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Management Implications for Invertebrate Assemblages in the Midwest American Agricultural Landscape

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Chapter 1

General Introduction

Introduction

Global population is growing ~ 1.1% per annum with projected populations reaching 9.6-12.3 billion by 2100 (Gerland *et al.*, 2014). Extreme poverty has declined globally by more than half falling from 1.9 billion in 1990 to 836 million in 2000 (Millennium Assessment, 2005). Increased agricultural production of food, fuel and fiber will be necessary to meet the needs of the growing population. Agricultural production of food, fuel and fiber involves socio-economic issues as well as environmental issues (Garnett, 2014). Controversy swirls around the use of food to produce fuel (Davis *et al.*, 2012), increase of production through genetic modification of seeds (Wisniewski *et al.*, 2002), pesticide use (Fernandez-Cornejo *et al.*, 1998), high fructose corn syrup food additives (Rippe and Angelopoulos, 2013), dietary preferences (Hansen and Gale, 2014), malnourishment and its counterpart obesity (Horvath *et al.*, 2014), and food access and security (Godfray and Garnett, 2016).

Apart from these issues around agriculture itself, goals to increase agricultural production are also often in competition with other societal goals. Water used to increase food production leads to reduced availability for other purposes, including human consumption (Haddeland *et al.*, 2014) and clearing forested land for use in growing agricultural products decreases biodiversity and carbon sequestration (Carlson *et al.*, 2012). The difficult and critically important challenge is to balance the multiple needs of society in the most sustainable way possible.

This thesis concentrates on how common vegetation management impacts invertebrate biodiversity, as a critical resource, in an area which is used for intensive agricultural production. Biodiversity conservation is the basis for preserving existing ecosystems and ecosystem services (Griggs *et al.*, 2013). The Earth Summit held in Rio de Janeiro, the United Nations developed a treaty called the Convention on Biological Diversity (CDB) that sets goals for biodiversity conservation on both national and global scales. The goals of the CDB are the conservation of biological diversity, sustainable use of components of biological diversity, and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources (Bell, 1992). In 2010 the international community set targets for biodiversity to be achieved within a decade. A mid-term analysis of progress toward these targets has shown little progress and some deterioration (Tittensor *et al.*, 2014).

This shows that increasing the efforts to conserve biodiversity is needed, including in agricultural areas. The aim of this thesis is to look at vegetation management within the agricultural landscape and determine which practices are most beneficial to invertebrate assemblages and the associated food web. The debate on how best to achieve biodiversity goals in relation to the need to increase agricultural production concentrates presently around two contrasting strategies, “land sparing” and “land sharing” (Phalan *et al.*, 2011; Grau *et al.*, 2013). My study is based on the question whether biodiversity conservation measures from the sharing strategy, which is traditionally applied in the countries like the Netherlands and United Kingdom in Europe, would be applicable in the Midwest of the USA, which follows traditionally a sparing strategy. The strategies find their theoretical bases in different interpretations of the ecological theories that describe the relationship between local populations or communities and the surrounding landscapes. Before I will discuss the research of this thesis, I will explore these ecological theories.

Ecological theory

Early ecological studies operated on the premise that species were distributed wherever there was appropriate habitat. At first, the abiotic characteristics of the habitat were thought to be the most important for the presence of species, later the biotic characteristics, i.e., species interactions, were added to the abiotic characteristics. These abiotic and biotic factors were the base of early niche theory for individual species (Soberón, 2007). Assembly theory uses the idea of species sorting to explain how abiotic and biotic factors influence certain species out of all possible species in the species pool to form a community.

The theory of island biogeography challenged this viewpoint (MacArthur and Wilson, 1967). They proposed the idea that species go extinct on a regular basis, leaving the habitat vacant until the next colonization event, but that extinction rate is highest on small islands and that colonization rate is smallest on islands far from the mainland. The theory is now applied to any patch of habitat, e.g., a mountain top, lake, park or conservation area, that is surrounded by a completely different type of habitat. For practical biodiversity conservation, this theory is usually interpreted as that conservation areas should be as large as possible and well connected to other areas with the same habitat in order to keep or get a high species richness within the conservation area.

In an expansion of this theory, the concept of metapopulations views populations of a single species in balance between colonization and extinction within a group of habitat patches (Hanski, 1998). A metapopulation of a species will have a high survival probability when the group of habitat patches is large and well connected. This theoretical paradigm further embraces the concept of source-sink dynamics, which supports the idea that a species can and does occupy suitable habitat as well as maintain stable populations in a large enough set of habitat patches that combines suitable and unsuitable patches (Pulliam, 1988).

Metacommunity theory expands the idea of metapopulations to a set of locally interacting species within a set of connected habitat patches and relate these to environment and regional processes (Logue *et al.*, 2011). Hubbell (2001), on the other hand, presumes in his neutral theory that both extinction and colonization may be largely stochastic processes so that the patterns of species distribution and abundance in sets of habitat patches that can actually largely be explained without taking the ecological traits of species or habitat characteristics into consideration, in other words without considering niches.

Of course, it was realized that habitat patches were seldom surrounded by 'empty' areas like seas. The study of the relationship between a local community and its surrounding landscape has led to a large body of literature and added further mechanisms, such as mass effects, spill over, dilution, etc., to ecological theory that may or may not be applicable in a certain specific situation. Tscharntke *et al.* (2012) has summarized these mechanisms into six hypotheses on the effect of surrounding landscape on local communities and populations and two hypotheses on the efficiency of biodiversity conservation measures in agricultural landscapes.

Vellend (2010) has tried to bring all theory discussed above together into a simple scheme of four key processes that determine a community at a certain location at a certain time: selection, drift, speciation and dispersal. Selection is the process that defines the relative abundance of species in a community based on abiotic and biotic factors. Drift is the stochastic process of species abundance fluctuations that can lead to local extinction. Speciation is the development of new species in an area and is probably mainly relevant at high levels of spatial and temporal scale. And dispersal is the process of colonization of species. In selection, the assembly theory and in drift, speciation and dispersal the neutral theory can be recognized.

Land sharing and sparing in agricultural areas. As said before, at the moment two main strategies for conserving biodiversity in relationship to agriculture are under discussion: land sharing vs land sparing. These strategies are discussed in view of the amount of biodiversity that can be conserved at the level of nations, regions or even at the global level. Traditional EU biodiversity conservation in agricultural areas follows a sharing strategy, while that in the USA follows a sparing strategy. Because this thesis partly focusses on the application of sharing techniques in the USA, it is worthwhile to explore both strategies a little further.

The discussion of balancing agriculture with nature has its roots in ecological theory. The problem of harmonizing agriculture and nature has long been a topic of research (i.e. Waggoner, 1995; Huguet, 1978). Green (2005) coined the terms 'land sharing' and 'land sparing' to express these opposing philosophies. Land sparing divides the land into homogeneous areas with distinctly different goals (Ausubel *et al.*, 2013). Agricultural land optimizes yield through the use of fertilizers, pesticides, and irrigation in order to use as small areas for agriculture as possible. Biological reserves target conservation of specific ecosystems and biodiversity. This strategy is associated with islands of nature being separate and protected from human disturbance (Higgs, 1981). Island theory is thought to be applicable here and the main goal of conservation is to establish large protected areas, connected by corridors if possible.

Land sharing integrates wildlife friendly farming techniques into a heterogeneous landscape (Fischer *et al.*, 2008; Pywell *et al.*, 2012). Proponents of this strategy emphasize interactions between farmed and unfarmed habitats. Larger farming areas may be required since farming is less intense resulting in lower agricultural production than would be possible if agriculture were optimized (Green *et al.*, 2005). Compensation may be given for the loss of yield that accompanies wildlife friendly farming techniques (Wilson and Hart, 2000). The eight hypotheses of Tscharntke *et al.* (2012) are applicable to this strategy.

Land sharing and land sparing strategies have been presented as dichotomous choices (Green *et al.*, 2005). Green (2005) presented yield density models to predict extinction risk of both individual and multiple avian species. These models make several assumptions regarding population density in non-farmed areas, impacts of chemical applications, water usage, and impacts of habitat fragmentation and dispersal corridors. This must take into account that reducing waste, increasing efficiency, and altering the food delivery system may have unintended consequences, as suggested by the Jevons paradox. The Jevons paradox, developed in 1866, was coined to explain the phenomenon of an action to conserve natural resources that allows more of the resource to be used and subsequently may harm that resource in the end (Polimeni, 2012). The land sparing model also assumes that as yields increase land will become freed for nature restoration. Freeing land from agricultural production with land sparing also provides land for other uses such as urbanization.

Law and Wilson (2015) provide analysis of land sharing and sparing philosophies and resulting policy decisions within an ecological context. Programs such as conservation set-asides, organic farming and environmental certification have a different impact in pristine environments than in areas degraded by agricultural practices (Law and Wilson, 2015; Cormont *et al.*, 2016). Law and Wilson (2015) examine two land sharing and three land sparing strategies under both pristine and agricultural baseline conditions. Their model shows that the initial proportion of the landscape devoted to agriculture as the most important parameter in predicting biodiversity changes.

Proposals have been made to reconcile these diametrically opposing strategies to address the challenges related to food security and access, ecosystem services and land scarcity (Fischer *et al.*, 2014; Grau *et al.*, 2013). Fischer et al. (2008) propose strategies for biodiversity conservation which draws on the strengths of both land sparing and land sharing philosophies. Phalan *et al.* (2011) suggests a more sophisticated land sparing philosophy that utilizes indigenous reserves, habitat banking, local knowledge and avoidance of agrochemicals and mechanization. Hayashi (2011) suggests the importance of management intensity as an important consideration when examining these opposing strategies. Application of various proposals requires consideration of social, political and technical issues (Phalan *et al.*, 2011). While specific proposals addressing biodiversity in Ghana are not directly applicable to Illinois, the concepts can be applied globally, e.g. decreasing management intensity through reduced tillage.

