These results, considered collectively, indicate that by managing components of the agricultural matrix sympathetically, there may be opportunities to enhance biodiversity and maintain ecosystem service delivery in agricultural landscapes. This has long been recognised in Europe, where ancient traditional agricultural landscapes have acquired and developed a diverse flora and fauna associated with production land components (Sutherland, 2004). However, in regions of the world where large-scale agriculture is a relatively recent landscape addition (‘frontier’ regions—Chapter 1), the traditional view has been that ‘islands’ of native indigenous vegetation are habitat, residing in a sea of non-habitat, the agricultural matrix (see Haila, 2002; Kupfer *et al*. 2006). Such a binary view of the landscape has been recently revised, with increasing recognition of the habitat and resource value of ‘countryside elements’ (*sensu* Haslem and Bennett, 2008a) and the influence of the structure and management intensity of the agricultural matrix for species that are considered to be ‘forest-dependent’ (Hughes, *et al*. 2002; Sekercioglu *et al*. 2007). Conservation management in agricultural landscapes in ‘frontier’ regions often focuses predominantly on remnants of native woodland or forest (Luck and Daily, 2003). This represents a sound conservation investment in part, but tends to neglect the spatially dominant land use in the landscape—agriculture. My work suggests that whilst patches of native vegetation are likely to be vital in conserving biological diversity in agricultural landscapes, areas not presently or commonly classified as habitat (e.g. pasture) may prove to be important refugia and resource pools for a range of taxa, particularly in the face of intensifying agricultural land use. Such approaches to conservation are becoming increasingly championed in Australia; for instance, Prober and Smith (2009) highlight the potential supportive role of perennial plant-based production systems in conserving the biodiversity of the Western Australian wheatbelt.

There is a growing body of recent scientific evidence (mainly focussed on birds associated with native vegetation) from Australia and elsewhere, that the agricultural matrix is far more ecologically important for biodiversity than previously thought, and accordingly this may present opportunities for integrating biodiversity conservation on private-land with agricultural management and policy (Hughes *et al.* 2002; Mattison and Norris, 2005; Park *et al.* 2007; Attwood *et al.* 2009; Sheahan, 2009). Such approaches, intended to complement the dominant conservation focus on native vegetation systems, may help to reduce threatening processes impacting upon native remnants, maintain or increase inter-remnant connectivity, reduce the impression that conservation is adversarial to production and forge better links between conservation and production policy and management. There are opportunities for conservation scenarios that improve conditions and resources for biodiversity, by modifying rather than excluding production, thus reducing conservation/production conflicts where feasible. Recent developments in the conservation policy climate in Australia, particularly relating to incentive schemes such as the Commonwealth Government's Environmental Stewardship Program (Commonwealth of Australia, 2007) and the Murray Catchment Management Authority's 'NestEgg' tender scheme (MCMA, 2008), indicate that a conservation approach more allied to production may be developing. Initiatives such as these may go some way to enabling land managers to undertake conservation actions whilst being compensated for the lost opportunity costs often associated with on-farm conservation management, particularly that focussing on the agricultural matrix (House *et al.* 2008).

6.4 Further research

Perhaps it is inevitable that any body of research generates more questions than it answers—this appears to have been the case with my thesis. Potential research questions that would follow logically from this thesis include a number relating to the importance of countryside elements (specific components of the agricultural matrix, such as pastures, linear vegetation strips, paddock trees, farm dams, etc.) for biodiversity conservation in Australia and other 'frontier' agricultural regions.

For instance, an important question relates to what roles the specific countryside elements of the production landscape play in maintaining biodiversity in recently created agricultural landscapes and how best might they be managed for the benefit of biodiversity and with minimal detriment to production? Whilst the countryside elements themselves are generally point features or patches of a particular land use or land cover type, the landscape in which such elements reside can also exert a considerable influence on ecological and conservation values. An important research question related to this issue is: do the biodiversity values of countryside elements such as pasture and paddock trees differ depending upon landscape context (e.g. landscapes with high percentage of native remnants remaining compared to predominantly agri-matrix landscapes)? Both of these questions apply at a broad level taxonomically, and to almost any taxonomic group.

In terms of the influence of countryside elements on arthropods, a useful area of research may be to investigate how countryside elements such as grass margins bordering cropping areas can be managed to increase populations of beneficial arthropods and reduce pest incursion into adjacent crops. This is related to management-specific responses of important arthropod groups. Two systematic reviews have examined this: one by Bengtsson *et al.* (2005) reported the effects of organic agriculture on numerous arthropod groups, and one by Attwood *et al.* (2008) (see Chapter 2) that revealed how reduced-input cropping in general can impact upon a range of arthropods. However, more detailed study is urgently required to advise farmers, land managers, researchers and policy makers on the detailed impacts of certain cropping and pasture management techniques (such as tillage, intercropping, stubble retention, grazing intensity, etc.) on various functionally important groups. As such, a meta-analytical study that details the impacts of various management regimes on different taxonomic and functional groups of arthropods would be valuable. The urgency of the dual need to utilise components of biodiversity in agricultural systems for ecosystem service provision and to conserve biodiversity in expanding and (often) intensifying agricultural landscapes leads to many other applied research questions; not least, the optimal management of countryside elements in order to increase the numbers of predatory and parasitic arthropods moving into cropping systems. Whilst such research is undertaken worldwide in many farming systems, the suite of land-use and crop-type specific studies has yet to yield strongly supported broad generalisations.

Another option for expanding on the type of 'general global response' meta-analyses performed in this thesis is to examine how effect size (e.g. Hedges' $E{+}{+}$ effect size) might differ between different biogeographical locations (e.g. tropical versus temperate), land forms (e.g. upland versus lowland), or agricultural historical development characteristics (e.g. 'frontier' versus 'traditional' systems). Some initial investigative analysis (not included in Chapter 2 due to space constraints) indicated that there was no significant correlation between the proportional analysis technique 'effect size' of arthropod richness differences between native vegetation ('NV') and agricultural land uses ('Ag') and the latitude where the study had taken place. However, this approach may have been severely hampered by the relative paucity of studies examining arthropod richness between native and agricultural systems at higher latitudes. Most of these studies (generally from Europe and North America) were far more focussed on the differences in arthropod richness among different agricultural land-use types. By contrast, those studies at lower latitudes principally focussed on native compared to agricultural systems. One potential means to explore such relationships would be to determine the agricultural history of each locality featured in a study. This would allow a more detailed examination of the time since agricultural development and the responses of arthropod taxa. However, such an undertaking would be no trivial exercise, and consequently is beyond the scope of this thesis.

Other potential research areas are more purely ecological than management-focussed. For example, does the relative influence of landscape and patch-scale factors differ in determining assemblage composition of taxa depending upon their dispersal and movement capabilities (e.g. Collembola might be more influenced by land use, whereas Hymenoptera might be more influenced by landscape composition and spatial arrangement). Finally, this thesis reported that some closely related ant taxa (from the same genus) displayed markedly different responses to land use and habitat preferences. Given the general lack of knowledge regarding the autecology and habitat associations of many arthropods, there is ample opportunity for more detailed research to be conducted at fine-scale taxonomic levels, in order to determine more exactly how taxon ecological and morphological traits are related to their habitat requirements and utilisation.

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Appendix A.1 Bird richness by country (total number of species, number of endemic species, number of IUCN Threatened species) for biodiversity/agricultural development correlations.

Birds Country	total # spp	endemics	IUCN Threatened	Birds Country	total # spp	endemics	IUCN Threatened
Afghanistan	501	0	17	**Nicaragua**	703	1	9
Albania	350	0	11	**Niger**	526	0	3
Algeria	397	1	12	**Nigeria**	944	4	18
American Samoa	66	0	6	**North Korea**	320	0	27
Andorra	161	0	0	**Norway**	471	0	7
Angola	976	12	18	**Oman**	472	0	12
Argentina	1026	18	46	**Pakistan**	738	0	29
Armenia	359	0	10	**Panama**	964	13	21
Australia	813	313	48	**Papua New Guinea**	823	75	34
Austria	434	0	13	**Paraguay**	708	1	28
Azerbaijan	368	0	13	**Peru**	1853	129	90
Bahamas	326	4	10	**Philippines**	591	177	64
Bahrain	332	0	6	**Poland**	451	0	14
Bangladesh	744	0	36	**Portugal**	502	0	14
Barbados	212	3	4	**Puerto Rico**	350	15	20
Belarus	318	0	8	**Qatar**	211	0	2
Belgium	433	0	11	**Romania**	380	0	12
Belize	622	0	4	**Russia**	769	2	49
Benin	600	0	3	**Rwanda**	720	0	8
Bermuda	356	1	7	**Saint Lucia**	176	5	6
Bhutan	681	0	22	**Samoa**	83	9	8
Bolivia	1434	24	31	**Sao Tome & Principe**	140	21	10
Bosnia-Herzegovina	319	0	11	**Saudi Arabia**	487	0	15
Botswana	585	0	8	**Senegal**	660	0	7
Brazil	1749	213	121	**Serbia & Montenegro**	380	0	10
Brunei	459	0	25	**Seychelles**	240	15	16
Bulgaria	397	0	12	**Sierra-Leone**	664	0	10
Burkina Faso	498	0	2	**Singapore**	389	0	16
Burundi	682	0	7	**Slovakia**	361	0	11
Cambodia	550	0	26	**Slovenia**	377	0	11
Cameroon	957	10	21	**Somalia**	704	7	14
Canada	657	6	22	**South Africa**	849	28	27
Cape Verde	184	4	4	**South Korea**	492	0	33
Cayman Islands	224	2	2	**Soviet Union**	849	4	51
Central African Republic	772	1	5	**Spain**	530	0	18
Chad	580	0	6	**Sri Lanka**	440	23	24
Chile	500	12	32	**St Kitts & Nevis**	139	0	2
China	1303	52	88	**St Vincent & Grenadines**	173	2	4
Colombia	1883	72	85	**Sudan**	994	1	9
Comoros	147	14	9	**Suriname**	718	0	2
Congo	714	0	9	**Swaziland**	510	0	11
Cook Islands	49	5	9	**Sweden**	476	0	9
Costa Rica	885	5	19	**Switzerland**	404	0	12

Country	total # spp	endemics	IUCN Threatened	Country	total # spp	endemics	IUCN Threatened
Cote d'Ivoire	743	0	12	**Syria**	388	0	12
Croatia	369	0	10	**Taiwan**	471	15	27
Cuba	368	22	17	**Tajikistan**	355	0	9
Cyprus	392	2	12	**Tanzania**	1097	20	34
Czech republic	413	0	14	**Thailand**	971	2	49
Czechoslovakia	423	0	13	**The Gambia**	575	0	2
Denmark	449	0	10	**The Netherlands**	462	0	12
Djibouti	393	1	8	**Togo**	662	0	4
Dominica	187	2	5	**Tonga**	73	2	8
Dominican Republic	289	0	14	**Trinidad & Tobago**	466	1	2
DRCongo	1161	20	29	**Tunisia**	373	0	9
Ecuador	1657	14	78	**Turkey**	490	0	14
Egypt	469	0	13	**Turkmenistan**	406	0	14
El Salvador	585	0	4	**Turks and Caicos**	200	0	4
Equatorial Guinea	844	0	8	**UAE**	435	0	10
Eritrea	563	0	9	**Uganda**	1044	2	18
Estonia	339	0	7	**Ukraine**	429	0	15
Ethiopia	914	20	19	**United Kingdom**	597	1	15
Faroes	273	0	1	**Uruguay**	479	19	5
Fiji	151	23	17	**USA**	885	13	38
Finland	441	0	10	**Uzbekistan**	365	0	15
France	567	1	16	**Vanuatu**	152	8	1
French Guiana	748	0	2	**Venezuela**	1406	45	27
French Polynesia	126	30	26	**Vietnam**	839	11	42
Gabon	747	0	11	**Western Sahara**	207	0	4
Georgia	358	0	11	**Yemen**	430	1	14
Germany	511	0	14	**Yugoslavia**	406	0	13
Ghana	737	0	10	**Zambia**	832	1	14
Greater Antilles	545	125	42	**Zimbabwe**	684	0	10
Greece	436	0	13				
Greenland	237	0	2				
Grenada	168	1	3				
Guatemala	739	1	11				
Guinea	725	0	10				
Guinea-Bassau	493	0	1				
Guyana	795	0	3				
Haiti	261	1	14				
Honduras	739	1	10				
Hong Kong	493	0	21				
Hungary	397	0	12				
Iceland	351	0	1				
India	1286	38	83				
Indonesia	1602	393	122				
Iran	521	1	19				
Iraq	411	0	14				
Ireland	473	0	11				
Israel	540	0	14				
Italy	534	0	16				
Jamaica	325	30	13				

Country	total # spp	endemics	IUCN Threatened
Japan	618	15	54
Jordan	412	0	12
Kazakhstan	504	0	21
Kenya	1119	7	21
Kyrgyzstan	377	0	10
Kuwait	362	0	8
Laos	700	0	26
Latvia	342	0	7
Lebanon	372	0	6
Lesotho	339	0	10
Lesser Antilles	401	31	21
Liberia	698	1	12
Libya	335	0	8
Liechtenstein	252	0	3
Lithuania	342	0	8
Luxembourg	299	0	4
Macau	88	0	2
Macedonia	333	0	10
Madagascar	296	105	31
Malawi	666	0	11
Malaysia	776	11	44
Maldives	124	0	2
Mali	611	1	6
Malta	388	0	10
Martinique	203	1	4
Mauritania	541	0	6
Mauritius	128	11	16
Mexico	1082	101	49
Micronesia	223	15	17
Moldova	301	0	9
Mongolia	427	0	24
Morocco	489	1	15
Mozambique	728	0	20
Myanmar	1056	5	52
Namibia	688	0	15
Nepal	898	1	33
Netherlands Antilles	286	0	4
New Caledonia	194	22	14
New Zealand	339	65	59

Appendix B.1 – **taxonomic and land-use/management terms used in literature searches.** Terms were used in a paired fashion (e.g. "acari & agri*"), resulting in a total of 476 search combinations.