I have elected to focus on those management practices that probably do not affect agricultural yield or management within agricultural fields. Yield was not measured in any of our studies. I was mostly interested in enhancing invertebrate biodiversity in the existing landscape, not influencing global or regional policy (Grau *et al.*, 2013). I believe it is important to acknowledge that high yielding agricultural areas (USDA, 2016) be maintained and valued for what they are as well as enhanced where they are lacking.

Agriculture

Overview of agricultural history in Europe and the USA. As said before, traditional EU biodiversity conservation in agricultural areas follows a sharing strategy, while that in the USA follows a sparing strategy. This is undoubtedly related to the history of agriculture in both regions. European and United States (US) agriculture is interconnected since the early 20th century. World War I disrupted European agriculture and the US responded by increasing production. After the war ended, demand dropped and crop prices fell dramatically in the USA (Sumner, 2007). American farmers struggled to make payments on the land and machinery they had purchased to meet production that was no longer needed. The agricultural system was already struggling when the depression hit in 1929 (Sumner, 2007). Prices fell further to a third of what they had been a decade earlier. In a reaction, the first farm bill was launched to raise commodity prices by paying farmers to limit production (Bowers *et al.*,1984).

In 1932 the Soil Conservation Service was formed to promote conservation practices and allow the land to recover after the severe erosion known as “the dust bowl years”. Practices included tree and grass plantings to anchor the soil, terraces and contour plowing, and crop rotation which included allowing the land to remain fallow during the rotation cycle (Bowers *et al.*, 1984). Crop prices again rose during World War II creating again an overproduction bubble that burst with the end of the war (Sumner, 2007). Since that time there have been opposing pressures on famers with the need from the agri-industry encouraging hedge-row to hedge-row planting and the societal need to conserve the land for future production. New technologies such as the combine harvester improved farming efficiencies (Dimitri, 2005). Current practices focus on reducing soil erosion and inputs to waterways (Reimer and Prokopy, 2014). Enhancing habitat for pollinators is a relatively new practice with the specific goals of reducing loss of honey bee colonies, providing habitat for Monarch butterflies, and the general goal of creating and restoring habitat (Obama, 2014).

As a result of the privations of WWII, food security in Europe became a high priority. In 1957, a group of 6 countries signed the treaty of Rome which was the precursor to the European Union (EU). In 1962 the Common Agricultural Policy (CAP) went into effect which had the result of assuring food security for Europe (European Commission 2012). Agri-Environment Schemes (AES) began in the EU in 1985 with the goal of compensating farmers for loss of yield and subsequent income loss that resulted from less intensive agricultural practices (Kleijn *et al.*, 2006). More developed countries in the north and west are the drivers of most AES which are now the main tool for biodiversity conservation in agricultural areas (Kleijn *et al.*, 2006). Currently all EU members are required to participate but may develop their own AES practices (Kleijn *et al.*, 2006). In addition to conserving high-value natural areas, AES provide subsidies for the protection of traditional farming as current farming practices replace traditional farming methods that are no longer economically practical (Kleijn *et al.*, 2006). Countries in the EU have the additional mission to preserve the cultural landscape and heritage (Antrop, 2005).

Programs in the EU and US have many goals in common. Both have subsidies for reducing water pollution and soil erosion. Both programs offer subsidies to stimulate organic farming and to address the decline in pollinators. But also, large differences exist. Government agriculture programs in the US remain mostly focused on conserving the soil and reducing input into the waterways, while EU programs now also offer subsidies to address species loss in the agricultural landscape. In the US, the protection of threatened species and habitats are often under the aegis of other agencies (Endangered Species Board 2011; Innes *et al.*, 1998) and private organizations (Dobson *et al.*, 1997; Kareiva *et al.*, 2014).

At the present time, biodiversity conservation in agricultural areas in the US is typically a sparing strategy, while that in western Europe is a sharing strategy (Batáry *et al.*, 2011; Boitani and Sutherland, 2015). In the Midwest United States, management is mostly focused on patches of habitat with buffer areas of protection. In contrast, practices in Europe are often focused on providing habitat for certain species or taxonomic groups: birds (Kleijn and Sutherland, 2003; Kragten *et al.*, 2008), mammals (Boatman, 1999), and insects (Desender and Turin, 1989; Noordijk *et al.*, 2009). Practices in the EU often focus on the edges, verges and hedgerows of agricultural fields and roadways creating a matrix of available habitat within the agricultural system.

Government incentive programs in the US generally have not been established to benefit invertebrates, but have probably enhanced invertebrate populations as a side-effect of practices with other end-goals. A recent addition of practices to enhance pollinators has uncertain funding (USDA FY 2015 Budget Summary and Annual Performance Plan, U.S. Department of Agriculture). Habitat restoration projects may require special effort to host specific native vegetation for highly specialized invertebrates or translocation of insect species where no local populations currently exist (Fischer and Lindenmayer, 2000).

Differences in conservation strategies in the EU and the US are somewhat understandable because of the differing lengths of time the landscape has been farmed. Farming began in the middle-east and moved gradually through Europe. First People (aboriginal people) farmed in close proximity to settlements in North America (Fritz, 1990). Indigenous farming practices were rudimentary and in relatively small areas of the landscape (Fritz, 1990). In Europe, much of the land has been intensively farmed since Roman times and in the US since European settlement, fewer than 200 years ago. Farmers came to the US mostly from Europe and brought European practices with them (Hewes and Jung, 1981). However, the European practices came not from a united Europe but from individual countries with vastly different practices. In the US, these practices were adapted to a landscape that differed in the amount of available space and access to support from developed communities. Farms in the Midwest were often begun with homesteads provided by the government for little or no cost and were isolated from population centers (Bell, 2012).

As the Midwest becomes more and more like Western Europe with few large areas left unaffected by agriculture, agri-systems may benefit from techniques developed for a more managed landscape. There is some support for moving to a sharing approach in the US (Rosenzweig, 2003). Adoption of a mix of land sharing and land sparing approaches may increase the odds of success (Fischer 2014; Grau *et al.*, 2013). This mix includes habitat restoration, expansion of remnant vegetation patches and restoration of both vegetative structure and function of waterways and riparian zones (Tscharntke *et al.*, 2005). Vegetation corridors are generally recognized as a means of linking isolated patches (Cook, 2002). Making optimal use of linking corridors through agricultural programs is an underutilized resource in the United States.

Understanding the published research. A survey of the literature provides much information about invertebrate assemblages in varied habitats across the globe. However, translating the results and conclusions of these studies requires some caution. Terminology, vocabulary and native language present opportunities for misunderstanding. Countries in the EU each have their own native language and generally have little difficulty with “scientific” English as the language for peer reviewed papers. But even English presents difficulties. Instructions to authors generally indicate that either “British” English or “American” English may be used, but not mixed within the same paper. Relevant to this dissertation, is a discussion of agricultural terminology which often differs in the US and EU. Terms are so well understood that they are not always defined. But they may have different definitions in the US and EU. For example, “hedgerow” creates different mental pictures in the Netherlands, Great Britain, France, and in the Midwest, United States. The misunderstanding of terminology may result in a lack of understanding of study results. A glossary of easily misunderstood terms is provided for the purposes of this dissertation.

Farming itself is different in the US and EU. The EU has a wide diversity of crop types including beets (*Beta vulgaris*), spelt (*Triticum spelta*), barley *(Hordeum vulgare*) and rye (*Secale cereale*). In the Midwest US, most crops are corn (*Zea mays*) and soybeans (*Glycine max*) with occasional winter wheat (*T. aestivum*). There is more emphasis on natural or organic crops in the EU while most crops in the Midwest are genetically modified to withstand chemical input of herbicides and pesticides (Wier and Calverley, 2002; Gaskell *et al*., 1999). Reduced tillage was promoted as a means of reducing soil erosion, soil compaction and chemical run-off, but is used to varying degrees in the US. Much of the landscape in the EU is kept open by farming and farm animals. In the US, management tools for grasslands include grazing and mowing (Jonas *et al*., 2002; Knapp *et al*., 1999). Additionally, fire is a frequently used tool for vegetation management in the US. Grazing by indigenous mammals is preferred over domestic livestock to preserve the prairie landscape (Knapp *et al*., 1999). Europe uses commercial production of food as an agricultural practice in the conservation of areas of high biodiversity (Boitani and Sutherland, 2015). Similarly, some forests in the US are managed by the department of agriculture with timber production a primary goal.

Glossary

Beetle bank: a strip of low semi-natural vegetation that runs in the middle of agricultural land that has been especially installed to promote predators in the field

Buffer strip: land maintained in permanent vegetation that helps to control air, soil, and water quality, along with other environmental problems, dealing primarily on land that is used in agriculture

Dike: a long wall or embankment to prevent flooding from the sea; a ditch or a watercourse

Drainage ditch: a ditch for removal of excess water

Field margin: a row of semi-natural vegetation alongside agricultural land

GM: crops with modified DNA to improve resistance to pests and diseases, environmental conditions, spoilage, chemical treatments or to improve the nutrient profile

Hay field: a field where grass, alfalfa, etc., are grown for making into hay

Headland: a row at ends of an agricultural field for turning equipment

Hedge-row: a row of bushes or small trees at the edge of an agricultural field

Lea: a tract of open ground, especially grassland; meadow

Meadow: a grassland, either in its natural state or used as pasture or for growing hay

Organic: a method of crop and livestock production that does not to use pesticides, fertilizers, genetically modified organisms, antibiotics and growth hormones. A GM crop can be organic in the US

Pasture: land covered with grass and other low plants suitable for grazing animals, especially cattle or sheep

Shrublands: naturally occurring or manmade plant community characterized by vegetation dominated by shrubs, often also including grasses, herbs, and geophytes.

Turn row: a row at the ends of an agricultural field for turning equipment

Verge: a row of semi-natural vegetation alongside a road, railway or agricultural land

Water way: broad, shallow channels designed to move surface water across farmland without causing soil erosion

Wood bank: a row of large trees at the edge of an agricultural field

Wood lot: a segment of a woodland or forest capable of small-scale production of forest products such as wood fuel, sap for maple syrup, as well as recreational uses like bird watching, bushwalking, and wildflower appreciation

Agricultural History of Illinois. The topography of the state was strongly influenced by the series of four Pleistocene glacial episodes. The last of the glaciers retreated about 13,000 years ago. As each of the great ice sheets advanced and retreated, it brought and left behind deposits of clay, sand, gravel, and boulders known as glacial till. Wind picked up the fine debris particles called loess and deposited it across the Illinois landscape. This material is rich in minerals, has a uniform consistency, and retains moisture (King, 1981). These qualities make excellent soil for growing crops.

Before the arrival of European settlers, what is now Illinois was covered with a mixture of grasslands and deciduous forest (King, 1981). Most of the central region was prairie, interspersed with wetlands and forested riparian areas. Fire (both natural and induced) was a major vegetation control factor, keeping the forests from encroaching on the grasslands. Indigenous people occupied the land from about 12,000 years ago. Cahokia (an area in southwestern Illinois) was the largest city in North America one thousand years before European contact (Fritz, 1990). Archeological sites document occupation in other areas of the state as well. There is evidence that fire was a tool often used by Native American people for a variety of reasons (Stewart, 1951; McClain and Elzinga, 1994).

Vegetative landscape was described by early explorers i.e. as Father Jacques Marquette and Louis Joliet in the 1670's (Shae, 1853). Illinois was controlled in succession by the French, British, and became a United States possession in 1778 (Wikipedia). In 1803, President Thomas Jefferson commissioned Meriwether Lewis and William Clark to document the plants, animals and geography of the region which included Illinois (Cutright, 2003). Illinois became a state in 1888. In the early part of the nineteenth century the Government Land Office (GLO) carried out the Public Land Surveys establishing the grid coordinate system for Township, Range, and Section lines. Vegetation composition was recorded in the surveys according to standard methodology (Hutchison, 1988). This has become the base line for understanding 200 years of change since European settlement. The Illinois invertebrate fauna has doubtless also been changed by human activity, although we lack the records to quantify the changes in invertebrate populations since the advent of the settlers. The vast expanses of land that have been given over to agriculture would seem to provide new kinds of ecosystems for certain insect species to exploit.

Settlers coming from Europe brought their farm practices to the "new world" (Hewes and Jung, 1981). Fences were used to exclude cattle from crops rather than enclose the crop fields. As settlers moved west, fencing large areas became less and less practical. Trees used for fencing were scarce in the prairie and used for construction of homes and barns when available. Digging ditches to mark field boundaries was labor intensive and the glacial loess did not have enough rocks to mark field edges. The development of barbed wire marked a turning point in Illinois agriculture (Hornbeck, 2010). Surveys were conducted regularly and sent to state agricultural departments to document type and amount of fencing (Hewes and Jung, 1981).

Field boundaries of agricultural fields recently cleared initially retain the character of the area that covered the land before clearing (Watts, 1975). Soil type and seed bank often remain in place for some time after clearing. Eventually the impacts of soil erosion and chemical amendments alter the character of the edge. In North America, fence rows may contain large canopy trees and dense shrubs and are generally left unmanaged (Fritz and Merriam, 1994). Seeds transported by the wind as well as those carried by birds and mammals repopulate the area with a new assemblage of plants (Poggio *et al.*, 2010). Fences are ideal perching points for birds and the edge provides a protective travel corridor for both small and large mammals (Gehring and Swihart, 2003). Many insects are dependent on specific plants for their existence. As the edges change in character, the invertebrates change as well.

One hundred years ago, farms were generally small and produced much of their own food (Shammas, 1982). Each farm would have chickens, a cow or two, maybe some pigs, and probably horses used as draft animals and for transportation. Livestock grazed in pastures; oats and grasses were planted to supplement the needs of the livestock. As time passed, agriculture has become more efficient (increasing yields) as well as utilizing more of the landscape (Table 1). While the area devoted to arable crops increased, other landcover types also changed. Tractors replaced draft animals; cows, chickens and pigs were moved to "confined feeding operations" (Burkholder *et al.*, 2007); wetlands were drained (Logan *et al.*, 1980); and city dwellers flocked to "McMansions" in the rural countryside (Nasar and Stamps, 2009). Forests increased and shrublands decreased (Table 2).

Farm-level intensification includes shortened crop rotation and increased chemical usage. On the landscape scale, fields have been consolidated and have increased in size resulting in a simplified landscape with the loss of non-crop field margins (Söderström and Pärt, 2000; Tscharntke *et al.*, 2005). At the level of the field, the use of chemicals, improved harvesting technologies, and increased tillage frequency has resulted in fewer invertebrates (Wilson and Hart, 2000). Crops are less diverse and planted in greater densities with uniform field margins (Table 1).

Table 1. Summary of land cover (in acres) number of cattle, human population and % change. Agricultural statistics are from the U.S. Department of Agriculture, National Agricultural Statistics Service: human population statistics are from the U.S. Census Bureau.

Central Illinois	1950's	2000's	%Change
Corn	1,473,000	2,512,000	+71
Soybeans	1,141,000	1,608,000	+41
Wheat	275,000	61,000	- 87
Oats	482,000	0	-100
Hay	338,000	46,000	-86
CRP	n/a	114,000	n/a
Forest	301,000	367,000	+22
Buildings	n/a	205,000	n/a
Cattle	556,000	132,000	-76
People	624,000	724,000	+16

Tillage practices vary greatly in the Midwest US as well as elsewhere in the world. Conventional tillage, reduced tillage, and conservation tillage are measures of crop residue left on the field surface. Impact on the soils is largely dependent on the type of machinery used, the frequency of equipment passage and chemical applications. The impact of tillage practices on invertebrates has been studied and is outside the scope of this dissertation (Stinner and House, 1990; Mirsky *et al.*, 2012; van der Laat *et al.*, 2015).

Table 2. Percent cover of crops, grasslands, forests, developed, shrublands and wetlands; number of land cover blocks, and average size of block (adapted from Taylor *et al.* 2009).

	% Cover		Number of Fields		Average Size (ha)	
Land Cover	1950's	2000's	1950's	2000's	1950's	2000's
Crop	62	59.6	313.3	165.9	7.4	13.8
Grassland	11.4	6.7	127.4	82	3.5	3.1
Forest	12.4	16.2	55.0	55.1	9.3	12.9
Buildings	4.6	8.5	50.0	42.4	3.3	7.0
Shrubland	2.2	0.5	22.3	10.1	3.4	2.0
Wetland	0.1	0.1	2.3	6.0	1.9	0.4

Vegetation Management. Vegetation management of both linear corridors and large blocks of land as wildlife habitat includes grazing, haying, mowing and prescribed fire. Often management techniques are selected for practical considerations such as controlling vegetation height as a traffic safety issue or fires being conducted under specified conditions of soil moisture and wind speeds with the proximate goal of averting succession or invasion of non-native species. The goal of much management in both the US and Europe, however, is to preserve or enhance biodiversity or a specific habitat type through management of the vegetation. Including biodiversity as well as other considerations requires an understanding of what management factors are less than optimal as well as those that can enhance ecological success.

Invertebrate management. Invertebrates make up the largest proportion of the biodiversity (MacArthur and Wilson, 1967). They play a major role in ecosystem services in agricultural systems as well as natural systems (Kellert, 1993). Attitudes cover a broad range from the need to protect commodity crops from pest depredation to focus on wider environmental costs of reducing complex ecosystems to simple ecosystems and removal of large parts of the food web or introduction of exotic species as pest control measures (Van Lenteren *et al.*, 2006). Current management in the agricultural landscape is focused on the fields. A more holistic approach would include the rest of the landscape. Refining common management practices within the agricultural landscape can help meet conservation goals within the broader ecological context. In this way, we offer land sharing techniques as an enhancement within an intensive agricultural system rather than a dichotomous choice.

As mentioned earlier, in the Midwest the crops are mostly genetically modified corn and soybeans. Application of herbicides, insecticides, and fertilizers and most drastic of all, fall harvesting virtually guarantees monospecific plant communities. Such simple communities offer a very limited number of ecological niches to be occupied. They are also drastically disrupted periodically by cultivation. Comparative studies of invertebrates inhabiting crop fields indicate that the most abundant species have high dispersal abilities (Young and Edwards, 1990). Since crop plants are removed at the end of the growing season, the invertebrates that repopulate the fields the following year are assumed to emigrate from adjacent habitats (woods, pastures, fencerows, etc.). Thus, crop fields are often inhabited chiefly by species that have superior dispersal powers and the ability to adapt to a highly artificial managed environment that is quite different from the natural ecosystems to which they have been fitted by a long history of natural selection (Hunter and Price, 1992).

Inventories of Illinois invertebrates are often restricted to 1) pest species such as soybean aphids (Tinsley *et al.*, 2012), emerald ash borer (Herms and McCullough, 2014), or gypsy moths (Manderino *et al.*, 2014); pollinators (Marlin and LaBerge, 2001), or rare butterflies (Panzer *et al.*, 1995). There are some long-term studies that monitor small areas and measure weather variables (Kendeigh, 1979; Marlin and LaBerge, 2001). In 1997, a statewide monitoring program (Critical Trends Assessment Project) was initiated to determine long term change in the biota of Illinois. As part of this effort collections of terrestrial insects are made. Unfortunately, due to funding constraints only a small portion are classified to species.