Taxonomic term	Land-use term
Acari	agri*
Araneae	crop
arthropod	farm*
Blattodea	fertilizer
Byrrhidae	forest
Carabidae	grassland
Chilopoda	herbicide
Coccinellidae	intercrop
Coleoptera	land use
Collembola	organic
Colydiidae	pasture
Cucujidae	pesticide
Dermaptera	tillage
Diplopoda	woodland
Elateridae	
Hemiptera	
Histeridae	
Homoptera	
Isopoda	
Isoptera	
Mantodea	
Neuroptera	
Opiliones	
Orthoptera	
Phasmida	
Pseudoscorpiones	
Scarabaeidae	
Scolytidae	
Scorpionidae	
Staphylinidae	
Symphyla	
Tenebrionidae	
Thysanoptera	
Thysanura	

Appendix B.2 – Papers included in meta-analyses. NV:Ag = native vegetation compared to agricultural land; WNV:IP = wooded native vegetation compared to improved/introduced pasture; NG:IP = native grassland compared to improved/introduced pasture; IP:C = improved/introduced pasture compared to cropping; RIC:CC = reduced-input cropping compared to conventional cropping. R = richness only calculated from paper, Ab = abundance only calculated from paper, R/Ab = both richness and abundance calculated from paper.

author(s)	year	country	Land-use comparisons	Land-use details	taxa	data source	richness / abundance	journal, vol., pp
Afun et al	1999	Côte d'Ivoire	RIC:CC	herbicide & non-herbicide rice	various	figures 5 & 6	Ab	Biological Agriculture and Horticulture, 17, 47-58
Akbulut et al	2003	Turkey	RIC:CC	intercropping	various	table 2	R/Ab	Journal of Agronomy & Crop Science, 189, 261-269
Altieri & Schmidt	1986	USA	RIC:CC	organic & sprayed orchards	predacious insects & spiders	table 2	Ab	Agriculture, Ecosystems and Environment, 16, 29-43
Altieri et al	1985	USA	RIC:CC	mulched & non-mulched tomatoes	various	table 2	Ab	Crop Protection, 4, 201-213
Alvarez et al	2001	England	RIC:CC	organic & conventional wheat	Collembola	fig. 4	R/Ab	Agriculture, Ecosystems and Environment, 83, 95-110
Andersen	2003	Norway	RIC:CC	tillage & reduced tillage cereals	various	table 2	Ab	Crop Protection, 22, 147-152
Arellano & Halffter	2003	Mexico	NV:Ag; RIC:CC	forest, polyculture coffee & monocrop coffee	Scarabaeidae	table 3 Arellano et al 2005	R	Biodiversity and Conservation, 14, 601-615
Armbrecht & Perfecto	2003	Mexico	NV:Ag	forest & coffee monoculture	Formicidae	figure 1	R/Ab	Agriculture, Ecosystems and Environment, 97, 107-115
Armbrecht et al	2005	Colombia	NV:Ag; RIC:CC	forest, shade coffee & sun coffee	Formicidae	table 2	R	Conservation Biology, 19, 897-907
Armbrecht et al	2006	Colombia	NV:Ag; RIC:CC	forest, shade coffee & sun coffee	Formicidae	table 2	R	Ecological Entomology, 31, 403-410
Arroyo et al	2005	Spain	NV:Ag; WNV:IP; IP:C	forest, pasture, crop	Oribatid mites	table 4	R/Ab	Journal of Natural History, 39, 3453-3470
Avendaño-Mendoza et al	2005	Guatemala	NV:Ag	forest & cropping	Dung beetles	results text and table 3	R/Ab	Biodiversity and Conservation, 14, 801-822
Badejo	1990	Nigeria	NV:Ag	forest & cassava	Acari	table 2	Ab	Biotropica, 22, 382-390
Badejo et al	2004	Brazil	NV:Ag; WNV:IP; IP:C;	forest, pasture & cropping	Acari	tables 2 & 3	R/Ab	Experimental and Applied Acarology, 34, 345-365

Badji et al	2004	Brazil	RIC:CC	no-till/no-insecticide maize & tilled & insecticide maize	various	table 1	Ab	Crop Protection, 23, 1031-1039
Badji et al	2006	Brazil	RIC:CC	tilled maize & no-till maize	Formicidae	table 1	R/Ab	Sociobiology, 48, 701-715
Baguette & Hance	1997	Belgium	RIC:CC	tilled crops & no-till crops	Carabids	table 1	R/Ab	Entomological Research in Organic Agriculture, 185-190
Baldi & Kisbenedek	1997	Hungary	NV:Ag; NG:IP	semi-natural meadow & grazed pasture	Orthoptera	table 2	R/Ab	Agriculture, Ecosystems and Environment, 66, 121-129
Baldissera et al	2004	Brazil	NV:Ag WNV:IP	forest & pasture	Araneae	figure 2	R/Ab	Biological Conservation, 118, 403-409
Balog & Marko	2006	Hungary	RIC:CC	conventional & IPM orchards	Staphylinidae	results text pg. 151	R/Ab	Journal of Fruit and Ornamental Plant Research, 14, 149-159
Banks et al	2007	Costa Rica	NV:Ag	forest & crops	Coleoptera & Araneae	figures 1 & 2; table 3	R/Ab	The Pan-Pacific Entomologist, 83, 152-160
Barros et al	2004	Brazil	NV:Ag; WNV:IP	forest & pasture	various	table 1	Ab	Applied Soil Ecology, 26, 157-168
Basore et al	1987	USA	RIC:CC	tilled corn & no-till corn	various	table 2	Ab	Wildlife Society Bulletin, 15, 229-233
Basu et al	1996	India	WNV:IP; NV:Ag	forest & pasture	Isoptera	table 2	R/Ab	European Journal of Soil Biology, 32, 113-121
Bedano & Ruf	2007	Argentina	NG:IP; IP:C; NV:Ag	various	Gamasina (Acari)	table 1	R/Ab	Applied Soil Ecology, 36, 22-31
Bedano et al	2006	Argentina	NG:IP; IP:C; NV:Ag	various	various	figures 3 & 4	Ab	European Journal of Soil Biology, 42, 107-119
Bedano et al	2006(b)	Argentina	NG:IP; IP:C; NV:Ag	various	Acari	figures 3-6	Ab	Applied Soil Ecology, 32, 293-304
Belaoussoff et al	2003	Canada	RIC:CC	no-tillage & high-tillage	Carabids	appendix 1 & results text	R/Ab	Biodiversity and Conservation, 12, 851-882
Belshaw & Bolton	1993	Ghana	NV:Ag	forest & cocoa	Formicidae	table 1	R	Biodiversity and Conservation, 2, 656-666
Bel'skaya & Esyunin	2003	Russia	RIC:CC	wheat with and without insecticide	Araneae	figure 2	Ab	Russian Journal of Ecology, 34, 359-362
Benito et al	2004	Brazil	WNV:IP; NV:Ag	cerrado & pasture	various	table 1	Ab	European Journal of Soil Biology, 40, 147-154

Berry et al	1996	New Zealand	RIC:CC	organic & conventional carrot crops	various	results text & figure 1	R/Ab	New Zealand Journal of Crop and Horticulture Science, 24, 307-314
Blackburn & Wallace	2001	UK	NV:Ag	woodland & field margin	Chilopoda	table 3	R	Basic and Applied Ecology, 2, 373-381
Blumberg & Crossley	1983	USA	RIC:CC	conventional tillage & no-tillage	soil arthropods	figure 2	R/Ab	Agro-Ecosystems, 8, 247-253
Bogya et al	2000	Hungary	RIC:CC	IPM orchard & conventional orchard	Araneae	table 3	R/Ab	International Journal of Pest Management, 46, 241-250
Borges & Brown	2001	Azores	NV:Ag; NG:IP	sown pasture & semi-natural grassland	various	appendix 1	R/Ab	Ecography, 24, 68-82
Bouyer et al	2007	Benin	NV:Ag & RIC:CC	wooded savannah, traditional and intensive cropping	Scarabaeidae	text results	R	Biological Conservation, 138, 73-88
Brennan et al	2006	Ireland	RIC:CC	eco-tillage & conventional tillage	Collembola	figure 1	R/Ab	Pedobiologia, 50, 145-155
Bromham et al	1999	Australia	NV:Ag; WNV:IP	woodland & pasture	various	tables 2 & 3	R/Ab	Australian Journal of Ecology, 24, 199-207
Brooks et al	2005	UK	RIC:CC	herbicide crop & non-herbicide crop	various	table 1	Ab	Proceedings of the Royal Society B, 272, 1497-1502
Brown et al	2001	Brazil	RIC:CC	no-tillage & tillage	macrofauna (various)	tables 5 & 6	R/Ab	http://www.unu.edu/env/plec/cbd/Montreal/presentations/BrownGeorge.pdf
Brown et al	2004	Mexico	NV:Ag; NG:IP	native grassland & introduced pasture	various	appendix b	Ab	Agriculture, Ecosystems and Environment, 103, 313-327
Buckelew et al	2000	USA	RIC:CC	conventional weed management & hand-weeded soy bean plots	various	table 7	Ab	Journal of Economic Entomology, 95, 1437-1443
Butts et al	2003	Canada	RIC:CC	barley monoculture & intercrop	Carabids	table 1	Ab	Environmental Entomology, 32, 535-541
Callaham Jr. et al	2006	USA	NV:Ag; WNV:IP; IP:C	hardwood, grass & cultivation	various	table 2 & figure 2a	R/Ab	European Journal of Soil Biology, 42, S150-S156
Cameron et al	2004	Northern Ireland	NV:Ag; WNV:IP; NG:IP	woodland, species-rich grassland & species-poor grassland	Araneae	table 5	R	Agriculture, Ecosystems and Environment, 102, 29-40
Cárdenas et al	2006	Spain	RIC:CC	organic & conventional olives	Araneae	results text & table 1	R/Ab	Biological Control, 38, 188-195

Castano-Meñeses & Palasios-Vargas	2003	Mexico	NV:Ag	forest & crop	Formicidae	table 1	R/Ab	Biodiversity and Conservation, 12, 1913-1919
Chauvat et al	2007	Germany	IP:C	grassland & crop	Collembola	figure 2	R/Ab	Ecography, 30, 183-192
Chen & Tso	2004	Taiwan	NV:Ag; WNV:IP	primary forest & grassland	Araneae	table 1	R/Ab	Zoological Studies, 40, 598-611
Clark	1999	USA	RIC:CC	organic & conventionally managed tomatoes	Carabids	text pg. 202	R	Applied Soil Ecology, 11, 199-206
Clement et al	2004	USA	RIC:CC	no-till & tilled cereal crops	Homoptera	table 2	Ab	Journal of the Kansas Entomological Society, 77, 165-173
Clough et al	2007	Germany	RIC:CC	organic & conventional fields	various	figure 3	R	Journal of Applied Ecology, 44, 804-812
Coll & Bottrell	1995	USA	RIC:CC	monoculture & diculture	various	tables 2 & 3	Ab	Agriculture, Ecosystems and Environment, 54, 115-125
Cortet et al	2002	France	RIC:CC	conventional & integrated cropping (tillage and insecticide)	various	table 2	Ab	European Journal of Soil Biology, 38, 239-244
Culik et al	2002	Brazil	RIC:CC	fertiliser, tillage and mulch crop treatments	Collembola	table 3 & figure 1	R/Ab	Applied Soil Ecology, 21, 49-58
Cunningham et al	2005	Australia	NV:Ag; WNV:IP	native woodland & annual pasture	Coleoptera & Formicidae	figure 4 & figure 9	R	Austral Ecology, 30, 103-117
Curry	1986	Sweden	RIC:CC; IP:C	barley with no fertiliser, barley with nitrate fertiliser & pasture	various	tables 1, 2 & 3	Ab	Journal of Applied Ecology, 23, 853-870
Dauber & Wolters	2004	Germany	IP:C	meadow & arable land	Formicidae	figures 2 & 3	R/Ab	Biodiversity and Conservation, 13, 901-915
Dauber & Wolters	2005	Germany	IP:C	>46 yr old pasture & arable	Formicidae	figures 1 & 2	R/Ab	Basic and Applied Ecology, 6, 83-91
Dauber et al	2005	Germany	IP:C	grassland & arable	various	table 2	R	Global Ecology and Biogeography, 14, 213-221
David et al	1999	France	NV:Ag	wooded sites & fields	microarthropods	table 2	R/Ab	Biodiversity and Conservation, 8, 753-767
Decaëns et al	2004	Brazil	NV:Ag; WNV:IP; NG:IP	forest, native savannah & introduced pasture	soil macrofauna	figures 2 & 4	R	Agriculture, Ecosystems and Environment,103, 301-312
Decaëns et al	1998	France	NV:Ag; WNV:IP	woodland & pasture	various	table 1	R/Ab	Applied Soil Ecology, 9, 361-367

Dias Loyola	2006	Brazil	NV:Ag; WNV:IP	forest & introduced pasture	various	table 2	R/Ab	Biodiversity and Conservation, 15, 25-42
Dittmer and Schrader	2000	Germany	RIC:CC	conservation tillage & conventional tillage	Collembola	table 1	R/Ab	Pedobiologia, 44, 527-538
Doles et al	2001	USA	NV:Ag; RIC:CC	scrub, organic apple orchard & conventionally managed apple orchard	various micro-arthropods	table 3, figures 4, 5 & 7	R/Ab	Applied Soil Ecology, 18, 83-96
Draney	1997	USA	NV:Ag; RIC:CC	forest, no-till cropping & conventional cropping	Araneae	table 4	Ab	The Journal of Arachnology, 25, 333-351
Drinkwater et al	1995	USA	RIC:CC	organic & conventional tomatoes	predators	table 5	R/Ab	Ecological Applications, 5, 1098-1112
Driscoll & Weir	2005	Australia	NV:Ag	remnant woodland & paddock	Coleoptera	results text	R/Ab	Conservation Biology, 19, 182-194
Dritschilo & Erwin	1982	USA	RIC:CC	organic & conventional crops	Carabids	table 1	R/Ab	Ecology, 63, 900-904
Dritschilo & Wanner	1980	USA	RIC:CC	organic & conventional fields	Carabids	table 2	R/Ab	Environmental Entomology, 9, 629-631
Duan et al	2004	USA	RIC:CC	potatoes with no pest-control & potatoes with permethrin	various	table 2	Ab	Environmental Entomology, 33, 275-281
Duelli & Obrist	1998	Switzerland	NV:Ag; NG:IP; IP:C	native & semi-natural grassland, improved pasture & wheat/maize crops	various	table 1	R/Ab	Biodiversity and Conservation, 7, 297-309
Easterbrook	1997	UK	RIC:CC	no-pesticide crop & insecticide-treated crop	various	table 3	Ab	Crop Protection, 16, 147-152
Eggleton et al	2002	Cameroon/Congo	NV:Ag	primary forest & mixed cropping	termites	figure 1	R	Agriculture, Ecosystems and Environment, 90, 189-202
Ellsbury et al	1998	USA	RIC:CC	high-input & low-input cropping	Carabids	table 3	R/Ab	Annals of the Entomological Society of America, 91, 619-625
Epstein et al	2000	USA	RIC:CC	pesticide use in apple orchards	various	figures 3, 4, 5 & 7	Ab	Environmental Entomology, 29, 340-348

Epstein et al	2001	USA	RIC:CC	apple orchards with and without insecticides	Carabids	figure 1	Ab	Biological Control, 21, 97-104
Escobar	2004	Colombia	NV:Ag; WNV:IP; IP:C	primary forest, pasture & cropping	Scarabaeidae	table 1	R/Ab	Tropical Zoology, 17, 123-136
Escobar et al	2007	Mexico & Colombia	NV:Ag; WNV:IP	forest & pasture	Scarabaeidae	table 1	R/Ab	Ecography, 30, 193-208
Estrada et al	1998	Mexico	NV:Ag; WNV:IP; IP:C	forest, pasture & cropping	dung & carrion beetles	table 1	R/Ab	Journal of Tropical Ecology, 14, 577-593
Ewuim et al	1997	Nigeria	NV:Ag	forest & crop fallow	Formicidae	table 3	Ab	Biotropica, 29, 93-99
Fan et al	1993	USA	RIC:CC	low-input & conventional bean production	various	table 2	Ab	Agriculture, Ecosystems and Environment, 43, 127-139
Favret & Voegtlin	2001	USA	NV:Ag	woodland, prairie & soy bean crop	Homoptera	table 1	Ab	Environmental Entomology, 30, 371-379
Feber et al	1998	UK	RIC:CC	organic & conventional cropping	Araneae	figures 1 & 2	R/Ab	The Journal of Arachnology, 26, 190-202
Fisher and Robertson	2002	Madagascar	WNV:IP; NV:Ag	forest & exotic grassland	Formicidae	table 1	R/Ab	Biotropica, 34, 155-167
Fournier & Loureau	2001	France	NV:Ag	woodland & barley	Collembola	table 3	R/Ab	Landscape Ecology, 16, 17-32
Frampton & Wratten	2000	England	RIC:CC	wheat with and without various fungicides	Collembola	figures 4-6	Ab	Ecotoxicology and Environmental Safety, 46, 64-72
Frampton et al	2007	England	RIC:CC	wheat with and without various insecticides	various	tables 1-3	R/Ab	Environmental Pollution, 147, 14-25
Fratello et al	1989	Italy	RIC:CC	organic fertilised & inorganic fertilised crops	Collembola & Acari	table 2(a)	Ab	Agriculture, Ecosystems and Environment, 27, 227-239
Furlong et al	2004	Australia	RIC:CC	brassicas with conventional and reduced insecticides	various	table 8	Ab	Journal of Economic Entomology, 97, 1814-1827
Gallo & Pekar	2001	Czech Republic	RIC:CC	conventional & reduced tillage	herbivores	tables 1 & 2	Ab	Journal of Pest Science, 74, 60-65
Gardi et al	2002	Italy	IP:C	pasture & cropping	Collembola	table 3	R	European Journal of Soil Biology, 38, 103-110
Goehring et al	2002	Costa Rica	NV:Ag	forest & coffee	various	tables 1-3	R/Ab	Journal of Insect Conservation, 6, 83-91