Research questions

As stated before, the aim of this thesis is to look at vegetation management within the agricultural landscape and determine which practices are most beneficial to invertebrate assemblages and the associated food web. I concentrate on invertebrates for several reasons. First of all, the richness of invertebrates is in itself a valuable aspect of biodiversity that has not yet received the due attention in the American agricultural landscapes. Secondly, invertebrates may play a crucial role in the ecological functioning of ecosystems that in the end may also be important for agriculture (Bengtsson, 1997; Weisser and Siemann, 2004.). Thirdly, invertebrates are an important source of food for birds that are highly appreciated inhabitants of the agricultural landscape. Measuring species richness and abundance is one means of quantifying ecosystem responses to conservation practices. Documentation of individual taxa can provide critical information about the impacts of conservation programs on ecosystem functioning. My study concentrates on the Midwest agricultural landscapes in central Illinois, being a typical USA landscape that might profit from a sharing strategy.

My general question is: How do different land sharing management practices in agricultural landscapes impact invertebrate assemblages and availability of food items during the avian breeding season? We used pitfall traps, sticky boards, and sweep netting to sample invertebrates under various management conditions.

More specifically, we focused on answering the following questions:

1) **How does mowing regime of agricultural roadsides impact invertebrate assemblages?**

2) **How does extreme earth-moving impact the invertebrate community in a newly created prairie restoration?**

3) **How does a mid-summer wildfire impact a grassland invertebrate community?**

4) **How do the invertebrate assemblages in agricultural fields and edges relate to local and landscape complexity?**

5) **How does the invertebrate population relate to food availability, particularly for birds during the breeding season?**

Research Design and Statistical Analysis

From the above summary of ecological theory it is clear that any study of local species assemblages should take the surrounding landscape into consideration. In this study, the effect of landscape on the local invertebrate assembly is the main focus of the two studies trying to answer the last two research questions. Here, the research design was the selection of ten study locations in different landscapes within three different regions (counties). The studies that tried to answer the first three research questions focused on the local effects of local management. For these studies, I made use of given situations: a road of which the edges were mowed according to different regimes, a prairie restoration project of which I was asked to assess the effects on the invertebrates and a wildfire that happened to occur in a restoration area to which I had access. None of these studies were properly designed to test the effect of an experimental treatment (Hurlbert, 1984). In spite of these limitations, I present these studies in this thesis because they give first-hand insight of potential effects of a sharing strategy. But these insights can only be preliminary and do not prove the applicability of a sharing strategy for the Midwest of the USA. For that, properly designed large-scale and long-term research is needed.

Independency of observations. A statistical problem that comes with the study of given situations is that the data collected cannot be regarded as independent observations. The way I dealt with this situation was to add “random effects” to most of the statistical models that were used for analysis. I often applied General Linear Mixed Models (GLMM’s) with random effect variables for location, year and sample method, the obvious sources of dependency. This allowed us to resolve the non-independence by assuming a different ‘baseline’ value for each sample. We then modeled the effect of the other variables of interest, such as the ‘treatment’, on the difference of the observed value and the ‘baseline’ value. Thus, the non-independence of data was resolved statistically with the mixed model (Winter, 2011).

Likelihood Ratio Testing. A problem with applying GLMM’s is that the classical tests for the significance of the differences between treatments or other categories of interest, such as t- or F-tests, can no longer be applied because the number of degrees of freedom have changed in an unknown way by correcting the residuals for the random effect variables. A solution for this problem is the comparison of the fit of the GLMM in which the variable of interest is included with that of the GLMM where the variable is left out: The Likelihood Ratio Test (LRT). When the GLMM’s are fit using a maximum likelihood approach, the difference between the log(likelihood) of two models follows a chi-square distribution with the difference in number of degrees of freedom of the two models as one degree of freedom (Winter, 2011). In this way, the LRT is a means of attaining p-values of the effect of a variable of interest, a method that I will apply in a large number of cases.

Multiple working hypotheses. As an alternative for traditional evaluation of effects of variables thru p-values, I applied an approach based on multiple working hypotheses in a number of cases. The method of multiple working hypotheses was developed in the 19th century by a geologist named Thomas Chamberlin (Rosen 2016, Chamberlin 1965). There has been a recent trend to resurrect this method as a means of addressing the complicated issues in ecological field work (Elliott and Brook 2007; Burnham and Anderson 2000; Rosen, 2016). Rather than using p-values for null-hypothesis testing of individual models, we used a model-selection technique introduced by Akaiki in the 1970’s (Burnham and Anderson, 2011). Akaiki’s information criterion (AIC) selection methods determine which set of models best explain the data collected (Elliott and Brook 2007; Burnham and Anderson, 2000). Burnham and Anderson (1998) suggest that models having ΔAICc (difference in AICc scores) within 1–2 of the best model have substantial support. Models within about 4–7 of the best model have considerably less support, while models with ΔAICc > 10 have essentially no support. This method of analysis is well matched to the field of ecology with the multitude of variables and degree of uncertainty in field work (Agresti and Kateri, 2011; Stephens *et al.*, 2005). An additional benefit is that some models which clearly do not fit the data can be eliminated and new models introduced during later research projects.

Outline of the thesis

This thesis is composed of this introduction (Chapter 1), 6 research chapters (Chapters 2-7) and a general discussion (Chapter 8).

In chapter 1, I introduce general background information, terminology, and statistical analysis.

In Chapter 2, we conducted a preliminary study to compare the influence of roadside management regime on biodiversity along a roadside with neighboring fields planted in no-till agriculture or land enrolled in a conservation set-aside program. Two of the management regimes are common in Illinois: mowing twice a year and regular mowing throughout the growing season, both leaving the clippings where they fall. The third regime was regular mowing and removing the clippings.

In Chapter 3, we looked at a relatively new restoration project with varied management including fire and regular mowing. We took the opportunity offered by a restoration project associated with a large-scale housing development in central Illinois to survey invertebrates in three phases of plant restoration that were part of a larger project. This cross-sectional study looked at invertebrate assemblages at two, four and five year's post-restoration.

In Chapters 4 and 5 we looked at the immediate and long-term results of an accidental wildfire that burned a hundred-hectare restoration of forest and grasslands. This was an unusual opportunity to study the effects of an unplanned fire that occurred mid-summer during a drought year. The study began 10 days post-fire and traced the re-establishment of invertebrates over a 3-year period. In Chapter 4 we looked at the immediate response of Lepidoptera to the flush of spring-like vegetation immediately following the fire. In Chapter 5 we looked at the long-term impact of the same wildfire on invertebrate assemblages in the burned and unburned areas of the same field for three growing seasons post fire.

In Chapter 6 we looked at the factors influencing invertebrate taxonomic richness and diversity in fields and edges at both local and landscape scales within the agricultural landscape. We sampled invertebrates in ten fields in each of three counties in central Illinois and measured local and landscape parameters that the literature has shown to influence invertebrate richness and diversity.

In Chapter 7 we looked at invertebrate availability for birds early in the breeding season as it relates to structural complexity at the local and landscape levels in three counties in central Illinois. We looked at linear agricultural areas as an opportunity to provide food for nestlings.

In Chapter 8, we discussed the results of the previous chapters and explored possible management recommendations and suggestions for further study as a result of our investigations.

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Chapter 2

Comparing Roadside Management Treatments to Enhance Invertebrate Diversity

Based on: T.R. Evans, M. J. Mahoney, E.D. Cashatt , J. Noordijk, G.R. de Snoo and C.J.M. Musters as submitted to Soil and Water Conservation 8/23/2016

Abstract

Roadside edges are an important part of the rural landscape that have the potential to contribute habitat for enhancing biodiversity. Roadside edges are generally managed with a variety of mowing regimes based on non-ecological objectives such as traffic safety, expense and aesthetic perceptions. We conducted a pilot study in rural Sangamon County, Illinois USA to compare the influence of roadside management regime on biodiversity along a roadside with neighboring fields planted in no-till agriculture or enrolled in a conservation program. We used sticky boards, pitfall traps and sweep netting to sample invertebrates on both the roadside and the neighboring fields. Three mowing regimes were applied to the roadside. Two of the management regimes are common in Illinois: mowing twice a year and regular mowing throughout the growing season, both leaving the clippings where they fall. The third regime was regular mowing and removing the clippings. Our study showed invertebrate richness was greatest in roadsides with regular mowing and clippings removed. When invertebrates were grouped as predators, parasites and parasitoids, omnivores, herbivores, flower visitors and detritivores, taxonomic richness remained highest in the area mowed with clippings removed, but abundance varied according to life history requirements of the invertebrates. Taxonomic diversity was not different between treatments. Our study indicates that small changes in management of roadside edges could increase invertebrate richness.

Keywords: biodiversity—central Illinois—invertebrates—mowing—removing clippings—taxonomic richness.

Biodiversity in the United States and Europe is declining as agricultural practices intensify (Stoate *et al.*, 2001; Stoate *et al.*, 2009; Hutchinson, 2011). Sustainable Development Goals have targeted biodiversity as a high priority in times of population growth and climate change (Sachs *et al.*, 2009; Griggs *et al.*, 2013). As invertebrates are the little things that run the world (Wilson, 1987) it is important to understand how management of many different habitats can enhance invertebrate biodiversity. Invertebrates are closely tied to vegetation composition and management (Sheridan *et al.*, 2008; Albrecht *et al.*, 2010). In the USA, studies often focus on stenotopic species, e.g., Lepidoptera: Hersperiidae (prairie skippers) (Schlicht and Orwig, 1992), Hemiptera: Auchenorrhyncha (prairie leafhoppers) (Hamilton, 2005; Wallner, *et al.*, 2012), and Hymenoptera: Apoidia (bees) (Slagle and Hendrix, 2009). Research in natural areas often focuses on the rare invertebrates associated with rare plants in the specialized habitat e.g. *Papiapena eryngii* and host plant *Eryngium yuccifolium* (Molano-Flores, 2001). Research in agricultural areas frequently focuses on pest species (Kogan and Kuhlman, 1982). Relatively few studies focus on invertebrate assemblages within roadsides in an agricultural landscape.

In the USA, financial incentives are provided to farmers to adopt environmentally friendly agricultural practices and take some land tracts out of agricultural production (Mausbach and Dedrick, 2004). These often-large tracts are believed to provide significant ecosystem services by reducing erosion in areas prone to losing topsoil, serving as flood storage and reducing chemical runoff into waterways (Ribaudo *et al.*, 2001). A host of smaller scale practices are also available to reduce agricultural contributions to pollution. These practices include riparian buffers, grass waterways and contour grass strips. Few of the smaller scale practices available are focused on biodiversity although attention to providing habitat for declining numbers of pollinators and other flower visitors is growing (Ries *et al.*, 2001; Potts *et al.*, 2010; Scheper *et al.*, 2013). European studies have led to management of roadsides for biodiversity in addition to safety-oriented objectives such as places to stop in emergencies, road maintenance staging areas and bikeways (Way, 1977).

Mowing regime is regarded as the most critical factor in roadside management (Parr and Way 1988, Noordijk *et al.*, 2009). Management of roadside edges has the potential to add linear connections between larger tracts of restored lands, dispersal corridors for wildlife moving through the landscape, and refugia for species unable to subsist on agricultural land (Bennett, 1991). Many invertebrates are dependent on the plants available in the environment, directly like flower visitors and herbivores, or indirectly like predators and parasitoids on herbivorous species. In this pilot study, we looked at the impact of agricultural roadside management, i.e., the mowing regime, on invertebrate diversity in the Midwest USA.

We asked three questions: 1) Does management of roadsides affect invertebrate taxonomic richness? 2) Does management of roadsides affect invertebrate taxonomic diversity? and 3) Does management of roadsides affect taxonomic richness and abundance within invertebrate functional groups? We compared three mowing regimes, two of which are common for roadsides in Illinois, USA while the third one is not. Based on studies in Europe, we expected the greatest taxonomic richness and diversity to be found in edges where clippings were removed, a practice not commonly followed in IL/US. This management technique removes biomass and keeps the vegetation nutrient-poor and species rich (Parr and Way, 1988). Invertebrates are closely tied to vegetation composition and management (Sheridan *et al*., 2008; Albrecht *et al*., 2010). In the Netherlands, for example, clippings are often baled and removed (Schaffers 2002a, b). Farmers in our area of study generally mow either twice per growing season or keep roadside edges quite short by mowing regularly, e.g., monthly in the growing season. Removal of roadside hay is not common. Our study area included a reduced tillage agricultural field and former agricultural field planted in native grasses and forbs separated by a narrow road with drainage ditches. This field is enrolled in the United States Department of Agriculture (USDA) Conservation Reserve Program (CRP) which makes payments to farmers in exchange for removing agricultural land from production and planting either trees or grassland species. We evaluated invertebrate diversity under three different mowing regimes to assess whether roadside management choice could be incorporated into practices that enhance local biodiversity. The three regimes we tested were 1) mowing twice per annum and leaving clippings, 2) mowing once ~ monthly and removing clippings; and 3) mowing ~ monthly and leaving clippings. Our hypothesis was that regime 2 would have greatest species richness and diversity followed by regime 1 and regime 3 having the least. Regime 1 has the greatest number of flowers and both regimes 1 and 3 have retained the nutrients of the clippings creating a nutrient-rich diversity-poor environment.

Materials and Methods

Study Area. The study area is located in Sangamon County in the state of Illinois, USA (39°45’23.34N, 89°28’22.34W). This is part of the Grand Prairie Natural Division (Schwegman 1973). The Grand Prairie was mostly tall-grass prairie with fertile soils developed from glacial outwash, lakebed sediments and deposited loess. It is currently modified for high yield agriculture. The topography is generally level to rolling with drainage improved by the use of tile lines and ditches. The local area has a high amount of land enrolled in CRP interspersed with agricultural fields almost exclusively sown in genetically modified corn or soybeans. For this investigation, we selected an area with row crops, CRP land, rural road and drainage ditches. This allowed control of some confounding variables such as historical roadside management, weather factors, and vegetation types. The CRP field had been sown in row crops for decades before being removed from agriculture and enrolled in CRP in 2001. The agricultural field has been managed as minimum tillage since 2001. Both fields are typical for the area. Our experimental site was a narrow oil and chip roadway (4 m) with vegetated edges including a drainage ditch (4 m) (Figure 1).

Figure 1. Photo of the study site

All plant species encountered were typical ruderal vegetation with a mix of native and introduced species. Of the latter, the dominant species were those typical of frequently mowed rural road sides: *Bromus inermis* (Hungarian brome), *Festuca arundinacea* (Common fescue), *Poa pratensis* (Kentucky bluegrass*), Plantago lanceolata* (Buckhorn plantain), *P. major* (Broadleaf plantain), *Achillea millefolium* (Yarrow), and *Taraxacum officinale* (Common dandelion). The native species, both herbaceous and woody, reflect the local floodplain community: e.g. *Leersia virginica* (White grass), *Celtis occidentalis* (Hackberry), *Morus rubra* (Mulberry), and *Urtica dioica* (Stinging nettle). Examples of this community remain nearby and may account for the surprisingly large number of species encountered in the roadside drainage ditches. Species distribution was often patchy and no species were dominant.

Illinois climate is typically continental with cold winter temperatures (mean −3.8 °C), warm summers (24.6 °C) and frequently fluctuating temperature, humidity, cloudiness and wind conditions. Precipitation averages 895 mm per year and temperatures average 11.2°C. The growing season is ~185 days. (Midwestern Regional Climate Center 2009; Springfield, Illinois http:/mcc.sws.uiuc.edu). During the first year of the study (2012) precipitation was 300-400 mm below average (950.7 mm) and ambient temperatures were 2.4 °C higher than average. A wildfire burned the CRP field on July 27, 2012 after data collection for this study was complete for the season. During the second year of the study (2013) conditions in central Illinois were closer to average, with precipitation ~ 974 mm and ambient temperature was ~11°C (National Oceanic and Atmospheric Administration).

Treatment. The study was designed to test three roadsides treatments during the growing season: mow 2 times per season and leave clippings (M2); mow ~ once/month and remove clippings (M6 + R); and mow ~ once/month and leave the clippings (M6). Treatments were placed 20 m apart with 9 sampling points per treatment spaced 10 m apart. The treatment areas were 120 m with the first sampling site at 20 m which meant 40 m between samples in the different treatments (Figure 2). Each of the mowing treatments was tested on the roadside adjacent to the agricultural field and the CRP field. An equal number of samples was also collected within the CRP field and agricultural field. The agricultural field was managed under a minimum tillage, 2-yr soybean (*Glycine max*, seeded in 2012) – corn (*Zea mays* seeded in 2013) rotation. The drainage ditches received no management during the two-year study period and might have acted as a refuge for a variety of invertebrates during mowing of the roadsides or when crops were harvested from the fields.

Mowing was done with a tractor and 1.5 m brush hog (a type of rotary mower), both typical pieces of farm equipment in the USA. All areas were mown in April and September. Mowing of treatment areas M6 and M6 + R was conducted ~once/month throughout the summer. Treatment area M6 + R was raked the day after being mown. Mowing dates in 2012 were April 15, May 15, June 15, July 16, August 16, and September 12 and in 2013 were April 30, June 4, July 9, August 7 and September 16.

Sampling. Invertebrates were sampled with sticky boards and pitfall traps. Traps were set June 8, 2012, and June 16, 2013. We selected this time period to be comparable to other studies (Bedford and Usher, 1994; Hendron, 2010) and consistent between years. The trapping methods were chosen to sample varied groups of invertebrates (flying and epigeic). Sampling sites in the field interiors were ~ 15 m from the roadway. Sites on the roadside edge were 1-2 m from the drainage ditch and between the ditch and roadway (Figure 2).

Each sample site had a pitfall and sticky board. Sticky boards (Sensor ~ 8 cm x 13 cm Yellow Monitoring Cards, GrowSmart), attached to a flag (~ 6 cm X 9 cm X 76 cm LimeGlo, Forestry Suppliers) were placed 10 m apart at the field edge parallel to the planting row. Boards were placed with ~½ above the vegetation. Boards were retrieved two days later and placed in a clear plastic cover for future identification.

Pitfall traps were 150 ml plastic cups with an aperture of 70 mm placed into the ground so that the mouths were flush with the ground and there was no discontinuity between the edge of the trap and the ground surface. Each trap was filled to ~ 2.5 cm with a solution of water and vinegar and a few drops of dish soap added to break the surface tension of the water. Pitfall traps were retrieved seven days after placement and contents placed in a labeled clear Ziploc bag containing 70% isopropyl alcohol.

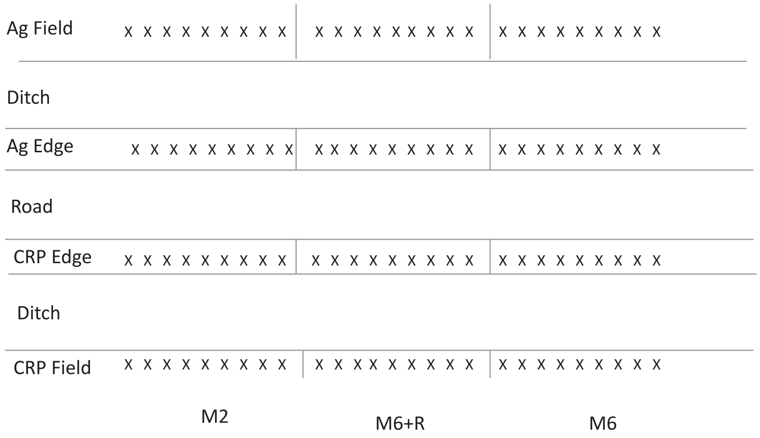

Figure 2. Sampling scheme (not drawn to scale) showing location of treatments and placement of sample locations in the agricultural (Ag) field, CRP field, and roadsides. The ditches are 4 m wide, the agriculture and CRP edges are 2 m wide and the road 4 m wide. X: address or sample site location. Sample locations are placed 10 m apart with 20 m between treatments. Treatment M2 is mowing twice per season, at the beginning and end of the growing season; treatment M6+R is mowing ~once per month and removing clippings, treatment M6 is mowing ~ once per month and leaving the clippings. The experimental area is 400 M long.