Gomez et al	2003	Spain	NV/Ag; WNV:IP; IP:C	forest, pasture & cropping	Formicidae	table 1	R/Ab	Biodiversity and Conservation, 12, 2135-2146
Good & Giller	1991	Ireland	IP:C; RIC:CC	pasture/hay meadow; cropping/silage; wheat with & without insecticide; crop with & without fungicide	Staphylinidae	tables 1, 3 & 4	R	Journal of Applied Ecology, 28, 810-826
Gormley et al	2007	Costa Rica	NV:Ag; WNV:IP	primary forest & pasture	Coleoptera	figure 2	R/Ab	Journal of Insect Conservation, 7, 131-139
Gove et al	2005	Mexico	NV:Ag; WNV:IP	forest & pasture	Formicidae	figure 1(b)	R	Biological Conservation, 126, 328-338
Green & Catterall	1998	Australia	NV:Ag; WNV:IP	native woodland & cleared grassland	various	figure 6	R/Ab	Wildlife Research, 25, 677-690
Greenwood et al	1991	UK	NV:Ag; WNV:IP; IP:C	woodland, pasture & arable	Staphylinidae & Carabidae	table 1	R/Ab	Regulated Rivers: Research and Management, 6, 321-332
Gudleifsson	2005	Iceland	NV:Ag; NG/IP	unimproved grassland & improved hayfield	Coleoptera	text results	R	Agriculture, Ecosystems and Environment, 109, 181-186
Hadjicharalampous et al	2002	Greece	RIC:CC	organic & conventional olives, vineyards and maize	various	table 3	R/Ab	Environmental Management, 29, 683-690
Harris & Burns	2000	New Zealand	NV:Ag; WNV:IP	forest & pasture	Coleoptera	figure 2	R/Ab	New Zealand Journal of Ecology, 24, 57-67
Harvey et al	2006	Nicaragua	NV:Ag; WNV:IP	riparian forest & pasture	Scarabaeidae	table 2	R/Ab	Ecological Applications, 16, 1986-1999
Hassall et al	2006	Malaysia	NV:Ag	primary forest & orchard	Isopoda	figure 1	R/Ab	European Journal of Soil Biology, 42, S197-S207
Hatten et al	2007	USA	RIC:CC	no-till & conventional tillage crops	Carabids	table 1	R/Ab	Environmental Entomology, 36, 356-368
Heithaus & Humes	2003	USA	NV:Ag	forest/woodland & crop/pasture	Formicidae	table 3	R	Ohio Journal of Science, 103, 89-97
Hidaka	1998	Japan	RIC:CC	traditional organic rice & conventionally intensive rice	various	table 2	Ab	Biological Agriculture and Horticulture, 15, 35-49

Hokkanen & Holopainen	1986	Germany	RIC:CC	biologically & conventionally managed fields	Carabids	table 2	R/Ab	Journal of Applied Entomology, 102, 353-363
Holland & Reynolds	2003	UK	RIC:CC	ploughed & un-ploughed crops	various	table 2	Ab	Pedobiologia, 47, 181-191
Holt & Coventry	1988	Australia	NV:Ag; WNV:IP	native woodland & introduced pasture	Isoptera	table 1	R/Ab	Australian Journal of Ecology, 13, 321-325
Horgan	2005	Peru	NV:Ag	forest & mixed cropping/plantations	Coleoptera	results text	R/Ab	Forest Ecology and Management, 216, 117-133
Horgan et al	2007	El Salvador	NV:Ag; WNV:IP; IP:C	forest, pasture & crop	Scarabaeidae	table 3	R	Biodiversity and Conservation, 16, 2149-2165
Horne & Edward	1998	Australia	RIC:CC	tillage & no-tillage crops	Carabids	figure 2	Ab	Australian Journal of Entomology, 37, 60-63
House	1989	USA	RIC:CC	no-till & tillage crops	various	figure 4	Ab	Agriculture, Ecosystems and Environment, 25, 233-244
House & Stinner	1983	USA	RIC:CC	tillage fields & no-tillage fields	various	table 1; figures 2A & 2B	R/Ab	Environmental Management, 7, 23-28
Hülsmann & Wolters	1998	Germany	RIC:CC	tillage & no-till crops	Acari	table 2	R/Ab	Applied Soil Ecology, 9, 327-332
Hulugalle	1997	Australia	RIC:CC	tilled, continuous cotton & minimum-till rotational cotton	various	table 6	Ab	Applied Soil Ecology, 7, 11-30
Hummel et al	2002(a)	USA	RIC:CC	chemical/biological & intercropping crop treatments	various	tables 4 & 5	Ab	Agriculture, Ecosystems and Environment, 93, 177-188
Hummel et al	2002(b)	USA	RIC:CC	biological & chemical treatment tomatoes	various	table 2	Ab	Agriculture, Ecosystems and Environment, 93, 165-176
Huusela-Veistola	1996	Finland	RIC:CC	reduced-pesticide and pesticide-treated crops	Carabids	figure 2	Ab	Annales Zoologici Fennici, 33, 197-205
Ishijima et al	2004	Japan	RIC:CC	tillage & no-tillage rice	Araneae & Homoptera	tables 1 & 3	Ab	Applied Entomology and Zoology, 39, 155-162
Janzen et al	1983	Costa Rica	NV:Ag; WNV:IP	forest & pasture	Scarabaeidae	table 2	Ab	Oikos, 41, 274-283
Jones et al	2003	Sumatra	NV:Ag; WNV:IP; IP:C	forest, pasture, cassava monoculture	Isoptera	table 2	R/Ab	Journal of Applied Ecology, 40, 380-391

Kajak & Łukasiewicz	1994	Poland	NV:Ag; WNV:IP; IP:C	forest, pasture & cropping	various	table 2	Ab	Agriculture, Ecosystems and Environment, 49, 149-161
Kannan et al	2004	India	RIC:CC	insecticide & non-insecticide plots	various	figure 1	Ab	Current Science, 86, 726-729
Keals & Majer	1991	Australia	NV:Ag	woodland & cropping	Formicidae	figure 2	R	Nature Conservation 2: The role of corridors; Eds Saunders and Hobbs
King et al	1998	Australia	NV/Ag; WNV/IP	rainforest & pasture	Formicidae	table 3	R/Ab	Biodiversity and Conservation, 7, 1627-1638
Kishimoto	2002	Japan	RIC:CC	orchards with and without pesticides	Acari	table 2	Ab	Applied Entomology and Zoology, 37, 603-615
Klein	1989	Brazil	NV:Ag; WNV:IP	forest & clearcut pastures	saprophagous and coprophagous Coleoptera	table 3	R/Ab	Ecology, 70, 1715-1725
Koivula et al	2004	Finland	NV:Ag	forest & farmland	Carabids	appendix 1	R	Journal of Insect Conservation, 8, 297-309
Koss et al	2004	USA	RIC:CC	conventional insecticide crops & organic crops	various predators	figure 2b	Ab	Environmental Entomology, 34, 87-95
Krogh	1994 (in Hansen et al 2001)	Denmark	RIC:CC	Integrated & conventional arable	Collembola & Acari	table 5	Ab	Agriculture, Ecosystems and Environment, 83, 11-26
Kromp	1989	Austria	RIC:CC	biological & conventional winter wheat	Carabids	figures 1 & 2	R/Ab	Agriculture, Ecosystems and Environment, 27, 241-251
Kromp	1990 (in Kromp 1999)	Austria	RIC:CC	biologically and conventionally managed potatoes	Carabids	figures 1(a) & 1(b)	R/Ab	Agriculture, Ecosystems and Environment, 74, 187-228
Kromp	1985 (in Kromp 1999)	Austria	RIC:CC	biologically and conventionally managed potatoes	Carabids	figures 1(a) & 1(b)	R/Ab	Agriculture, Ecosystems and Environment, 74, 187-228
Kromp & Hartl	1991 (in Kromp 1999)	Austria	RIC:CC	biological & conventional winter wheat	Carabids	figure 1(b)	R/Ab	Agriculture, Ecosystems and Environment, 74, 187-228

Kroos & Schaefer	1998	Germany	RIC:CC	conventional/reduced input farming; tilled wheat compared to no-till wheat	Staphylinidae	tables 3 & 4	R/Ab	Agriculture, Ecosystems and Environment, 69, 121-123
Larsen et al	2003	USA	NV:Ag	woodland & cropping	Carabids	table 1	R/Ab	Pedobiologia, 47, 288-299
Lavelle & Pashanasi	1989	Peru	NV:Ag; WNV:IP; IP:C; RIC:CC	primary forest, pasture, low-input & high-input maize	various	tables 2 & 3	R/Ab	Pedobiologia, 33, 283-291
Leather et al	1999	UK	NV:Ag; WNV:IP	woodland & pasture	Coccinellidae	figure 1	Ab	European Journal of Entomology, 96, 23-27
Liang et al	2007	Australia	RIC:CC	orchards with & without synthetic pesticides	soil arthropods	figure 2	R/Ab	Australian Journal of Entomology, 46, 79-85
Lobry de Bruyn	1993	Australia	NV:Ag	woodland, heathland & farmland	Formicidae	table 3	R/Ab	Soil Biology and Biochemistry, 25, 1043-1056
Loranger et al	1998	Martinique	NV:Ag; WNV:IP; IP:C	forest, old pasture & market gardening	various	figure 2	R/Ab	European Journal of Soil Biology, 34, 157-165
Luff & Rushton	1989	UK	NV:Ag; NG:IP	unimproved grassland & improved grassland	Carabids & Araneae	tables 2 & 3	R/Ab	Agriculture, Ecosystems and Environment, 25, 195-205
Lundgren et al	2006	USA	IP:C	vegetable cropping & pasture	various	figures 1 & 2; results text	Ab	Renewable Agriculture and Food Systems, 21, 227-237
Magagula	2006	Swaziland	NV:Ag	wooded savannah & orchard	various	figure 1; tables 2 & 3	R/Ab	Biodiversity and Conservation, 15, 453-463
Majer	1978	Australia	NV:Ag; WNV:IP	unburnt jarrah & pasture	various	tables 1 & 3	R/Ab	Forest Ecology and Management, 1, 321-334
Marasas et al	2001	Argentina	RIC:CC	no-tillage & conventional tillage	various	table 2	Ab	Applied Soil Ecology, 18, 61-68
Marquini et al	2002	Brazil	RIC:CC	beans with and without insecticide application	Araneae	tables 1 & 2	Ab	Journal of Applied Entomology, 126, 550-556
Mathieu et al	2005	Brazil	NV:Ag; WNV:IP; IP:C	primary forest, pasture & rice cropping	various	figure 3	R/Ab	Conservation Biology, 19, 1598-1605
Meissle & Lang	2005	Germany	RIC:CC	crops with & without insecticide	Araneae	table 3	R	Agriculture, Ecosystems and Environment, 107, 359-370

Melnychuck et al	2003	Canada	RIC:CC	annual grain rotation & diversified grain rotation	Carabids	results text	R/Ab	Agriculture, Ecosystems and Environment, 95, 69-72
Menalled et al	2007	USA	RIC:CC	no-till & conventional corn	Carabids	table 1	R/Ab	Agriculture, Ecosystems and Environment, 118, 49-54
Michereff-Filho et al	2004	Brazil	RIC:CC	cornfields with and without insecticide	various	table 1; figures 3 & 5	R/Ab	International Journal of Pest Management, 50, 91-99
Minarro & Dapena	2003	Spain	RIC:CC	herbicide treatment & natural soil control treatment	Carabids	tables 2 & 3	R/Ab	Applied Soil Ecology, 23, 111-117
Minor & Cianciolo	2007	USA	NV:Ag	forest & cornfield	Acari	table 2	R/Ab	Applied Soil Ecology, 35, 140-153
Miyazawa et al	2002	Japan	RIC:CC	conventional tillage compared to reduced tillage	Collembola & Acari	table 3	Ab	Plant Production Science, 5, 257-265
Moreby & Sotherton	1997	UK	RIC:CC	organic and conventional wheat	various	table 3	Ab	Biological Agriculture and Horticulture, 15, 51-60
Moreby et al	1994	UK	RIC:CC	organic and conventional wheat	various	table 4	Ab	Annals of Applied Biology, 125, 13-27
Moron/Moron & Lopez-Mendez	1987 & 1985	Mexico	NV:Ag	rainforest & shade coffee plantation	Scarabaeidae	table 3 Nestel et al 1993	R	Biodiversity and Conservation, 2, 70-78
Mukhopadhyay et al	2003	India	RIC:CC	organic & chemically intensive tea	various	tables 1 & 2	R/Ab	Journal of Environmental Biology, 24, 471-476
Munyuli et al	2007	Uganda	RIC:CC	insecticide/non-insecticide; cowpea monoculture & intercrop	various	tables 2, 4, 6 & 7	R/Ab	Crop Protection, 26, 114-126
Mussury et al	2002	Brazil	IP:C	pasture & cropping	Collembola and Acari	figure 1	Ab	Brazilian Archives of Biology and Technology, 45, 257-264
Nakamoto & Tsukamoto	2006	Japan	RIC:CC	inorganic & non-inorganic fertilised crops	Collembola and Acari	figure 3	Ab	Agriculture, Ecosystems and Environment, 115, 34-42
Nakamoto et al	2006	Japan	RIC:CC	tillage & non-tillage fields	various	figure 1	Ab	Soil and Tillage Research, 85, 94-106
Nakamura et al	2003	Australia	NV:Ag; WNV:IP	forest remnants & pasture	various	table 2	R/Ab	Ecological Management and Restoration, 4 (supp.), S20-S28

Neave & Fox	1998	Canada	RIC:CC	no-till & tillage	various	tables 1 & 2	R/Ab	Applied Soil Ecology, 9, 423-428
Nestel et al	1993	Mexico	RIC:CC	shaded & unshaded coffee	various	table 1	R/Ab	Biodiversity and Conservation, 2, 70-78
Nicholls et al	2000	USA	RIC:CC	cover crop & no-cover crop	various	table 2	Ab	Agricultural and Forest Entomology, 2, 107-113
Nkem et al	2002	Australia	RIC:CC	N-fertilised wheat & non-fertilised wheat	various	table 3	Ab	Applied Soil Ecology, 20, 69-74
Okwakol	2001	Uganda	NV:Ag	forest & cultivation	various	table 1 & figure 1	R/Ab	African Journal of Ecology, 32, 273-282
O'Neal et al	2005	USA	RIC:CC	blueberry crop with clover & bare ground cover	Carabids	figure 5	Ab	BioControl, 50, 205-222
Osler & Murphy	2005	Australia	NV:Ag	woodland & cropping	Acari	table 1	R/Ab	Applied Soil Ecology, 29, 93-98
Paoletti et al	1999	China	IP:C	meadow & vegetable lot	various	tables 1 & 2	Ab	Critical Reviews in Plant Sciences, 18, 457-465
Parajulee et al	2006	USA	RIC:CC	tillage & conservation-tillage crops	Thysanoptera & Homoptera	table 3	Ab	International Journal of Pest Management, 52, 249-260
Pardo-Locarno et al	2007	Colombia	NV:Ag; WNV:IP; IP:C	woodland, pasture & coffee	Scarabaeidae	table 2	R/Ab	Florida Entomologist, 88, 355-363
Parisi et al	2005	Italy	NV:Ag	woodland & cropping	various	table 5	R	Agriculture, Ecosystems and Environment, 105, 323-333
Pavuk et al	1997	USA	RIC:CC	corn without weeds and corn with mixed weeds	Carabids	tables 3 & 4	R/Ab	American Midland Naturalist, 138, 14-28
Peachey et al	2002	USA	RIC:CC	tillage & direct drill (no-tillage) crops	various	table 2 & figure 3	Ab	Applied Soil Ecology, 21, 59-70
Peck et al	1998	USA	IP:C; RIC:CC	hay fields, corn fields, conventional till/conservation-till fields	Formicidae	tables 2 & 4	R/Ab	Environmental Entomology, 27, 1102-1110
Pekár	1999	Czech Republic	RIC:CC	orchards with IPM & conventional spraying	Araneae	tables 2 & 3	R/Ab	Agriculture, Ecosystems and Environment, 73, 155-166
Pekár & Kocourek	2004	Czech Republic	RIC:CC	orchards with & without insecticide	Araneae	figure 2 & table 1	R/Ab	Journal of Applied Entomology, 128, 561-566
Penagos et al	2003	Mexico	RIC:CC	maize with and without mechanical weed control	various	table 2	Ab	International Journal of Pest Management, 49, 155-161