Arthropods were examined under a binocular microscope for identification. Ten percent of the samples were examined a second time as quality control. An independent expert adjudicated conflicting identifications. Numbers of arthropods smaller than 2 mm were estimated. Invertebrates larger than 2 mm were identified using taxonomic keys (Triplehorn and Johnson, 2005) and reference collections housed at the Illinois State Museum Research and Collections Center (ISM RCC). Identifications were made to lowest operational taxonomic unit (OTU) possible which in most cases was family. All OTUs were characterized to functional group (Table S1), i.e. herbivores, detritivores, flower visiting, omnivores, predators, parasites and parasitoids (Kaufman *et al.*, 2015; Evans, 2008).

Data Analysis. We used a block design in which the two edges are the blocks within which the mowing treatment was performed. The location of the treatment was selected to minimize the landscape gradient and not randomly selected. Sampling was done in two successive years at fixed sampling sites (addresses). We regarded the addresses as random sampling sites nested within locations within blocks. We applied linear mixed models for analyzing the data, in which address, year, and method are the random effect variables. Treatment (mowing regime) was the fixed effect variable. All our models were maximum random effect models, i.e., including the effects on both the intercept and the regression coefficient (Barr *et al.*, 2013). By applying a mixed effects model, samples can be regarded as corrected for the dependency that might have been introduced by the address, year or sampling method (Lazic 2010, Millar and Anderson 2004, Winter 2013). Our dependent variables were Taxonomic Richness (TR), i.e., the number of OTUs, and Taxonomic Diversity (TD), the exponentially transformed Shannon Weaver H', making it Hill numbers of order 1 (Hill, 1973; Jost, 2007). Residuals were checked in all analyses and were normally distributed for TR and TD and required log transformation when testing abundance. Data is reported as $\bar{x}$ ± sd. For testing, we applied in all cases a Likelihood-Ratio Test (LRT, for more explanation see chapter 1 of this thesis). We performed the statistical analyses using R software 3.0.2 (R Development Core Team 2014), i.e., lmer () of the package lme4 (Bates and Maechler, 2010), version 1.1-7.

Results

Mowing regime had a significant effect on taxonomic richness (TR) with the monthly mowing and removing clippings treatment having the greatest TR followed by monthly mowing and mowing twice per season and leaving clippings. The LRT shows that the effect of treatment is significant (LRT: Chi Sq = 7.4013, df = 1, p = 0.02471) (Figure 3).

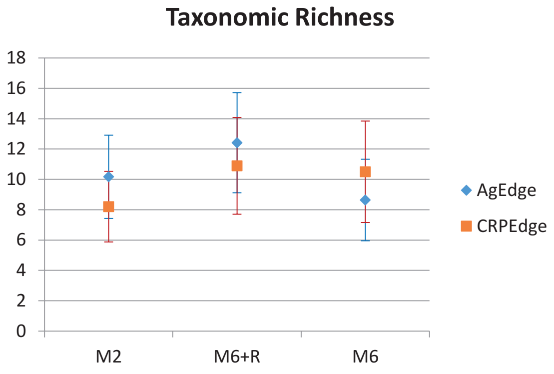

Figure 3. Average taxonomic richness (TR) per sample of roadside edges under three roadside treatments for study period. Treatment M2 is mowing twice per season, at the beginning and end of the growing season; treatment M6+R is mowing ~once per month and removing clippings, treatment M6 is mowing ~ once per month and leaving the clippings.

Taxonomic richness (TR), i.e., the number of OTUs, in the complete study area averaged 9.5 ± 3.1 (2 to 21) per sample (i.e. pitfall + sticky board at a single location) (Table 1). TR was higher in 2012 than in 2013 (10.4 vs 8.62; LRT: Chi Sq = 4.547; df = 1; p = 0.033; random variables: address and method, n = 432) and roadside edges had a higher average TR than fields but the difference was not significant (10.1 vs 8.8; LRT: Chi Sq = 1.602; df = 1; p = 0.206; random variables: address, method and year, n = 432). TR associated with agriculture (field and roadside) tended to be higher but not significantly different from the TR associated with CRP (9.6 vs 9.3; LRT: Chi Sq = 0.0621, df = 1, p = 0.803; random variables: address, method and year; n = 432).

Table 1. Average taxonomic richness (TR) and diversity (TD) (± sd) per location (n=54) for 2012 and 2013 and overall (n=216).

Complete study	**TR**		**TD**	
	2012	**2013**	**2012**	**2013**
Ag Edge	11.4 ± 3.1	9.4 ± 3.2	4.7 ± 2.0	4.4 ± 1.1
CRP Edge	11.1 ± 3.3	8.7 ± 2.6	4.6 ± 2.3	4.2 ± 1.1
Ag Field	8.6 ± 2.6	9.0 ± 2.0	4.9 ± 1.7	4.2 ± 1.6
CRP Field	10.3 ± 3.3	7.3 ± 2.7	4.9 ± 1.7	3.9 ± 1.3
All locations	10.4 ± 3.3	8.6 ± 2.8	4.8 ± 1.9	4.2 ± 1.3
Overall	9.5 ± 3.1		4.3 ± 1.7	

Mowing regime did not have a significant impact on taxonomic diversity (TD) (LRT: Chi Sq = 2.04037, df = 1, p = 0.3006; random variables: address and method, n=432). TD in the complete study area averaged 4.3 ± 1.7 (1.4 to 11.4) per sample (Table 1). TD was less in 2012 than in 2013 (4.8 vs 4.2; Table 1; LRT: Chi Sq = 14.19; df = 1; p < 0.001; random variables: address and method); TD in roadside edges was not different than fields (4.5 vs 4.5; LRT: Chi Sq = 0.0035; df = 1; p = 0.953; random variables: address, method and year, n = 432). TD associated with CRP was not significantly different from the TD associated with agriculture (4.4 vs 4.6; Chi Sq = 1.1255; df = 1; p = 0.289; random variables: address, method and year, n = 432).

Of the functional groups tested, only omnivores TR was significantly impacted with parasites trending toward significance (Figure 4). Omnivores had significantly different TR in treatment areas with M2 being greatest (LRT: Chi Sq = 6.4446; df = 1; p = 0.0399; random variables: address, method and year, n = 216). TR of omnivores averaged 2.0 (0 to 4) per sample. TR for parasites followed with an average of 1.2 (0 to 6) per sample. Parasite TR tended toward significance with treatment M6 + R being greatest (LRT: Chi Sq = 5.942; df = 1; p = 0.05125; random variables: address, method and year, n = 216). The remaining functional groups (detritivores, herbivores, flower visitors, predators) did not achieve statistical significance. Detritivore TR followed with an average of 1.7 (0 to 4) per sample (LRT: Chi Sq = 5.2032; df = 1; p = 0.07415; random variables; address, method and year, n = 216). This was followed by herbivores which averaged 3.1 (1 to 10) per sample (LRT: Chi Sq = 2.3131; df = 1; p = 0.3146; random variables; address, method and year, n = 216). The TR of flower visitors averaged 1.1 (1 to 4) per sample (LRT: Chi Sq = 0.9635; df = 1; p = 0.6177; random variables; address, method and year, n = 216). Predators averaged 2.4 (1 to 10) per sample (LRT: Chi Sq = 3.0852; df = 1; p = 0.2138; random variables; address, method and year, n = 216).

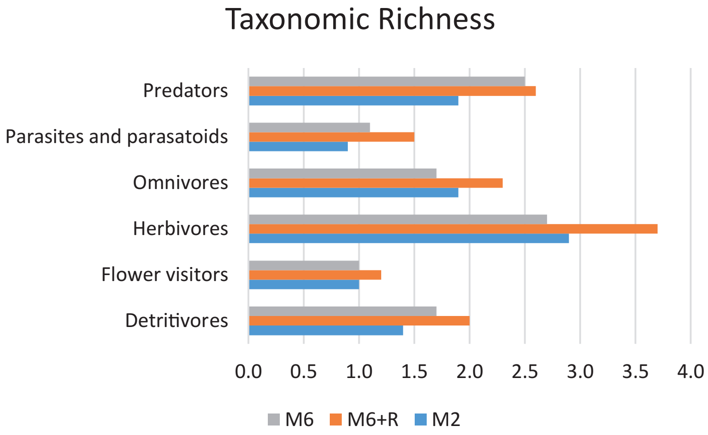

Figure 4. Taxonomic richness per sample within functional groups in each of the three treatments. Treatment M2 is mowing twice per season, at the beginning and end of the growing season; treatment M6+R is mowing ~once per month and removing clippings, treatment M6 is mowing ~ once per month and leaving the clippings. Omnivores; P = 0.0399, n = 216); parasites P = 0.05125, n = 216).

Abundance of individual detritivores was greatest (x̄= 51.3 individuals per sample) followed by omnivores (x̄ = 23.6), herbivores (x̄ = 15.5), predators (x̄ = 13.8), and parasites and parasitoids (x̄ = 4.8) (Table 2, Figure 5). Abundance was not significantly different in the three treatments (LRT: Chi Sq = 2.0554; df-1; p = 0.3578; random variables; address, method and year, n = 216). Most abundant taxa were Araneae; Isopoda; Collembola; Hemiptera: Cicadellidae and Aphidae; Coleoptera: Scarabaeidae, Mordellidae, and Curculionidae; Hymenoptera: Braconidae and Formicidae; and Diptera: Chironomidae, Culicidae, Mycetophilidae, Dolichopodidae, Muscidae, and Ulidiidae.

Table 2. Average abundance ± sd within functional groups of each of the three management treatments of the roadside edges (n=72) and overall (n=216). Treatment M2 is mowing twice per season, at the beginning and end of the growing season; treatment M6+R is mowing ~once per month and removing clippings, treatment M6 is mowing ~ once per month and leaving the clippings.