Pereira et al	2005	Brazil	RIC:CC	herbicide and insecticide crop & untreated control	various	figures 2-7	Ab	Journal of Environmental Science and Health, B, 40, 45-54
Perfecto et al	1997	Costa Rica	RIC:CC	traditional & unshaded coffee	Coleoptera & Formicidae	table 3	R/Ab	Biodiversity and Conservation, 6, 935-945
Perner & Malt	2003	Germany	IP:C	grassland & arable	Araneae & Coleoptera	figure 1	R/Ab	Agriculture, Ecosystems and Environment, 98, 169-181
Petersen	2002	Denmark	RIC:CC	non-inversion & conventional tillage	Collembola	figure 1 and author's data	Ab	European Journal of Soil Biology, 38, 177-180
Peveling et al	1999	Niger	RIC:CC	insecticide & control treatments	Formicidae & Carabids	figures 3 & 5	Ab	Crop Protection, 18, 323-339
Pfiffner & Niggli	1996	Switzerland	RIC:CC	organic & conventional wheat	various	tables 1 & 3	R/Ab	Biological Agriculture and Horticulture, 12, 353-364
Philpott et al	2006	Mexico	RIC:CC	extensive & intensive coffee	Formicidae	table 2	R	Biodiversity and Conservation, 15, 139-155
Pik et al	1999	Australia	NV/Ag; WNV/IP	woodland regrowth and pasture	Formicidae	figure 1	R	Australian Journal of Ecology, 24, 555-562
Pineda et al	2005	Mexico	NV:Ag	forest & shade coffee	Scarabaeidae	table 1	R/Ab	Conservation Biology, 19, 400-410
Pinkus-Rendón et al	2006	Mexico	NV:Ag; RIC:CC	forest, organic coffee & conventional coffee	Araneae	table 1 & results text	R/Ab	The Journal of Arachnology, 34, 104-112
Pinkus-Rendón et al (b)	2006	Mexico	NV:Ag; WNV:IP; IP:C; RIC:CC	forest, pasture & crop	Araneae	table 3	R	Diversity and Distributions, 12, 61-69
Piqué et al	1998	Spain	RIC:CC	crop with & without carbofuran insecticide	corn borers	table 2	Ab	Crop Protection, 17, 557-561
Pokarzhevskii & Krivolutskii	1997	Russia	NV:Ag; NG:IP; IP:C	steppe, pasture & barley	various	table 1	R/Ab	Agriculture, Ecosystems and Environment, 62, 127-133
Ponge et al	2003	France	NV:Ag	forest & agriculture	Collembola	table 3	R/Ab	Soil Biology and Biochemistry, 35, 813-826
Prasse et al	1985	Germany	RIC:CC	cropping with differing herbicide rates	Collembola & Acari	figure 1	R	Agriculture, Ecosystems and Environment, 13, 205-215
Purtauf et al	2005	Germany	RIC:CC	organic & conventional wheat	Carabids	results text & appendix	R/Ab	Oecologia, 142, 458-464
Purtauf et al	2004	Germany	IP:C	pasture & arable	Carabids	table 2; appendix A	R/Ab	Landscape and Urban Planning, 67, 185-193

Purvis et al	2001	Ireland	IP:C	pasture & cropping	Carabids	appendix 1	R/Ab	Annals of Applied Biology, 139, 351-360
Quirozrobledo & Valenzuela-González	1995	Mexico	NV:Ag; WNV:IP	rainforest & pasture	Formicidae	table 1	R/Ab	Southwestern Entomologist, 20, 203-213
Rand & Louda	2006	USA	NV:Ag	remnant grassland & crop	Coccinellidae	results text	Ab	Conservation Biology, 20, 1720-1729
Ratschker & Roth	2000	Germany	IP:C	grassland & cereal fields	Araneae	table 2	R/Ab	Ekológia Bratislava, 19, 213-225
Rebek et al	2002	USA	RIC:CC; IP:C	pasture, chemical fertilised corn & manure fertilised corn	Collembola	tables 3 & 4	R/Ab	Environmental Entomology, 31, 37-46
Reeleder et al	2006	Canada	RIC:CC	rye cover crop & no cover crop	Acari	figure 2	Ab	Applied Soil Ecology, 33, 243-257
Rinaldi & Forte	1997	Brazil	NV:Ag; WNV:IP; IP:C	forest, pasture, crop	Araneae	table 1	R/Ab	Studies on Neotropical Fauna and Environment, 32, 244-255
Risch	1979	Costa Rica	RIC:CC	monoculture cropping & diculture cropping	various	table 1	R/Ab	Oecologia, 42, 195-211
Rodrĺguez et al	2006	Spain	RIC:CC	no-tillage & conventional tillage barley	various	table 1	Ab	Soil and Tillage Research, 85, 229-233
Rojas et al	2001	Costa Rica	RIC:CC	unshaded coffee monoculture & shaded coffee polycultures	Homoptera	table 2	R	Agroforestry Systems, 53, 171-177
Rossi & Blanchart	2005	India	NV:Ag; WNV:IP	primary forest & pasture	various	table 1	Ab	Soil Biology and Biochemistry, 37, 1093-1104
Roth et al	1994	Costa Rica	NV:Ag	forest & banana crop	Formicidae	table 5	R	Ecological Applications, 4, 423-436
Ruano et al	2004	Spain	RIC:CC	conventional & organic olives	various	tables 3 & 4	Ab	Agricultural and Forest Entomology, 6, 111-120
Samways	1983	South Africa	IP:C	grassland & orchard	Formicidae	table 3	R	Journal of Applied Ecology, 20, 833-847
Sánchez-Bayo et al	2007	Japan	IP:C; RIC:CC	pasture & crop; insecticide crop & control	vegetation arthropods	figures 2a & 2b	R	Journal of Environmental Science and Health Part B, 42, 279-286

Santos et al	2007	Portugal	RIC:CC	organic & integrated olive groves	various	table 2	Ab	Chemosphere, 67, 131-139
Scheffler	2005	Brazil	NV:Ag; WNV:IP	forest & pasture	Scarabaeidae	table 3	R/Ab	Journal of Tropical Ecology, 21, 9-19
Schmidt & Tscharntke	2005	Germany	IP:C	grassland & crop	Araneae	figures 2a & 2b	R/Ab	Agriculture, Ecosystems and Environment, 105, 235-242
Schmidt et al	2004	Germany	RIC:CC	mulched & unmulched crop	various	table 1 & figure 1	Ab	Entomologia Experimentalis et Applicata, 113, 87-93
Schmidt et al	2005	Germany	RIC:CC	organic & conventional crop	Araneae	figure 2	Ab	Journal of Applied Ecology, 42, 281-287
Schnell et al	2003	Australia	NV/Ag; WNV/IP	native woodland & pasture	Formicidae	figure 2	R	Austral Ecology, 28, 553-565
Schonberg et al	2004	Costa Rica	NV/Ag; WNV/IP	primary forest & pasture	Formicidae	text p. 404	R	Biotropica, 36, 403-409
Schulze et al	2004	Sulawesi	NV:Ag	forest & agricultural fields	Scarabaeidae	figure 1	R	Ecological Applications, 14, 1321-1333
Shah et al	2003	UK	RIC:CC	organic & conventional cropping	various	tables 1-3	R/Ab	Agricultural and Forest Entomology, 5, 51-60
Shahabuddin et al	2005	Indonesia	NV:Ag	forest compared to maize	Scarabaeidae	figure 1b	R/Ab	Biodiversity and Conservation, 14, 863-877
Showler & Greenberg	2003	USA	RIC:CC	weedy & weed-free cropping	various	figures 1 & 2	Ab	Environmental Entomology, 32, 39-50
Siepel	1996	Holland	NV:Ag; WNV:IP	old-growth forest & high input grassland	microarthropods	table 1	R/Ab	Biodiversity and Conservation, 5, 251-260
Sileshi & Mafongoya	2006	Zambia	NV:Ag	Miombo woodland & maize	various	table 3	R/Ab	Applied Soil Ecology, 33, 49-60
Skelton & Barrett	2005	USA	RIC:CC	wheat monocrop & intercrop	Homoptera & Araneae	figures 2a, 2b & 2c	Ab	Renewable Agriculture and Food Systems, 20, 38-47
Smith et al	2000	Guatemala	RIC:CC	insecticide-treated crops & non-insecticide crops; monocrop & intercrop	various	table 2	Ab	Florida Entomologist, 83, 358-362
Sousa et al	2004	Portugal	NV:Ag; WNV:IP; IP:C	woodland, pasture & agricultural	Collembola	table 4	R/Ab	Pedobiologia, 48, 609-622
Souty-Grosset et al	2005	France	NV:Ag; NG:IP; IP:C	pasture (>3years), pasture (<3 years) & alfalfa crop	Isopoda	tables 2 & 3	R/Ab	European Journal of Soil Biology, 41, 109-116

Squitier & Capinera	2002	USA	WNV:IP	scrub, pasture & crops	Orthoptera	results text	R	Florida Entomologist, 85, 235-244
Stamps et al	2002	USA	RIC:CC	walnut monocrop & intercrop	various	tables 3, 4, 5 & 7	R/Ab	Agroforestry Systems, 56, 167-175
Stinner et al	1986	USA	RIC:CC	till & no-till crops	various	figures 1 & 2	Ab	Agriculture, Ecosystems and Environment, 15, 11-21
Suckling et al	1999	New Zealand	RIC:CC	orchards with biological & conventional pest control	various	figures 2 & 3	R	Agriculture, Ecosystems and Environment, 73, 129-140
Tabu et al	2003	Kenya	NV:Ag	native forest & cropping	various	figure 34.4	R/Ab	In: Bationo, A.(ed.). Managing nutrient cycles to sustain soil fertility in sub-Saharan Africa, 487-500.
Tajovský	1993	Czech Republic	NV:Ag; WNV:IP; IP:C	forest, pasture & field	Diplopoda	table 2	R/Ab	Ekologia-Bratislava, 12, 277-283
Taylor et al	2006	USA	RIC:CC	herbicide applications	beneficial insects	table 4	Ab	Agriculture, Ecosystems and Environment, 116, 157-164
Teodorescu & Cogălniceanu	2005	Romania	RIC:CC	crops with & without pesticides	various	table 2	R	Applied Ecology and Environmental Research, 4, 55-62
Thomson & Hoffmann	2007	Australia	RIC:CC	vines with bare earth & compost mulch	various	table 1	Ab	Agricultural and Forest Entomology, 9, 173-179
Tillman et al	2004	USA	RIC:CC	monocropped & intercropped cotton	various	tables 2 & 6	Ab	Journal of Economic Entomology, 97, 1217-1232
Topping & Lovei	1997	New Zealand	IP:C; RIC:CC	pasture, conventional wheat & organic wheat	Araneae	table 1	R/Ab	New Zealand Journal of Ecology, 21, 121-128
Torres	1984	Puerto Rico	NV:Ag; WNV:IP; IP:C	forest, pasture & agricultural land	Formicidae	table 1	R	Biotropica, 16, 284-295
Tsai et al	2006	China	NV:Ag; WNV:IP	natural forest & grassland	Araneae	table 1	R/Ab	Ecography, 29, 84-94
Van den Berg et al	1998	Indonesia	RIC:CC	pesticide application	various	figures 2 & 5	Ab	Biocontrol Science and Technology, 8, 125-137
Vanbergen et al	2005	Scotland	NV:Ag	Caledonian forest & agricultural landscape	Carabids	figures 2a & 2b	R/Ab	Ecography, 28, 3-16
Vink	2004	New Zealand	IP:C	pasture & cropping	Araneae	table 1	R/Ab	New Zealand Journal of Zoology, 31, 149-159
Weibull & Ostman	2003	Finland	IP:C	pastures and cereal fields	Carabids	appendix	R	Basic and Applied Ecology, 4, 349-361

Weibull et al	2003	Sweden	IP:C; RIC:CC	pasture, organic cropping, conventional cropping	Carabids	appendix 1	R/Ab	Biodiversity and Conservation, 12, 1335-1355
Wells et al	2001	USA	RIC:CC	non-insecticide cotton & insecticide-treated cotton	Coccinellidae	table 2	Ab	Environmental Entomology, 30, 785-793
Wickramasinghe et al	2004	UK	NV:Ag; WNV:IP; IP:C; RIC:CC	woodland, pasture, organic cropping, conventional cropping	various	table 3	Ab	Conservation Biology, 14, 1283-1292
Wilson et al	1999	Australia	RIC:CC	treated & untreated cotton	Coccinellidae & Homoptera	table 1	Ab	Australian Journal of Entomology, 38, 242-243
Wisniewska & Prokopy	1997	USA	RIC:CC	apple orchard with & without pesticides	Araneae	figure 1(b)	Ab	Environmental Entomology, 26, 763-776
Witmer et al	2003	USA	RIC:CC	intensive & extensive cropping (various)	Carabids & Araneae	table 4	Ab	Environmental Entomology, 32, 366-376
Witt & Samways	2004	South Africa	NV:Ag; RIC:CC	Fynbos, non-pesticide apple orchards & pesticide-treated orchards	various	table 2	R/Ab	African Entomology, 12, 89-95
Yardim & Edwards	2002	USA	RIC:CC	herbicide & non-herbicide crop	various	figures 2-4	Ab	Phytoparasitica, 30, 1-8

Appendix C.1 All morphospecies collected and land-use occurrence.

Morphospecies numbering system is authors own, and reflects order in which each taxon was identified from pitfall samples.

Sub-family	**Genera**	**Morpho sp.**	**Total**	**WC**	**WE**	**PC**	**CE**	**CC**
Formicinae	***Paratrechina***	**1(a)**	571	0	0	4	567	0
	Paratrechina	**1(b)**	66	29	28	2	2	4
	Paratrechina	**2**	2	0	1	1	0	0
	Camponotus	**1(a)**	24	9	6	4	5	0
	Camponotus	**1(b)**	14	14	0	0	0	0
	Camponotus	**2**	20	7	0	3	10	0
	Camponotus	**3(a)**	2	0	0	2	0	0
	Camponotus	**3(b)**	1	1	0	0	0	0
	Camponotus	**4**	7	6	1	0	0	0
	Camponotus	**8**	4	2	2	0	0	0
	Camponotus	**9**	2	2	0	0	0	0
	Camponotus	**N**	2	2	0	0	0	0
	Melophorus	**1**	36	12	13	10	1	0
	Melophorus	**2(a)**	85	37	46	2	0	0
	Melophorus	**2(b)**	24	0	4	8	8	4
	Melophorus	**3**	2	0	0	2	0	0
	Melophorus	**4**	36	2	5	18	11	0
	Melophorus	**9**	29	3	15	13	0	0
	Melophorus	**10**	3	3	0	0	0	0
	Melophorus	**11**	2	0	0	2	0	0
	Melophorus	**13**	3	0	0	1	1	1
	Melophorus	**14**	2	0	1	0	1	0
	Notoncus	**1**	74	28	46	0	0	0
	Notoncus	**2**	270	0	16	212	42	0
	Polyrhachis	**1**	1	1	0	0	0	0
	Polyrhachis	**2**	1	0	0	1	0	0
	Polyrhachis	**3**	1	0	1	0	0	0
	Stigmacros	**1**	2	2	0	0	0	0
	Opisthopsis	**1**	5	0	5	0	0	0
Dolichoderinae	***Iridomyrmex***	**1**	7804	1791	1851	1666	2144	352
	Iridomyrmex	**3**	520	50	428	38	3	1
	Iridomyrmex	**2**	2	0	2	0	0	0
	Iridomyrmex	**4**	4	1	1	1	0	1
	Iridomyrmex	**7**	51	1	11	0	4	35
	Iridomyrmex	**9**	32	5	0	26	1	0
	Tapinoma	**2**	48	2	38	8	0	0
	Tapinoma	**3**	2	1	1	0	0	0
	Dolichoderus	**2**	2	2	0	0	0	0
	Doleromyrma	**1**	2	0	0	2	0	0
	Ochetellus	**1**	7	3	4	0	0	0
	Ochetellus	**2**	2	2	0	0	0	0
	Anonychomyrma	**1**	2	2	0	0	0	0
	Anonychomyrma	**2**	2	0	2	0	0	0
Ponerinae	***Rhytidoponera***	**1**	744	54	132	144	211	203
	Rhytidoponera	**3**	58	15	26	8	6	3
	Rhytidoponera	**4**	26	1	1	6	18	0

Sub-family	Genera	Morpho sp.	Total	WC	WE	PC	CE	CC
	Rhytidoponera	**5**	64	2	3	36	22	1
	Rhytidoponera	**6**	63	10	19	26	8	0
	Pachycondyla	**1**	39	13	17	8	1	0
	Pachycondyla	**2**	1	1	0	0	0	0
	Pachycondyla	**3**	1	0	0	0	1	0
	Heteroponera	**1**	1	0	1	0	0	0
	Leptogenys	**1**	1	0	1	0	0	0
Myrmeciinae	***Myrmecia***	**1**	2	1	1	0	0	0
	Myrmecia	**2**	2	0	2	0	0	0
Myrmicinae	***Meranoplus***	**1**	32	7	10	15	0	0
	Meranoplus	**2**	52	1	22	21	8	0
	Meranoplus	**3**	10	0	4	2	4	0
	Solenopsis	**1**	13	3	2	2	5	1
	Monomorium	**1**	83	43	24	14	2	0
	Monomorium	**2**	376	8	2	312	54	0
	Monomorium	**3**	22	7	10	5	0	0
	Monomorium	**5(a)**	11	1	9	1	0	0
	Monomorium	**5(b)**	39	2	34	1	2	0
	Monomorium	**7**	6	6	0	0	0	0
	Monomorium	**8**	24	15	9	0	0	0
	Cardiocondyla	**1**	1	0	1	0	0	0
	Pheidole	**2**	272	75	174	22	1	0
	Pheidole	**3**	787	32	152	412	145	46
	Pheidole	**5(a)**	91	0	0	3	52	36
	Pheidole	**5(b)**	130	49	29	23	29	0
	Pheidole	**7**	81	35	30	16	0	0
	Pheidole	**8**	1	1	0	0	0	0
	Pheidole	**10**	1	0	0	0	0	1
	Pheidole	**13**	6	6	0	0	0	0
	Crematogaster	**1**	5	5	0	0	0	0
	Crematogaster	**2**	16	4	3	5	4	0
	Crematogaster	**3**	119	4	15	65	35	0
	Crematogaster	**4**	1	1	0	0	0	0
	Crematogaster	**5**	1	1	0	0	0	0
	Crematogaster	**6**	8	0	8	0	0	0
	Oligomyrmex	**1**	1	0	0	0	0	1
	Colobostruma	**1**	1	1	0	0	0	0
Cerapachyinae	***Cerapachys***	**1**	1	0	0	0	0	1
	Cerapachys	**2**	2	0	1	0	1	0
Totals				**2425**	**3270**	**3173**	**3409**	**691**

<u>Appendix C.2</u> Papers used for data extraction for the functional group literature analysis, list of taxa (mostly at level of genera), functional group attributions and list of authorities used to determine functional group categorisation (at foot of table).

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
Armbrecht & Perfecto	2003	Agriculture, Ecosystems & Environment, 97, 107-115	Mexico	*Crematogaster*	Generalised Myrmicinae	5	0
				Pheidole 1	Generalised Myrmicinae	53	21
				Pheidole 3	Generalised Myrmicinae	3	0
				Pheidole 4	Generalised Myrmicinae	16	4
				Pheidole 5	Generalised Myrmicinae	4	0
				Pheidole 6	Generalised Myrmicinae	3	0
				Pheidole 7	Generalised Myrmicinae	1	0
				Solenopsis 1	Hot Climate Specialist	7	4
				Solenopsis 2	Hot Climate Specialist	2	0
				Solenopsis 3	Hot Climate Specialist	5	1
				Solenopsis geminata	Hot-climate Specialist	3	29
				Solenopsis 4	Hot Climate Specialist	14	0
				Gnamptogenys sulcata	Opportunist	6	11
				Hypoponera 1	Cryptic	27	0
				Hypoponera 2	Cryptic	10	0
				Odontomachus 1	Opportunist	3	2
				Pachycondyla 1	Specialist Predator	7	0
				Brachymyrmex 1	Cryptic	1	11
				Brachymyrmex 2	Cryptic	0	21

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Brachymyrmex 3	Cryptic	9	1
Bos *et al*.	2007	Biodiversity & Conservation, 16, 2429-2444	Indonesia	*Dolichoderus*	Cold Climate Specialist	3	78
				Tapinoma	Opportunist	0	22
				Gnamptogenys	Opportunist	102	0
				Anoplolepis	Opportunist	1	287
				Camponotus	Subordinate Camponotini	2	9
				Echinopla	Subordinate Camponotini	13	7
				Oecophylla	Tropical Climate Specialist	8	0
				Paratrechina	Opportunist	1	78
				Polyrhachis	Subordinate Camponotini	289	297
				Cataulacus	Specialist Predator	0	4
				Crematogaster	Generalised Myrmicinae	276	61
				Paratopula	Unknown		
				Pheidole	Generalised Myrmicinae	2	0
				Secostruma	Unknown		
				Tetramorium	Opportunist	0	15
				Tetraponera	Specialist Predator	0	7
Bromham *et al*.	1999	Australian Journal of Ecology, 24, 199-207	Australia	*Camponotus*	Subordinate Camponotini	0.36	0.15
				Iridomyrmex	Dominant Dolichoderinae	0.13	0.26
				Rhytidoponera	Opportunist	3.89	16.26
Castaño-Meneses & Palacios-Vargas	2003	Biodiversity & Conservation, 12, 1913-1919	Mexico	*Brachymyrmex*	Cryptic	1	0
				Crematogaster	Generalised Myrmicinae	0	1
				Solenopsis	Hot Climate Specialist	6	1
				Solenopsis	Hot Climate Specialist	7	6
				Leptothorax	Opportunist	1	5
				Leptothorax	Opportunist	0	1
				Paratrechina	Opportunist	0	1
				Rogeria	Trop. Clim. Spec.	2	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
Fisher & Robertson	2002	Biotropica, 34, 155-167	Madagascar	*Hypoponera*	Cryptic	35	1
				Hypoponera	Cryptic	13	1
				Hypoponera	Cryptic	14	0
				Hypoponera	Cryptic	27	0
				Hypoponera	Cryptic	0	2
				Oligomyrmex	Cryptic	0	15
				Plagiolepis	Cryptic	4	0
				Plagiolepis	Cryptic	0	43
				Prionopelta	Cryptic	0	1
				Pyramica	Cryptic	0	1
				Pyramica	Cryptic	0	4
				Strumigenys	Cryptic	6	0
				Strumigenys	Cryptic	0	1
				Strumigenys	Cryptic	1	0
				Strumigenys	Cryptic	2	0
				Strumigenys	Cryptic	32	0
				Strumigenys	Cryptic	9	0
				Strumigenys	Cryptic	1	0
				Strumigenys	Cryptic	0	1
				Crematogaster	Generalised Myrmicinae	3	0
				Crematogaster	Generalised Myrmicinae	2	0
				Monomorium	Generalised Myrmicinae	4	0
				Monomorium	Generalised Myrmicinae	0	90
				Monomorium	Generalised Myrmicinae	0	29
				Monomorium	Generalised Myrmicinae	17	0
				Pheidole	Generalised Myrmicinae	22	0
				Pheidole	Generalised Myrmicinae	42	1
				Pheidole	Generalised Myrmicinae	0	168
				Pheidole	Generalised Myrmicinae	0	76
				Anoplolepis	Opportunist	3	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Aphaenogaster	Opportunist	0	65
				Cardiocondyla	Opportunist	0	11
				Cardiocondyla	Opportunist	0	11
				Leptothorax	Opportunist	6	0
				Leptothorax	Opportunist	1	0
				Leptothorax	Opportunist	2	0
				Paratrechina	Opportunist	0	58
				Technomyrmex	Opportunist	0	23
				Tetramorium	Opportunist	1	0
				Tetramorium	Opportunist	45	0
				Tetramorium	Opportunist	36	0
				Tetramorium	Opportunist	0	60
				Tetramorium	Opportunist	0	68
				Tetramorium	Opportunist	0	4
				Tetramorium	Opportunist	0	6
				Cerapachys	Specialist Predator	11	0
				Cerapachys	Specialist Predator	0	1
				Cerapachys	Specialist Predator	0	4
				Pachycondyla	Specialist Predator	0	8
				Camponotus	Subordinate Camponotini	0	16
				Camponotus	Subordinate Camponotini	0	9
Gómez *et al.*	2003	Biodiversity & Conservation, 12, 2135-2146	Spain	*Hypononera*	Cryptic	2	0
				Aphaenogaster	Opportunist	12	0
				Aphaenogaster	Opportunist	14	1
				Crematogaster	Generalised Myrmicinae	57	9
				Crematogaster	Generalised Myrmicinae	6	0
				Leptothorax	Cold Climate Specialist	3	0
				Leptothorax	Cold Climate Specialist	90	0
				Leptothorax	Cold Climate Specialist	14	0
				Messor barbarus	Hot Climate Specialist	4	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Myrmica scabrinodis	Opportunist	0	239
				Myrmica sabuletti	Opportunist	7	0
				Pheidole	Generalised Myrmicinae	218	0
				Solenopsis	Cryptic	9	1
				Tetramorium	Opportunist	1	0
				Tetramorium	Opportunist	0	7
				Tapinoma	Opportunist	2	17
				Camponutus	Subordinate Camponotini	4	0
				Camponutus	Subordinate Camponotini	11	0
				Camponutus	Subordinate Camponotini	12	0
				Camponutus	Subordinate Camponotini	7	0
				Camponutus	Subordinate Camponotini	2	0
				Cataglyphis	Hot Climate Specialist	1	0
				Formica	Opportunist	0	43
				Formica	Opportunist	93	7
				Formica	Opportunist	0	36
				Lasius	Cold Climate Specialist	2	0
				Lasius	Cold Climate Specialist	0	40
				Lasius	Cold Climate Specialist	1	0
				Plagiolepis	Cryptic	36	0
Gove *et al.*	2005	Biological Conservation, 126, 238-338	Mexico	*Dolichoderus*	Cold Climate Specialist	4	0
				Solenopsis (diplorhoptrum)	Cryptic	2	7
				Solenopsis (diplorhoptrum)	Cryptic	4	4
				Wasmannia auropunctata	Cryptic	3	0
				Brachymyrmex	Cryptic	0	5
				Brachymyrmex	Cryptic	0	4
				Azteca	Dominant Dolichoderinae	0	1

Author	**Year**	**Journal, Vol, pp**	**Country**	**Genus**	**Functional Group**	**Abundance in NV**	**Abundance in Ag**
				Azteca	Dominant Dolichoderinae	4	0
				Forelius pruinosus	Dominant Dolichoderinae	0	5
				Crematogaster	Generalised Myrmicinae	2	1
				Cephalotes	Generalised Myrmicinae	1	0
				Crematogaster	Generalised Myrmicinae	1	0
				Crematogaster	Generalised Myrmicinae	4	1
				Monomorium	Generalised Myrmicinae	1	11
				Pheidole	Generalised Myrmicinae	4	0
				Pheidole	Generalised Myrmicinae	0	1
				Pheidole	Generalised Myrmicinae	6	0
				Pheidole	Generalised Myrmicinae	0	2
				Pheidole	Generalised Myrmicinae	2	9
				Pheidole	Generalised Myrmicinae	1	3
				Pheidole	Generalised Myrmicinae	1	2
				Pheidole	Generalised Myrmicinae	2	2
				Pheidole	Generalised Myrmicinae	2	0
				Pogonomyrmex	Hot Climate Specialist	0	2
				Forelius sp.	Hot Climate Specialist	0	3
				Solenopsis geminata	Hot-Climate Specialist	5	5
				Solenopsis	Hot-Climate Specialist	3	0
				Leptothorax	Opportunist	0	1
				Leptothorax	Opportunist	2	0
				Tetramorium	Opportunist	1	4
				Dorymyrmex	Opportunist	0	11
				Paratrechina	Opportunist	1	3