Treatment	M2	M6 + R	M6	Overall
Detritivores	37.8 ± 42.5	54.8 ± 40.6	61.3 ± 63.6	51.3 ± 50.8
Flower visitors	2.0 ± 2.6	2.1 ± 2.0	1.9 ± 2.5	2.0 ± 2.4
Herbivores	12.9 ± 15.2	19.5 ± 27.2	14.0 ± 13.8	15.5 ± 19.8
Omnivores	28.0 ± 39.3	23.7 ± 28.7	19.1 ± 25.1	23.6 ± 31.7
Parasites and Parasitoids	4.6 ± 5.9	5.7 ± 7.2	4.1 ± 4.4	4.8 ± 6.0
Predators	12.8 ± 43.0	9.5 ± 18.2	19.2 ± 43.1	13.4 ± 36.7

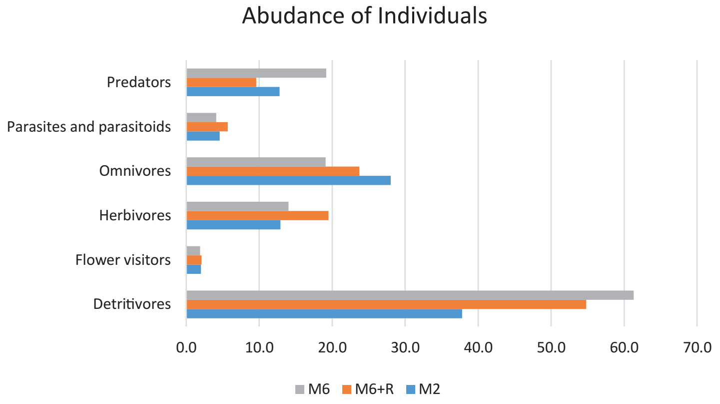

Figure 5. Average abundance per sample ± sd within functional groups in each of the three treatments. Treatment M2 is mowing twice per season, at the beginning and end of the growing season; treatment M6+R is mowing ~once per month and removing clippings, treatment M6 is mowing ~ once per month and leaving the clippings. Abundance was not significantly different between treatments.

In total, there were 98 OTUs sampled from both fields and roadside edges (Table S1). There were 43,366 individuals sampled from all sites over the two years of the study. There were 10 fewer OTUs in 2013 than in 2012. In contrast, 43% of the individuals were trapped in 2012 and 57% in 2013. Common taxa such as Heteroptera: Aphidae and Cicadellidae, Diptera: Muscidae, Hymenoptera: Braconidae and Isopoda became more abundant in the second year of sampling, while Lepidoptera and less common Diptera families dropped out of the samples. From the roadside edges 23,254 individuals were sampled over the two years of the study. There were 12 fewer OTUs in 2013 than in 2012. In contrast, 51.6% of the individuals were trapped in 2012 and 48.4% in 2013.

Discussion

Our study shows that taxonomic richness is affected by roadside treatment method and was greatest in the roadside edges that were mown regularly with clippings removed. Based on European studies, this was not unexpected (Morris, 1981; Parr and Way, 1988; Noordijk *et al*., 2009). In Spanish olive groves, removal of the natural cover below the olive trees resulted in higher abundance, family richness and dominance of epigeal beetles (Cotes, 2009). In the US, prescribed fire is a common method of removing biomass. This management technique is controversial in many areas. Of particular relevance to our study is the safety issue with smoke obscuring traffic visibility. Mowing has been shown to cause insect decline but of a shorter duration and less intensity than a similarly timed prescribed burn (Bulan and Barrett, 1971).

However, we also expected that mowing twice per year would provide similar habitat improvement for invertebrates as mowing and removing clippings. Mowing twice per year would provide a savings in money and manpower as well as having an aesthetic value. This did not prove to be the case in our study. Unfortunately, in this pilot study we were not able to test the regimen of mowing twice a year with removal of the clippings. This management type proved to be the most beneficial regimen for invertebrates in grasslands (Parr and Way 1988, Noordijk *et al*., 2009), although in low-productivity grasslands a less intensive regimen (mowing once a year with removal of hay) might be the most beneficial management type (Noordijk *et al*., 2010).

Differences in TR between the three management regimens in our study were small. This could be due to the short duration of our experiment and the fact that the sites were in close proximity. The vegetation in the study area was typical of many agricultural roadside edges and very dense. Vegetation grew quickly in the spring. When cut by the brush hog, it created a dense mat of non-living material. This was, in essence, a barrier that inhibited access to the ground surface as well as slowing new growth. We believe the area that was mown and had clippings removed allowed invertebrates access to new growth (for herbivorous insects, like the groups Hemiptera: Aphidae and Cicadellidae, and Orthoptera: Acrididae that were encountered abundantly), access to the ground for making nests and laying eggs e.g. Hymenoptera: Formicidae, and possibilities for ground dwelling species to receive warmth from the sun that allowed sufficient activity and the development of the juvenile stages in or on the ground e.g. Araneae; Coleoptera: Carabidae. On the other hand, some detritivores and hydrophilic invertebrates e.g. Gastropoda; Isopoda; and some Diptera apparently benefitted when the clippings were not removed.

The differences in TR and TD between treatments show the same pattern over the two years, although the effect of treatment on TR is significant while that on TD is not. It is also notable that TD shows no differences between roadside edges and fields, while TR does show differences. So, in our study area, TD as a measure of invertebrate biodiversity was less sensitive to treatment and differences between locations than TR. Diversity indices are not generally sensitive to species with low abundance while richness values give equal weight regardless of abundance (Magurran, 2004). We found no differences in abundance between treatments. This indicates that the differences we found in TR is because of the locally rare species found in the treatment area M6 + R rather than in increase in total abundance between treatments.

The landscape-moderated insurance hypothesis provides resiliency and stability of ecological processes in highly disturbed environments (Tscharntke, 2012). Redundancy theory suggests that the more redundancy the more an ecosystem can recover from disturbance (Naeem, 1997). In general, more species result in more stability (Naeem, 1998; Cardinale *et al.*, 2012). Different species do better under different conditions. When disruption occurs, it is likely that some species will do well and conserve the functional niche within the community. Maintaining invertebrate biodiversity can only be managed indirectly and the options for such management are not always clear (Brussaard, 2007). Until recently, the focus on invertebrate biodiversity within the agricultural landscape has mostly been on pest control (Bianchi, 2006). Loss of pollinators and impacts of neonicotinoids have drawn recent attention (e.g. Seagraves and Lundgren, 2012; Kielmanowicz *et al.*, 2015).

Our study shows that for most of the functional groups of invertebrates (detrivores, flower visitors, herbivores, parasites and parasitoids, and predators) enhancing the area between the edges of the agricultural fields and roads provides a biotope which is generally stable and increases taxonomic richness. TR was greatest in the M6 + R treated area, and this was fairly consistent across functional groups.

There was considerable difference in weather between years. The extreme drought conditions in 2012 probably affected survival and ultimately reproductive success the following year. Collections in 2012 were made early in the season before the drought had much of an impact. Water was available in the ditches and there was residual moisture in the soil. As the season progressed, the ditches dried and there was almost no rainfall during the reproductive season. The drought conditions carried over into the spring of 2013 when conditions returned to normal. Collections were made 24 days after the first mowing event in 2012 and 16 days in 2013. This difference in number of days after the mowing was related to vegetation growth. In 2012 there was little growth and in 2013 the growth was considerably richer. We attempted to collect at the same stage of vegetation growth in both years and still be consistent with collection dates. Although the weather conditions in both years was quite different, the effect of treatment was not different in the two years of our study.

This study was designed as a pilot study to provide information and guidance for a more elaborate future study. The study was initially designed with multiple sites. Permissions were obtained from the land owners and land managers who were different people, some of whom were located at some distance from the research sites. Within weeks of study initiation, the management protocols had been violated from a variety of sources and treatments. Some edges had been sprayed with herbicide and most had been mowed by well-intentioned neighbors or diligent township and county employees. This left us with the results of only two roadsides of one road that could be used for this study. So, the replication of our treatments is poor, which hinders strong conclusions and generalizations.

Summary and Conclusions

This study indicates potential for using roadside management to improve biodiversity. We belief that our results justify future research. However, issues exist that will need to be addressed before additional studies can be conducted. These same issues suggest that any change in mowing regimes will be difficult to implement within the existing agricultural culture.

A future study design should include four treatments: mowing 2X and leaving clippings, mowing 2X and removing clippings, mowing 6X and leaving clippings, and mowing 6X and removing clippings.

Any future research will need to address the issue of the involvement of well-intentioned neighbors or diligent township and county employees. Raking and removing clippings is labor intensive. Future studies should consider the use of mechanical bailing equipment. The limitations of this study are sufficiently great that it should not be considered applicable to roadsides in general and further study is indicated.

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Table S1.

Abundance of individuals in 2012, 2013 and total abundance. Guilds are mostly detritivores (D), flower visitors (F), herbivores (H), omnivores (O), parasites and parasitoids (PA), predators (PR), or not feeding as adults (NA).