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Ectatomma	Opportunist	0	7
				Odontomachus	Opportunist	1	2
				Leptogenys	Specialist predator	1	0
				Pachycondyla	Specialist Predator	3	1
				Camponotus	Subordinate Camponotini	1	2
				Camponotus	Subordinate Camponotini	1	0
				Camponotus	Subordinate Camponotini	2	0
				Camponotus	Subordinate Camponotini	7	1
				Camponotus	Subordinate Camponotini	0	1
				Camponotus	Subordinate Camponotini	2	0
				Camponotus	Subordinate Camponotini	3	0
				Camponotus	Subordinate Camponotini	2	0
				Cyphomyrmex	Tropical Climate Specialist	2	0
				Cyphomyrmex	Tropical Climate Specialist	3	2
				Mycocepurus	Tropical Climate Specialist	6	0
				Trachymyrmex	Tropical Climate Specialist	7	5
				Neivamyrmex adnepos	Tropical Climate Specialist	0	1
				Neivamyrmex opacithorax	Tropical Climate Specialist	0	1
				Pseudomyrmex	Tropical Climate Specialist	0	1
				Pseudomyrmex	Tropical Climate Specialist	1	0
				Pseudomyrmex	Tropical Climate Specialist	0	1
Keals & Majer	1991	In: (eds. D. A. Saunders & R. J. Hobbs) Nature Conservation 2: The Role of Corridors. Surrey Beatty and Sons, Sydney. 387-393	Australia	Dominant Dolichoderinae	Dominant Dolichoderinae	14	25.5
				Subordinate Camponotini	Subordinate Camponotini	8	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Cryptic	Cryptic	3.5	0
				Opportunists	Opportunist	11	8.25
				Generalised Myrmicinae	Generalised Myrmicinae	27	58.25
				Specialist Predator	Specialist Predator	3	0
King *et al.*	1998	Biodiversity & Conservation, 7, 1627-1638	Australia	*Cryptopone*	Cryptic	1	0
				Heteroponera	Cryptic	1	0
				Hypoponera	Cryptic	1	0
				Hypoponera	Cryptic	1	0
				Oligomyrmex	Cryptic	1	0
				Solenopsis	Cryptic	0	3
				Strumigenys	Cryptic	1	0
				Iridomyrmex	Dominant Dolichoderinae	0	1
				Crematogaster	Generalised Myrmicinae	1	0
				Pheidole	Generalised Myrmicinae	14	0
				Pheidole	Generalised Myrmicinae	1	0
				Pheidole	Generalised Myrmicinae	1	0
				Pheidole	Generalised Myrmicinae	1	0
				Pheidole	Generalised Myrmicinae	5	0
				Rhytidoponera	Opportunist	2	0
				Rhytidoponera	Opportunist	2	0
				Rhytidoponera	Opportunist	13	22
				Aphaenogaster	Opportunist	0	32
				Cardiocondyla	Opportunist	0	1
				Tetramorium	Opportunist	1	0
				Ochetellus	Opportunist	0	2
				Technomyrmex	Opportunist	1	0
				Paratrechina	Opportunist	2	20
				Paratrechina	Opportunist	1	0
				Myrmecia	Specialist Predator	1	0
				Onychomyrmex	Specialist Predator	1	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Polyrhachis	Subordinate Camponotini	1	0
Lobry de Bruyn (Yellow sand site)	1993	Soil Biology & Biochemistry, 25, 1043-1056	Australia	*Iridomyrmex*	Dominant Dolichoderinae	2	317
				Iridomyrmex	Dominant Dolichoderinae	263	148
				Iridomyrmex	Dominant Dolichoderinae	32057	26
				Iridomyrmex	Dominant Dolichoderinae	103	3
				Iridomyrmex	Dominant Dolichoderinae	35	15
				Iridomyrmex	Dominant Dolichoderinae	189	4
				Iridomyrmex	Dominant Dolichoderinae	23	67
				Tapinoma	Opportunist	7	0
				Tapinoma	Opportunist	52	0
				Camponotus	Subordinate Camponotini	1	0
				Camponotus	Subordinate Camponotini	5	0
				Camponotus	Subordinate Camponotini	20	0
				Camponotus	Subordinate Camponotini	162	3
				Camponotus	Subordinate Camponotini	16	1
				Camponotus	Subordinate Camponotini	3	0
				Camponotus	Subordinate Camponotini	1557	8
				Camponotus	Subordinate Camponotini	0	4
				Camponotus	Subordinate Camponotini	27	0
				Camponotus	Subordinate Camponotini	3	0
				Camponotus	Subordinate Camponotini	31	0
				Camponotus	Subordinate Camponotini	32	0
				Camponotus	Subordinate Camponotini	6	0
				Camponotus	Subord. Camponotini	9	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Camponotus	Subordinate Camponotini	12	0
				Camponotus	Subordinate Camponotini	1	0
				Aphaenogaster	Opportunist	89	3
				Cerapachys	Specialist Predator	3	1
				Cerapachys	Specialist Predator	1	2
				Melophorus	Hot Climate Specialist	37	0
				Melophorus	Hot Climate Specialist	16	72
				Melophorus	Hot Climate Specialist	14	0
				Melophorus	Hot Climate Specialist	71	181
				Melophorus	Hot Climate Specialist	2	7
				Melophorus	Hot Climate Specialist	67	0
				Melophorus	Hot Climate Specialist	32	28
				Melophorus	Hot Climate Specialist	1	0
				Melophorus	Hot Climate Specialist	15	0
				Melophorus	Hot Climate Specialist	15	0
				Meranoplus	Hot Climate Specialist	3	0
				Meranoplus	Hot Climate Specialist	1	0
				Meranoplus	Hot Climate Specialist	2	0
				Notoncus	Cold Climate Specialist	2	0
				Notoncus	Cold Climate Specialist	1	0
				Stigmacros	Cold Climate Specialist	2	0
				Stigmacros	Cold Climate Specialist	1	1
				Stigmacros	Cold Climate Specialist	1	0
				Paratrechina	Opportunist	3	0
				Tetramorium	Opportunist	7	10

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Tetramorium	Opportunist	2	25
				Tetramorium	Opportunist	0	10
				Tetramorium	Opportunist	0	9
				Rhytidoponera	Opportunist	93	237
				Rhytidoponera	Opportunist	25	0
				Crematogaster	Generalised Myrmicinae	5	0
				Crematogaster	Generalised Myrmicinae	120	0
				Crematogaster	Generalised Myrmicinae	79	0
				Monomorium	Generalised Myrmicinae	645	3014
				Monomorium	Generalised Myrmicinae	9	1
				Monomorium	Generalised Myrmicinae	20	608
				Monomorium	Generalised Myrmicinae	22	0
				Pheidole	Generalised Myrmicinae	37	0
				Pheidole	Generalised Myrmicinae	24	1833
				Pheidole	Generalised Myrmicinae	18	3873
				Pheidole	Generalised Myrmicinae	35	79
				Pheidole	Generalised Myrmicinae	2	67
				Pheidole	Generalised Myrmicinae	0	9
				Anochetus	Specialist Predator	2	0
				Bothroponera	Specialist Predator	2	0
Lobry de Bruyn (Grey sandy loam site)	1993	Soil Biology & Biochemistry, 25, 1043-1056	Australia	*Iridomyrmex*	Dominant Dolichoderinae	140	87
				Iridomyrmex	Dominant Dolichoderinae	88	1
				Iridomyrmex	Dominant Dolichoderinae	79645	72
				Iridomyrmex	Dominant Dolichoderinae	13	18
				Iridomyrmex	Dom. Dolichoderinae	13	3

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Iridomyrmex	Dominant Dolichoderinae	0	9
				Iridomyrmex	Dominant Dolichoderinae	15	23
				Iridomyrmex	Dominant Dolichoderinae	12	1
				Iridomyrmex	Dominant Dolichoderinae	3	0
				Ochetellus	Opportunist	1	0
				Tapinoma	Opportunist	129	0
				Tapinoma	Opportunist	1	0
				Camponotus	Subordinate Camponotini	32	0
				Camponotus	Subordinate Camponotini	2	0
				Camponotus	Subordinate Camponotini	37	0
				Camponotus	Subordinate Camponotini	11	0
				Camponotus	Subordinate Camponotini	17	0
				Camponotus	Subordinate Camponotini	11	0
				Camponotus	Subordinate Camponotini	1	0
				Camponotus	Subordinate Camponotini	44	0
				Camponotus	Subordinate Camponotini	2	0
				Camponotus	Subordinate Camponotini	15	0
				Camponotus	Subordinate Camponotini	29	0
				Camponotus	Subordinate Camponotini	6	0
				Camponotus	Subordinate Camponotini	42	0
				Polyrhachis	Subordinate Camponotini	3	0
				Polyrhachis	Subordinate Camponotini	2	0
				Aphaenogaster	Opportunist	16	1
				Cerapachys	Specialist Predator	3	0
				Cerapachys	Specialist Predator	1	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Cerapachys	Specialist Predator	0	36
				Dolichoderus	Cold Climate Specialist	5	0
				Melophorus	Hot Climate Specialist	6	0
				Melophorus	Hot Climate Specialist	56	5
				Melophorus	Hot Climate Specialist	187	0
				Melophorus	Hot Climate Specialist	57	86
				Melophorus	Hot Climate Specialist	1	0
				Melophorus	Hot Climate Specialist	66	0
				Melophorus	Hot Climate Specialist	7	29
				Melophorus	Hot Climate Specialist	27	0
				Melophorus	Hot Climate Specialist	2	1
				Melophorus	Hot Climate Specialist	7	0
				Melophorus	Hot Climate Specialist	0	1
				Melophorus	Hot Climate Specialist	1	0
				Meranoplus	Hot Climate Specialist	32	0
				Meranoplus	Hot Climate Specialist	43	0
				Meranoplus	Hot Climate Specialist	58	0
				Meranoplus	Hot Climate Specialist	50	0
				Meranoplus	Hot Climate Specialist	65	0
				Notoncus	Cold Climate Specialist	2	0
				Podomyrma	Cold Climate Specialist	12	0
				Stigmacros	Cold Climate Specialist	1	0
				Stigmacros	Cold Climate Specialist	14	0
				Stigmacros	Cold Clim. Specialist	3	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Stigmacros	Cold Climate Specialist	6	0
				Stigmacros	Cold Climate Specialist	1	0
				Strumigenys	Cryptic	2	0
				Tetramorium	Opportunist	5	45
				Tetramorium	Opportunist	0	13
				Tetramorium	Opportunist	5	0
				Tetramorium	Opportunist	5	0
				Tetramorium	Opportunist	1	0
				Tetramorium	Opportunist	2	0
				Rhytidoponera	Opportunist	147	983
				Rhytidoponera	Opportunist	239	0
				Rhytidoponera	Opportunist	10	0
				Crematogaster	Generalised Myrmicinae	12	36
				Crematogaster	Generalised Myrmicinae	36	0
				Crematogaster	Generalised Myrmicinae	2	0
				Crematogaster	Generalised Myrmicinae	1470	2116
				Monomorium	Generalised Myrmicinae	223	0
				Monomorium	Generalised Myrmicinae	166	863
				Monomorium	Generalised Myrmicinae	3	0
				Monomorium	Generalised Myrmicinae	1	0
				Monomorium	Generalised Myrmicinae	1	0
				Monomorium	Generalised Myrmicinae	3	0
				Monomorium	Generalised Myrmicinae	6	0
				Pheidole	Generalised Myrmicinae	26	0
				Pheidole	Generalised Myrmicinae	6	3468
				Pheidole	Generalised Myrmicinae	1	1958
				Pheidole	Gen. Myrmicinae	34	1598

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
Majer	1978	Forest Ecology & Management, 1, 321-334	Australia	*Pheidole*	Generalised Myrmicinae	203	17
				Pheidole	Generalised Myrmicinae	1	44
				Anochetus	Specialist Predator	1	0
				Anochetus	Specialist Predator	27	2
				Bothroponera	Specialist Predator	2	0
				Odontomachus	Opportunist	1	0
				Rhytidoponera	Opportunist	9	2
				Heteroponera	Cryptic	1	0
				Pheidole	Generalised Myrmicinae	1	10
				Xiphomyrmex	Opportunist	1	0
				Monomorium	Generalised Myrmicinae	3	0
				Monomorium	Generalised Myrmicinae	10	0
				Meranoplus	Hot Climate Specialist	9	0
				Crematogaster	Generalised Myrmicinae	21	0
				Iridomyrmex	Dominant Dolichoderinae	26	0
				Iridomyrmex	Dominant Dolichoderinae	15	0
				Iridomyrmex	Dominant Dolichoderinae	0	3
				Iridomyrmex	Dominant Dolichoderinae	101	0
				Iridomyrmex	Dominant Dolichoderinae	3	0
				Iridomyrmex	Dominant Dolichoderinae	6	0
				Iridomyrmex	Dominant Dolichoderinae	1	0
				Prolasius	Cold Climate Specialist	2	0
				Melophorus	Hot Climate Specialist	0	15
				Melophorus	Hot Climate Specialist	1	0
				Melophorus	Hot Climate Specialist	2	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Camponotus	Subordinate camponotini	2	0
				Camponotus	Subordinate Camponotini	1	0
Nakamura *et al.*	2003	Ecological Management & Restoration, 4, S20-S28	Australia	*Anillomyrma*	Cryptic	0	1.8
				Anisopheidole	Hot Climate Specialist	0.8	0
				Anonychomyrma	Dominant Dolichoderinae	0	1.6
				Cardiocondyla	Opportunist	0.2	0
				Colobostruma	Specialist Predator	2.8	0
				Discothyrea	Cryptic	0.2	0
				Eurhopalothrix	Cryptic	0.2	0
				Heteroponera	Cryptic	2.8	0.4
				Hypoponera	Cryptic	11.4	0
				Lordomyrma	Climate Specialist	0.6	0
				Mayriella	Tropical Climate Specialist	1.2	0
				Meranoplus	Hot Climate Specialist	0.4	0
				Monomorium	Generalised Myrmicinae	2	16.4
				Myrmecina	Cryptic	0.2	0
				Notoncus	Cold Climate Specialist	0	0.2
				Oligomyrmex	Cryptic	7.4	17
				Pachycondyla	Specialist Predator	0	1.6
				Paratrechina	Opportunist	0.4	0.8
				Pheidole	Generalised Myrmicinae	0.6	2.6
				Plagiolepis	Cryptic	0	1
				Prionopelta	Cryptic	0.4	0
				Rhytidoponera	Opportunist	4	0
				Solenopsis	Cryptic	8.4	10.8
				Strumigenys	Cryptic	2.2	0
				Tapinoma	Opportunist	0	0.6
				Tetramorium	Opportunist	0	0.8
Room	1975	Australian Journal of Zoology, 23, 71-89	PNG	*Anoplolepis longipes*	Opportunist	3	4

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Pseudolasius	Unknown	2	0
				Lordomyrma	Cold Climate Specialist	1	0
				Monoceratoclinea	Cold Climate Specialist	2	0
				Brachyponera	Cryptic	7	17
				Cryptopone	Cryptic	1	0
				Mesoponera	Cryptic	2	0
				Hypoponera	Cryptic	2	5
				Strumigenys	Cryptic	1	0
				Strumigenys	Cryptic	1	0
				Strumigenys	Cryptic	1	0
				Eurhopalothrix	Cryptic	0	1
				Myrmecina	Cryptic	0	1
				Myrmecina	Cryptic	1	1
				Pheidologeton	Cryptic	9	6
				Acropyga	Cryptic	1	0
				Leptomyrmex	Dominant Dolichoderinae	2	3
				Iridomyrmex	Dominant Dolichoderinae	3	0
				Iridomyrmex	Dominant Dolichoderinae	2	0
				Crematogaster	Generalised Myrmicinae	1	0
				Rhoptromyrmex	Generalised Myrmicinae	1	5
				Pheidole	Generalised Myrmicinae	7	1
				Pheidole	Generalised Myrmicinae	2	2
				Pheidole	Generalised Myrmicinae	2	0
				Pheidole	Generalised Myrmicinae	1	0
				Pheidole	Generalised Myrmicinae	2	0
				Pheidole	Generalised Myrmicinae	1	1
				Pheidole	Generalised Myrmicinae	1	1
				Pheidole	Gen. Myrmicinae	3	2

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Meranoplus	Hot Climate Specialist	1	0
				Rhytidoponera	Opportunist	0	4
				Gnamptogenys sulcata	Opportunist	1	0
				Odontomachus	Opportunist	4	0
				Odontomachus	Opportunist	1	6
				Odontomachus	Opportunist	7	2
				Aphaenogaster	Opportunist	25	3
				Aphaenogaster	Opportunist	3	0
				Tetramorium	Opportunist	1	1
				Cardiocondyla	Opportunist	0	1
				Technomyrmex	Opportunist	3	6
				Technomyrmex	Opportunist	2	1
				Paratrechina	Opportunist	0	1
				Paratrechina	Opportunist	0	1
				Paratrechina	Opportunist	7	1
				Paratrechina	Opportunist	1	0
				Paratrechina	Opportunist	1	0
				Paratrechina	Opportunist	1	0
				Anochetus	Specialist Predator	0	1
				Myopias	Specialist Predator	2	0
				Myopias	Specialist Predator	1	0
				Leptogenys	Specialist Predator	1	0
				Ectomomyrmex	Specialist Predator	6	1
				Ectomomyrmex	Specialist Predator	1	0
				Orectognathus	Specialist Predator	1	0
				Camponotus	Subordinate Camponotini	0	1
				Polyrhachis	Subordinate Camponotini	5	0
				Polyrhachis	Subordinate Camponotini	1	0
				Pristomyrmex	Tropical Climate Specialist	0	2
				Oecophylla	Tropical Climate Specialist	2	2
Roth *et al.*	1994	Ecological Interactions, 4, 423-436	Costa Rica	*Aphaenogaster*	Opportunist	0.171	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Cardiocondyla	Opportunist	0	0.011
				Crematogaster	Generalised Myrmicinae	0.046	0
				Cyphomyrmex	Tropical Climate Specialist	0	0.011
				Pheidole	Generalised Myrmicinae	0.026	0
				Pheidole	Generalised Myrmicinae	0.062	0
				Pheidole	Generalised Myrmicinae	0.058	0
				Pheidole	Generalised Myrmicinae	0.079	0
				Pheidole	Generalised Myrmicinae	0	0.116
				Pheidole	Generalised Myrmicinae	0.05	0
				Pheidole	Generalised Myrmicinae	0.005	0
				Pheidole	Generalised Myrmicinae	0.033	0
				Pheidole	Generalised Myrmicinae	0	0.033
				Pheidole	Generalised Myrmicinae	0.241	0
				Pheidole	Generalised Myrmicinae	0.039	0
				Pheidole	Generalised Myrmicinae	0.009	0
				Pheidole	Generalised Myrmicinae	0.01	0
				Pheidole	Generalised Myrmicinae	0.025	0
				Pheidole	Generalised Myrmicinae	0.067	0
				Pheidole	Generalised Myrmicinae	0.004	0
				Pheidole	Generalised Myrmicinae	0.017	0.011
				Pheidole	Generalised Myrmicinae	0.005	0
				Pheidole	Generalised Myrmicinae	0	0.005
				Pheidole	Generalised Myrmicinae	0.005	0
				Pheidole	Gen. Myrmicinae	0.005	0

Author	**Year**	**Journal, Vol, pp**	**Country**	**Genus**	**Functional Group**	**Abundance in NV**	**Abundance in Ag**
				Pheidole	Generalised Myrmicinae	0.13	0
				Pheidole	Generalised Myrmicinae	0.118	0.005
				Pheidole	Generalised Myrmicinae	0.005	0
				Pheidole	Generalised Myrmicinae	0.065	0
				Pheidole	Generalised Myrmicinae	0	0.045
				Pheidole	Generalised Myrmicinae	0	0.258
				Pheidole	Generalised Myrmicinae	0	0.049
				Pheidole	Generalised Myrmicinae	0.085	0
				Pheidole	Generalised Myrmicinae	0.005	0
				Solenopsis	Hot Climate Specialist	0.004	0
				Solenopsis	Hot Climate Specialist	0	0.007
				Solenopsis	Hot Climate Specialist	0.004	0.013
				Solenopsis	Hot Climate Specialist	0.046	0
				Solenopsis	Hot Climate Specialist	0.004	0
				Solenopsis	Hot Climate Specialist	0.004	0
				Solenopsis	Hot Climate Specialist	0.005	0
				Solenopsis	Hot Climate Specialist	0	0.013
				Tetramorium	Opportunist	0	0.005
				Trachymyrmex	Tropical Climate Specialist	0.004	0
				Wasmannia	Cryptic	0	0.011
				Wasmannia	Cryptic	0.044	0
				Gnamptogenys	Opportunist	0	0.007
				Hypononera	Cryptic	0.019	0
				Hypononera	Cryptic	0.005	0
				Hypononera	Cryptic	0	0.005
				Hypononera	Cryptic	0	0.011

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Odontomachus	Opportunist	0	0.04
				Odontomachus	Opportunist	0.004	0
				Odontomachus	Opportunist	0.08	0
				Odontomachus	Opportunist	0.017	0.043
				Odontomachus	Opportunist	0.062	0
				Odontomachus	Opportunist	0.005	0
				Pachycondyla	Specialist Predator	0.042	0
				Pachycondyla	Specialist Predator	0.0325	0.046
				Pachycondyla	Specialist Predator	0.005	0
				Paratrechina	Opportunist	0.092	0.013
Schnell *et al*.	2003	Austral Ecology, 28, 553-565	Australia	Dominant Dolichoderinae	Dominant Dolichoderinae	9	24
				Subordinate Camponotini	Subordinate Camponotini	3	0.5
				Opportunists	Opportunist	66	42
				Generalised Myrmicinae	Generalised Myrmicinae	17	21
				Hot Climate Specialist	Hot Climate Specialist	0.5	2
Schonberg *et al*.	2004	Biotropica, 36, 402-409	Costa Rica	*Solenopsis*	Hot Climate Specialist	5	5
				Camponotus	Subordinate Camponotini	5	5
				Camponotus	Subordinate Camponotini	4	5
				Stenamma	Cold Climate Specialist	5	1
				Pheidole diana	Generalised Myrmicinae	3	4
				Brachymyrmex	Cryptic	3	2
				Myrmelachista	Tropical Climate Specialist	2	3
				Leptothorax	Opportunist	2	4
				Solenopsis	Hot Climate Specialist	3	1
				Pheidole innupta	Generalised Myrmicinae	3	1
				Myrmelachista	Tropical Climate Specialist	3	1
				Pheidole exarata	Generalised Myrmicinae	0	4
				Brachymyrmex	Cryptic	1	0

Author	Year	Journal, Vol, pp	Country	Genus	Functional Group	Abundance in NV	Abundance in Ag
				Hypoponera	Cryptic	1	1
				Brachymyrmex	Cryptic	0	2
				Myrmelachista	Tropical Climate Specialist	1	1
				Brachymyrmex	Cryptic	1	0
				Pheidole monteverdensis	Generalised Myrmicinae	1	0
				Paratrechina	Opportunist	0	1
				Wasmannia auropunctata	Cryptic	0	1
				Adelomyrmex	Cryptic	0	1
				Hypoponera	Cryptic	1	0
				Pachycondyla aenescens	Specialist Predator	1	0
				Pheidole hizempos	Generalised Myrmicinae	1	0
				Pheidole specularis	Generalised Myrmicinae	0	1

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Appendix C.3 Bray Curtis Similarity Matrix for 4th Rt transformed ant morphospecies data at each location and treatment for intensification gradient (WC = woodland core, WE = woodland/pasture edge, PC = pasture core, CE = pasture/cropping edge, CC = cropping core).

	Rice 1 CC	Rice 1 CE	Rice 1 PC	Rice 1 WE	Rice 1 WC	Rice 2 CC	Rice 2 CE	Rice 2 PC	Rice 2 WE	Rice 2 WC	Kowitz CC	Kowitz CE	Kowitz PC	Kowitz WE	Kowitz WC	Radke CC	Radke CE	Radke PC	Radke WE	Radke WC
Rice 1 CC																				
Rice 1 CE	35.4																			
Rice 1 PC	31.7	47.0																		
Rice 1 WE	20.9	58.1	48.7																	
Rice 1 WC	23.0	43.4	32.8	57.2																
Rice 2 CC	60.1	41.0	29.8	26.6	29.2															
Rice 2 CE	62.4	33.5	30.9	27.4	31.7	50.1														
Rice 2 PC	39.5	59.1	37.5	54.0	38.6	47.8	43.4													
Rice 2 WE	27.9	54.8	43.7	53.4	51.8	33.9	34.4	53.6												
Rice 2 WC	27.9	51.3	30.1	53.1	42.1	34.2	29.4	63.7	62.7											
Kowitz CC	54.7	24.3	27.8	20.8	22.7	35.4	51.4	25.7	24.7	17.7										
Kowitz CE	38.4	40.9	30.1	32.4	31.3	32.3	42.5	37.4	32.3	31.1	40.1									
Kowitz PC	24.1	34.5	38.3	40.5	29.8	23.8	25.7	38.9	39.3	34.2	32.1	51.6								
Kowitz WE	14.5	25.9	18.6	43.3	37.9	15.9	22.9	24.8	29.7	26.9	22.6	32.5	49.8							
Kowitz WC	7.8	18.2	17.2	34.5	31.7	11.9	7.0	21.0	26.1	30.0	11.6	25.3	29.2	56.8						
Radke CC	56.0	30.0	20.6	22.9	26.1	55.6	36.0	44.8	24.1	36.0	28.0	21.7	10.1	6.9	6.6					
Radke CE	27.3	52.9	31.5	39.8	36.9	32.2	40.6	47.0	55.9	40.9	30.1	55.8	43.3	20.8	11.7	22.8				
Radke PC	38.5	51.7	54.2	43.2	48.8	38.7	29.6	38.4	55.9	50.4	27.2	29.7	38.2	22.3	19.5	32.5	45.5			
Radke WE	38.4	39.1	42.3	45.3	48.1	38.2	32.9	43.0	51.4	39.9	33.4	31.7	33.5	31.7	26.6	28.6	37.4	52.3		
Radke WC	26.8	40.6	34.6	52.0	42.6	30.9	21.3	35.9	49.3	57.1	24.3	22.2	30.6	37.8	40.8	31.4	30.0	51.1	48.9	
Halford 1 CC	88.4	42.1	38.3	26.0	26.6	68.1	68.4	46.2	34.3	30.0	50.1	42.9	28.8	18.2	7.6	57.4	33.4	39.9	43.6	28.7
Halford 1 CE	37.9	38.4	43.4	26.4	27.4	38.4	29.6	27.4	35.5	25.3	32.9	30.3	28.3	19.5	24.4	13.0	20.2	41.2	33.2	23.4
Halford 1 PC	15.1	32.5	9.6	35.4	36.9	23.6	18.2	33.4	31.5	40.6	14.4	47.4	40.4	34.9	20.5	26.0	41.1	24.8	24.8	30.1
Halford 1 WE	8.8	22.7	14.3	37.5	37.3	7.4	7.4	19.9	30.1	40.3	14.2	18.5	36.8	62.2	55.9	8.8	8.3	24.5	35.2	53.5
Halford 1 WC	33.4	37.9	21.0	38.9	33.3	28.0	24.5	38.9	41.4	60.6	19.6	26.7	31.5	35.4	34.0	34.5	23.8	32.0	38.7	59.5
Halford 2 CC	58.9	39.1	34.1	25.0	27.3	56.1	43.0	42.9	38.0	35.0	56.4	47.6	33.6	16.5	6.8	51.3	47.3	41.8	42.1	33.4
Halford 2 CE	42.5	42.5	36.8	33.9	31.1	36.1	50.7	39.4	40.4	37.3	37.5	54.9	42.8	29.1	19.1	28.8	62.3	39.1	45.0	36.5
Halford 2 PC	34.1	25.1	23.7	24.6	26.6	43.9	36.8	38.0	39.4	44.5	29.8	38.5	30.7	26.3	25.9	37.1	43.2	39.1	35.8	43.0
Halford 2 WE	26.7	21.5	23.6	44.4	34.4	18.7	26.2	27.5	36.1	40.2	32.4	42.7	44.2	58.1	40.3	19.1	27.2	29.3	34.9	53.1
Halford 2 WC	23.9	21.0	16.9	27.0	33.5	20.3	26.9	22.3	27.8	31.1	23.0	27.0	21.4	29.5	29.2	22.2	16.4	22.9	26.8	33.9
Postle CC	45.8	20.3	18.9	16.6	13.4	47.2	33.3	28.4	16.3	27.5	42.3	28.2	11.6	6.7	11.7	32.9	28.1	23.1	22.0	20.2
Postle CE	32.0	34.4	16.1	26.7	28.5	48.8	32.6	38.4	33.7	42.7	28.8	22.4	6.7	14.7	14.1	46.7	40.5	28.0	21.9	35.3
Postle PC	28.5	53.4	43.8	48.4	40.4	41.4	38.3	44.7	47.8	46.3	31.4	33.3	28.3	25.2	15.0	24.9	46.2	51.0	44.0	41.2
Postle WE	20.9	36.5	13.9	33.7	33.9	23.5	16.9	24.6	30.6	39.7	19.6	24.8	18.2	44.2	47.2	24.5	22.5	22.5	30.9	46.4
Postle WC	21.5	23.2	20.8	30.0	34.0	18.4	31.0	21.4	32.8	42.4	22.5	19.8	17.2	31.5	31.4	21.6	24.4	30.1	29.4	41.8
Thallon CC	81.3	36.4	32.7	22.0	22.6	57.9	65.3	39.5	29.0	23.3	49.7	38.8	28.7	18.1	7.6	43.3	28.4	33.8	37.7	22.9
Thallon CE	41.1	44.1	40.1	37.3	32.1	54.0	40.8	49.0	44.0	37.2	27.1	41.8	39.9	29.3	25.1	34.2	37.5	41.9	36.7	23.4
Thallon PC	32.8	31.3	46.9	45.4	33.0	35.2	39.8	33.7	39.8	40.7	28.3	39.6	22.2	26.2	21.5	25.5	31.1	29.9	41.2	34.7
Thallon WE	28.4	35.5	35.2	52.6	38.2	50.6	24.3	40.2	40.3	38.0	19.6	25.2	29.7	30.6	28.9	25.8	35.1	38.5	44.0	46.6
Thallon WC	18.9	26.0	18.7	36.6	36.4	26.8	28.3	24.2	29.6	38.6	23.2	24.8	32.1	53.1	39.0	13.7	20.9	30.8	32.2	45.8
McCreath PC	26.3	44.4	51.0	43.3	27.4	21.6	27.4	45.6	44.3	36.6	28.5	34.8	46.3	47.1	45.4	9.0	24.8	35.6	44.5	31.1
McCreath WE	13.8	25.4	27.1	42.4	21.0	17.0	18.6	24.5	24.5	28.4	25.6	14.6	28.0	50.3	41.4	8.1	14.7	26.4	29.0	38.2
McCreath WC	22.6	34.2	26.7	53.0	54.2	30.2	29.9	37.7	57.2	41.7	22.3	23.4	30.0	51.1	43.0	22.1	39.1	42.6	47.9	54.6

	Halford 1 CC	**Halford 1 CE**	**Halford 1 PC**	**Halford 1 WE**	**Halford 1 WC**	**Halford 2 CC**	**Halford 2 CE**	**Halford 2 PC**	**Halford 2 WE**	**Halford 2 WC**	**Postle CC**	**Postle CE**	**Postle PC**	**Postle WE**	**Postle WC**	**Thallon CC**	**Thallon CE**	**Thallon PC**	**Thallon WE**	**Thallon WC**	**McCreath PC**	**McCreath WE**	**McCreath WC**
Rice 1 CC																							
Rice 1 CE																							
Rice 1 PC																							
Rice 1 WE																							
Rice 1 WC																							
Rice 2 CC																							
Rice 2 CE																							
Rice 2 PC																							
Rice 2 WE																							
Rice 2 WC																							
Kowitz CC																							
Kowitz CE																							
Kowitz PC																							
Kowitz WE																							
Kowitz WC																							
Radke CC																							
Radke CE																							
Radke PC																							
Radke WE																							
Radke WC																							
Halford 1 CC																							
Halford 1 CE	37.3																						
Halford 1 PC	17.9	9.3																					
Halford 1 WE	8.3	21.5	30.6																				
Halford 1 WC	32.7	20.8	29.8	46.2																			
Halford 2 CC	59.6	25.2	32.0	7.0	26.5																		
Halford 2 CE	44.5	32.7	33.7	10.9	32.2	51.0																	
Halford 2 PC	36.0	20.5	34.1	28.8	27.8	50.3	47.2																
Halford 2 WE	25.3	26.8	38.8	51.9	44.6	26.5	34.9	48.2															
Halford 2 WC	22.8	23.6	22.6	31.2	32.7	26.1	21.4	29.3	48.5														
Postle CC	42.3	30.8	9.6	7.2	22.8	41.5	23.9	25.2	20.7	18.7													
Postle CE	34.6	8.1	47.3	13.7	31.9	48.9	34.5	34.7	20.1	16.3	37.7												
Postle PC	32.9	25.5	24.3	19.5	25.6	37.7	40.3	32.5	34.5	23.4	16.6	37.9											
Postle WE	22.8	20.3	32.6	48.1	42.4	22.7	27.5	25.0	40.4	31.7	16.0	29.9	38.5										
Postle WC	20.5	12.6	19.0	28.1	43.0	17.7	28.9	20.1	32.6	30.4	15.8	28.3	37.4	43.0									
Thallon CC	84.9	37.0	11.1	8.3	27.2	50.2	38.0	29.1	23.4	21.3	42.2	25.6	28.2	17.8	17.9								
Thallon CE	49.8	37.1	28.8	13.1	29.3	45.8	42.1	40.6	27.5	28.4	22.6	39.0	38.3	31.2	19.7	42.0							
Thallon PC	40.3	30.8	27.8	22.3	26.3	36.2	49.1	26.6	25.4	20.1	24.5	37.0	43.9	36.2	26.4	33.9	44.1						
Thallon WE	30.7	32.9	33.4	21.5	22.6	32.7	44.0	38.0	36.0	19.6	26.0	40.4	37.9	24.8	17.4	25.8	38.3	47.9					
Thallon WC	18.2	22.2	27.8	39.7	48.4	16.1	32.4	29.8	49.4	35.8	21.8	31.2	34.1	37.5	50.1	18.2	35.7	31.8	35.8				
McCreath PC	31.1	42.1	18.2	45.7	30.4	18.8	31.0	30.7	35.4	18.4	13.9	12.2	28.0	27.1	21.0	30.0	47.0	40.5	35.6	31.5			
McCreath WE	13.3	16.2	15.4	52.1	19.5	11.6	20.5	36.4	46.8	23.0	11.8	22.4	42.7	35.7	25.2	13.2	26.9	29.6	44.2	41.3	51.0		
McCreath WC	28.7	16.5	38.9	41.7	41.8	27.2	27.2	30.6	40.9	38.8	12.5	31.3	34.2	34.8	43.6	23.8	25.3	35.3	43.9	43.7	30.5	31.9	

Appendix D.1 Bray Curtis Similarity Matrix for 4th rt transformed ant morphospecies data at each location and treatment for directional pitfall trapping (Wedge = wood-edge, Wcrop = wood-crop, Hedge = linear-edge, Hcrop = linear-crop).

	LWedge1	LWedge2	LWedge3	LWcrop1	LWcrop2	LWcrop3	LHedge1	LHedge2	LHedge3	LHcrop1	LHcrop2	LHcrop3
LWedge1												
LWedge2	70.62											
LWedge3	65.98	63.09										
LWcrop1	64.80	78.10	68.90									
LWcrop2	53.79	73.58	53.17	75.03								
LWcrop3	50.09	53.14	48.73	61.88	47.48							
LHedge1	35.14	59.48	45.06	40.08	42.68	23.58						
LHedge2	55.29	58.46	63.36	49.60	40.91	39.63	52.49					
LHedge3	27.05	48.39	40.05	35.79	37.64	19.81	75.83	56.35				
LHcrop1	44.36	56.52	33.17	49.40	40.36	60.60	48.34	30.57	39.96			
LHcrop2	34.40	25.91	32.04	34.91	17.46	48.14	0.00	34.36	13.24	37.19		
LHcrop3	29.26	43.71	35.87	34.12	21.58	54.54	55.22	32.63	45.33	69.35	21.59	
MWedge1	68.45	52.28	47.15	38.13	41.89	26.76	37.47	50.23	51.86	19.29	10.45	18.84
MWedge2	50.45	34.59	51.05	41.82	37.93	42.28	11.14	42.51	19.93	22.57	54.57	27.41
MWedge3	54.65	44.15	62.31	51.12	38.84	42.87	22.04	33.23	19.85	29.56	30.67	31.19
MWcrop1	62.45	65.82	51.19	54.47	45.63	48.28	44.42	46.82	33.31	49.08	26.78	41.04
MWcrop2	47.11	38.14	45.91	43.77	27.42	68.85	0.00	37.44	0.00	36.79	58.14	28.06
MWcrop3	47.45	41.98	39.81	64.26	32.74	70.30	0.00	22.88	0.00	42.99	48.14	23.94
MHedge1	49.22	58.29	63.10	47.29	40.16	28.84	46.23	48.28	36.93	30.14	13.11	31.93
MHedge2	63.82	65.61	51.44	53.13	56.46	44.48	37.75	41.92	28.85	48.17	38.77	34.11
MHedge3	67.29	59.13	40.14	44.65	49.10	31.64	38.95	34.13	29.66	37.47	16.20	19.68
MHcrop1	43.69	46.63	29.63	47.41	39.28	77.91	24.95	28.98	20.41	67.10	46.10	57.93
MHcrop2	29.89	44.29	32.03	50.25	36.74	58.76	20.35	25.97	16.74	48.85	52.33	30.29
MHcrop3	44.96	43.35	31.78	55.98	35.99	76.81	19.12	24.95	15.90	65.02	50.90	51.61
QWedge1	68.35	65.59	59.17	65.23	59.05	50.24	39.42	41.51	29.98	51.40	32.76	35.82
QWedge2	55.58	52.50	56.70	62.01	45.26	46.78	28.30	30.02	25.45	46.33	33.49	31.58
QWedge3	64.14	60.93	56.18	71.17	58.32	69.34	20.74	34.50	18.19	53.65	35.52	40.94
QWcrop1	38.74	34.81	32.26	49.89	40.12	47.92	9.35	22.25	8.51	33.89	31.34	22.55
QWcrop2	52.60	51.27	45.53	61.41	57.07	73.28	21.27	35.13	18.59	54.87	38.23	42.13
QWcrop3	49.84	46.08	50.55	59.59	42.01	54.13	14.86	20.29	13.12	46.53	37.32	33.91
QHedge1	51.19	51.96	45.87	60.26	47.40	58.09	38.99	38.17	49.30	55.56	42.28	40.03
QHedge2	47.65	55.55	49.81	69.31	47.82	55.77	44.49	42.27	39.29	65.68	39.24	38.26
QHedge3	46.38	64.65	43.03	61.16	50.39	55.82	58.89	40.40	51.25	88.31	34.60	63.23
QHcrop1	22.46	34.60	45.06	46.22	41.46	49.39	39.11	38.10	33.31	34.95	28.75	46.70
QHcrop2	55.34	73.63	52.02	67.78	51.12	56.29	75.72	55.03	59.64	71.59	36.56	57.50
QHcrop3	47.29	56.22	47.18	67.39	63.08	64.25	43.32	41.13	37.39	63.81	40.76	47.06
CWedge1	64.95	64.67	51.18	67.51	64.32	69.05	39.04	48.38	33.89	59.00	32.74	41.67
CWedge2	57.51	61.01	46.37	55.56	52.62	58.53	35.78	48.47	27.49	46.99	33.59	32.12
CWedge3	46.06	47.31	38.13	49.34	69.78	58.07	33.12	33.97	28.35	43.40	17.11	28.13
CWcrop1	63.40	60.57	54.59	72.00	66.89	56.88	28.05	46.92	35.05	48.83	39.65	33.64
CWcrop2	59.12	56.16	52.26	56.42	59.42	39.91	32.88	41.79	37.02	45.01	34.90	29.77
CWcrop3	56.98	56.29	44.53	63.69	68.96	55.61	27.57	29.90	24.00	60.18	34.48	43.64
CHedge1	42.23	44.06	27.96	44.50	46.86	45.31	40.03	27.44	34.08	52.10	22.24	29.39
CHedge2	39.69	37.94	21.63	47.46	42.86	44.69	30.84	21.23	26.31	51.49	21.98	28.93
CHedge3	60.09	59.49	44.17	65.41	62.06	45.93	43.65	29.80	37.09	52.70	22.50	29.84
CHcrop1	37.84	35.66	16.11	46.85	41.24	29.29	0.00	0.00	0.00	30.66	27.66	0.00
CHcrop2	61.69	60.03	49.65	55.28	51.65	39.28	33.45	38.19	25.88	44.14	36.40	29.80
CHcrop3	60.29	59.79	38.12	55.87	40.34	50.98	45.23	45.86	33.85	55.97	31.04	38.96

	MWedge1	MWedge2	MWedge3	MWcrop1	MWcrop2	MWcrop3	MHedge1	MHedge2	MHedge3	MHcrop1	MHcrop2	MHcrop3
LWedge1												
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LHcrop3												
MWedge1												
MWedge2	44.64											
MWedge3	46.82	59.89										
MWcrop1	47.33	31.71	39.86									
MWcrop2	12.05	40.87	29.02	31.70								
MWcrop3	11.08	29.53	30.91	28.68	67.59							
MHedge1	52.06	27.99	54.06	56.05	15.00	13.85						
MHedge2	54.40	44.88	49.22	68.40	26.58	30.73	66.93					
MHedge3	65.88	40.59	42.92	58.63	12.56	18.72	58.77	72.97				
MHcrop1	15.17	25.34	25.72	49.48	48.26	51.22	26.34	47.39	35.78			
MHcrop2	0.00	17.59	16.33	33.20	56.26	59.36	27.38	34.76	20.46	65.12		
MHcrop3	12.04	29.86	27.81	46.16	52.41	67.67	26.39	45.57	32.97	84.28	69.37	
QWedge1	45.90	40.35	47.99	69.44	30.71	48.22	60.29	81.20	62.27	49.79	39.47	58.63
QWedge2	34.32	32.40	50.52	54.29	27.23	42.32	51.20	58.71	49.02	43.83	34.83	51.97
QWedge3	39.47	43.14	50.59	53.59	49.32	62.15	41.59	57.34	47.40	57.01	45.07	65.40
QWcrop1	14.52	35.69	30.30	33.85	35.77	54.55	16.26	34.69	19.55	36.35	30.52	45.74
QWcrop2	24.58	43.53	40.04	41.53	53.49	64.30	26.42	51.30	31.61	58.69	46.37	64.04
QWcrop3	25.42	35.23	46.14	47.18	32.72	52.14	43.33	53.06	41.88	53.25	42.16	62.44
QHedge1	41.84	39.28	46.74	44.69	34.14	42.42	38.40	44.42	47.39	55.73	58.88	58.27
QHedge2	23.12	26.04	34.16	49.06	32.71	53.37	42.23	48.26	38.99	53.24	56.30	62.43
QHedge3	19.63	21.38	29.37	47.64	33.73	44.18	39.30	46.97	36.82	61.09	60.76	64.51
QHcrop1	12.99	42.73	31.79	30.65	25.91	27.19	36.41	37.17	13.49	43.80	46.91	45.69
QHcrop2	31.21	23.64	32.08	59.12	34.00	44.69	50.45	57.06	47.77	55.47	58.61	62.35
QHcrop3	19.44	35.60	32.52	48.83	39.78	53.49	41.17	58.27	37.39	65.68	69.12	75.92
CWedge1	37.05	39.59	40.15	54.57	50.20	61.84	35.39	62.98	44.79	62.52	42.46	64.74
CWedge2	47.22	38.97	38.01	54.59	39.14	46.17	51.57	72.59	57.60	44.58	35.42	47.87
CWedge3	32.93	31.81	33.87	38.68	38.53	39.09	21.20	45.93	36.25	45.55	22.15	38.51
CWcrop1	45.80	52.23	45.21	53.58	42.01	60.15	38.61	60.70	43.93	46.73	35.87	53.08
CWcrop2	45.87	41.53	42.69	56.75	22.87	36.23	50.82	69.03	52.78	44.47	30.42	47.03
CWcrop3	30.91	42.65	39.93	60.63	33.60	45.61	40.68	68.11	48.44	60.83	44.39	66.02
CHedge1	26.58	10.87	21.53	70.04	18.34	27.21	25.28	44.00	46.06	53.76	30.44	49.15
CHedge2	20.57	10.77	19.18	49.75	18.07	42.25	19.57	37.79	39.64	52.90	29.97	56.25
CHedge3	41.97	23.99	33.91	62.62	18.60	38.34	39.89	59.65	62.21	54.61	30.91	57.91
CHcrop1	15.18	15.08	13.98	33.99	24.17	51.03	14.32	35.45	37.56	40.65	40.91	51.07
CHcrop2	42.59	42.43	47.76	61.74	23.36	37.97	54.55	81.46	56.93	41.34	30.40	45.90
CHcrop3	35.05	19.01	27.97	73.50	29.54	48.63	42.67	59.93	52.27	58.39	39.72	60.75

	QWedge1	QWedge2	QWedge3	QWcrop1	QWcrop2	QWcrop3	QHedge1	QHedge2	QHedge3	QHcrop1	QHcrop2	QHcrop3
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MHcrop3												
QWedge1												
QWedge2	72.73											
QWedge3	69.28	63.04										
QWcrop1	46.36	43.78	56.03									
QWcrop2	58.85	54.10	64.05	65.45								
QWcrop3	70.41	75.57	68.84	50.33	48.10							
QHedge1	49.59	48.75	49.05	37.13	51.68	46.19						
QHedge2	63.38	58.73	54.85	43.55	52.04	53.83	66.26					
QHedge3	53.24	48.25	53.97	35.02	53.05	47.25	64.92	77.57				
QHcrop1	42.28	31.76	33.48	36.00	49.45	35.48	52.03	61.78	45.99			
QHcrop2	65.65	54.42	52.16	35.79	53.61	47.47	64.70	71.47	81.35	49.56		
QHcrop3	70.07	53.57	61.04	48.84	71.70	54.55	70.53	73.87	76.52	67.66	73.87	
CWedge1	71.94	55.34	66.37	53.95	77.48	47.97	52.45	62.99	60.68	44.25	63.92	77.25
CWedge2	65.57	47.96	51.27	55.81	64.48	50.37	49.04	53.07	45.90	42.29	58.97	59.63
CWedge3	47.85	32.95	46.93	44.84	67.30	28.12	39.14	38.74	42.14	33.50	40.06	57.20
CWcrop1	73.41	57.18	67.73	61.53	69.73	54.42	45.72	58.71	50.72	38.11	53.17	64.79
CWcrop2	81.41	65.70	59.99	41.70	51.25	61.66	41.26	52.01	47.02	33.22	53.49	59.15
CWcrop3	76.34	59.94	68.57	48.38	66.64	61.15	53.25	56.73	61.37	45.83	56.48	77.71
CHedge1	47.23	42.34	41.78	33.70	42.79	34.89	45.79	49.99	50.15	18.85	51.74	51.75
CHedge2	52.15	43.66	49.73	39.77	44.16	44.95	44.06	55.31	52.53	18.61	47.72	57.71
CHedge3	71.22	63.78	66.21	30.80	45.09	57.89	46.24	60.12	55.07	19.09	57.82	59.05
CHcrop1	49.66	42.47	54.67	25.84	29.04	53.11	24.63	35.91	33.19	0.00	29.15	38.20
CHcrop2	85.60	69.75	58.39	44.23	48.45	67.35	40.67	53.07	46.08	33.03	54.70	57.47
CHcrop3	73.34	54.96	53.98	43.03	49.27	49.60	50.09	65.56	57.76	28.71	68.03	61.20

	CWedge1	CWedge2	CWedge3	CWcrop1	CWcrop2	CWcrop3	CHedge1	CHedge2	CHedge3	CHcrop1	CHcrop2	CHcrop3
LWedge1												
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QHedge3												
QHcrop1												
QHcrop2												
QHcrop3												
CWedge1												
CWedge2	70.71											
CWedge3	73.56	55.77										
CWcrop1	78.21	61.79	65.36									
CWcrop2	65.87	54.03	55.41	76.18								
CWcrop3	73.59	56.68	67.49	76.41	77.31							
CHedge1	57.12	42.97	50.18	44.75	42.88	49.55						
CHedge2	56.14	37.09	46.71	54.90	44.76	53.90	74.72					
CHedge3	67.48	45.28	50.78	64.23	64.59	72.33	66.08	67.22				
CHcrop1	37.20	20.37	22.80	44.21	43.74	54.61	33.72	48.99	71.89			
CHcrop2	62.16	57.89	40.93	67.85	72.29	66.11	40.24	51.20	60.60	41.23		
CHcrop3	69.41	58.31	41.76	63.83	59.68	58.54	67.12	80.08	65.75	39.39	68.77	