Taxa	2012	2013	Total	Guild
Class Oligochaeta: Earthworms	15	99	114	D
Class Gastropoda				
Snails	35	38	73	H
Slugs	4	9	13	H
Order Araneae: Spiders				PR
Linyphiidae: Sheet Web Spiders	85	22	107	PR
Lycosidae: Wolf Spiders	252	473	725	PR
Gnaphosidae: Parson Spiders	8	1	9	PR
Thomisidae: Crab Spiders	86	22	108	PR
Salticidae: Jumping Spiders	7	0	7	PR
Spider hatchlings	2424	510	2934	PR
Order Opiliones: Harvestmen	153	91	244	PR
Order Acari: Ticks	2	2	4	PA
Order Isopoda: Isopods				
Common Pillbugs	284	2415	2699	O
Order Diplopoda: Millipedes	45	14	59	D
Order Chilopoda: Centipedes	11	4	15	PR
Order Collembola: Springtails	3262	3120	6382	D
Order Orthoptera				
Acrididae: Grasshoppers	296	127	423	H
Gryllidae: Crickets	15	23	38	H
Order Phasmatodea: Walkingsticks				
Heteronemiidae: Stick Bugs	0	1	1	H
Order Blattaria: Cockroaches				
Blattidae: Cockroaches	0	1	1	O
Order Hemiptera:True Bugs				
Miridae: Plant Bugs	6	0	6	H
Anthocoridae: Minute Pirate Bugs	13	37	50	PR
Reduviidae : Assassin Bugs	11	4	15	PR
Lygaeidae: Seed Bugs	2	0	2	H
Largidae: Plant Bugs	7	7	14	H
Coreidae: Leaf-footed Bugs	2	0	2	H
Pentatomidae: Stink Bugs	4	2	6	H
Cicadellidae: Leafhoppers	663	1861	2524	H
Fulgoroidea: Plant Hoppers	3	28	31	H
Aphidae: Aphids	353	3702	4055	H
Order Thysanoptera: Thrips	26	0	26	H
Order Coleoptera: Beetles				
Cicindelidae: Tiger Beetles	1	9	10	PR
Carabidae: Ground Beetles	74	111	185	PR
Histeridae: Hister Beetles	2	4	6	PR

Taxa	2012	2013	Total	Guild
Silphidae: Carrion Beetles	5	3	8	D
Scaphidiidae: Shining Fungus Beetles	13	34	47	D
Staphylinidae: Rove Beetles	42	25	67	PR
Trogidae: Trox Beetles	16	31	47	D
Scarabaeidae: Scarab Beetles	360	146	506	H
Melolonthinae: June Bugs	1	1	2	H
Buprestidae: Jewel Beetles	1	0	1	H
Elateridae: Click Beetles	48	56	104	H
Phengodidae: Railroad Fireflies	2	1	3	PR
Lampyridae: Fireflies	4	2	6	PR
Cantharidae: Soldier Beetles	31	6	37	PR
Cleridae: Checkered Beetles	3117	10	27	PR
Nitidulidae: Sap Beetles	1	9	10	D
Erotylidae: Pleasing Fungus Beetles	2	0	2	D
Byturidae: Fruitworm Beetles	6	0	6	H
Coccinellidae: Lady Beetles	3	15	18	PR
Mordellidae: Tumbling Flower Beetles	146	128	274	F
Tenebrionidae: Darkling Beetles	1	1	2	H
Meloidae: Blister Beetles	1	0	1	H
Cerambycidae: Long-horned Beetles	3	0	3	H
Chrysomelidae: Leaf Beetles	41	34	75	H
Microrhopala vittata: Goldenrod Leaf Miners	0	2	2	H
Curculionidae: Weevils	72	51	123	H
Coleoptera larva ssp •	9	66	75	H
Order Neuroptera: Antlions, Lacewings	1	0	1	PR
Order Hymenoptera: Wasps, Bees, Ants				
Symphyta: Sawfly ssp	2	4	6	H
Ichneumonidae: Ichneumon Wasps	22	2	24	PA
Braconidae: Parasitic Wasps	145	784	929	PA
Chrysididae: Cuckoo Wasps	50	9	59	PA
Megachilidae: Resin Bees	59	8	67	F
Sphecidae: Thread-Waisted Wasps	1	0	1	F
Halictidae: Sweat Bees	54	9	63	F
Apidae: Bees	22	3	25	F
Bombus pensylvanicus: Bumble Bees	3	0	3	F
Mutillidae: Velvet Ants	3	1	4	PA
Vespidae: Hornets, Wasps	6	2	8	F
Formicidae: Ants	1823	1479	3302	O
Trichoptera: Caddisflies	19	7	26	NA
Lepidoptera: Butterflies and Moths				
Micro-lepidoptera ••	13	6	19	F
Hesperiidae: Skippers	33	2	35	F
Pieridae: Sulphurs	6	0	6	F
Lycaenidae: Coppers/Gossamers	14	0	14	F
Nymphalidae: Brush-footed Butterflies	3	0	3	F
Heliconinae: Fritillaries	3	0	3	F

Taxa	2012	2013	Total	Guild
Noctuidae: Owlet Moths	3	4	7	F
Lepidoptera larva ssp •	0	7	7	H
Order Diptera: Flies				
Tipulidae: Crane Flies	2	1	3	F
Chironomidae: Midges	91	142	233	NA
Culicidae: Mosquitoes	535	203	738	PA
Simuliidae: Black Flies	2	1	3	PA
Mycetophilidae: Fungus Gnats	5525	5410	10935	D
Tabanidae: Horse Flies, Deer Flies	1	1	2	PA
Dolichopodidae: Long-legged Flies	53	95	148	PR
Phoridae: Hump-backed Flies	52	1	53	O
Pipunculidae: Big-headed Flies	4	25	29	PA
Syrphidae: Flower Flies	31	40	71	F
Calliphoridae: Blow Flies	8	4	12	D
Tachinidae: Tachinid Flies	1	0	1	PA
Muscidae: House Flies	364	495	859	O
Sarcophagidae: Flesh Flies	14	28	42	O
Tephritidae: Fruit Flies	8	0	8	F
Ulidiidae: Picture-winged Flies	130	112	242	F
Diptera ssp •	1107	2647	3754	O
Diptera larva ssp •	44	313	357	O
	19239	25197	44436	

• Other species not identified due to damage of features or difficulty in identification

•• Small Lepidoptera of the Super Families Gelechioidea, Pyraloidea, Tiniodea, Gracillarioidea, Incurvarioidea, and Families Tortricidae and Pterophoridae

Chapter 3

Development of invertebrate assemblages in a recently restored prairie

Based on: Tracy R. Evans, Meredith J. Mahoney, E.D. Cashatt, Bryon W. Cross, Geert R. de Snoo and C.J.M. Musters. Invertebrate communities associated with three early phases of a prairie restoration project. 2016 .*In Press* Great Lakes Entomologist

Abstract

While specific invertebrate groups have been studied in prairie restorations, there are few studies that look at terrestrial invertebrate assemblages. We took the opportunity offered by a restoration project associated with a large-scale housing development in central Illinois to survey invertebrates in three phases of plant restoration that were part of a larger project. This cross-sectional study of invertebrate recovery at two, four and five year's post-restoration showed that there was no overall difference in invertebrate taxa richness and diversity. Overall abundance was greatest in the most recently restored area. Richness, diversity and abundance of six functional groups did not differ. The restoration phases of our study were apparently all characterized by an early pioneer assemblage that did not differ significantly from each other. The conclusion is that all phases are still characterized by pioneer invertebrate assemblages, and that development to more diverse and richer assemblages might take more than five years in prairie restoration projects. The new and unexpected finding was that the reestablishment of invertebrate assemblages was not closely tied to vegetation restoration.

Keywords: invertebrate diversity, prairie restoration, species richness, taxonomic richness, urban watershed protection

Introduction

Illinois was once part of a vast grassland which became known by the French word for grassland, “prairie”. Early European settlers soon realized the agricultural potential and converted the rich prairies to croplands. Only a few thousand hectares of the original prairie remains, mostly pioneer cemeteries and linear elements along railroad rights-of-way and highways (Johnson and Anderson, 1986; Walk and Warner, 1999). There is a growing movement to restore prairie, a difficult task considering the lack of scientific documentation of the original ecosystem. Our best records come from descriptions of the vegetation, mammals, and birds during early exploration (Audubon, 1843; Wheeler, 1904).

Historically the focus of prairie restoration projects has been to establish the prairie flora. From an ecological point of view, the traditional focus on vegetation restoration makes sense because of the strong relationship between floral and faunal diversity (Labandeira *et al.*, 1994). The habitat heterogeneity hypothesis predicts invertebrate species richness should be greater with greater structural and vegetation complexity (Nilsson *et al.*, 1988). There are three general layers in the above ground vegetation structure of an established prairie. These include above ground structures that have low growing forbs and grasses, a highly diverse intermediate layer, and later in the season tall perennials. Together these layers provide a diverse microhabitat for invertebrates.

Restorations are planned with careful selection of various seeding mixes and hay spreading from existing prairies, as well as the use of specific management techniques including prescribed fire and mowing (Schramm, 1990; Kindscher and Tieszen, 1998; Dickson and Busby, 2009). However, when a restoration plan succeeeds in establishment of the prairie vegetation it does not automatically mean that the prairie ecosystem is also fully functional. As with plants, many animals and most micro-organisms have limited dispersal capabilities. But since neither animals nor micro-organisms are usually aided by translocations, the recovery of the complete prairie community may take time, if it happens at all (Woodcock *et al.*, 2012a; Woodcock *et al.*, 2012b). This might be especially true when soils are strongly disturbed during the establishment of the restoration. This bares the risk that the prairie under restoration, although having a recovered vegetation, is not functioning well because some functional groups are missing or depending on too few species. Such a prairie could be unstable or have low resilience (Peterson *et al.*, 1998).

Subjective appraisals of restoration projects were characteristic in the early history of restoration ecology. This was partially the result of the feeling of urgency that resulted from the rapid degradation of ecological systems. The pragmatic approach of visually assessing the end product of a restoration continues to be one method of utilizing scarce financial and manpower resources (personal observation). A more rigorous scientific approach includes monitoring fundamental parameters of the restoration and comparison of indigenous species during and after the restoration (Bradshaw, 1993; Ruiz-Jaen and Mitchell Aide, 2005). Post-restoration monitoring ranges from one or two years to a minimum of 15 years for some mine reclamation projects (Craft *et al.*, 2002). Plant and invertebrate diversity and abundance are the most common measures of ecosystem recovery (Ruiz-Jaen and Mitchell Aide, 2005). Invertebrate studies of restored prairie include soil arthropods (Lussenhop, 1976), invertebrate herbivory (Gibson *et al.*, 1990), and invertebrate response to management techniques (Benson *et al.*, 2007). Most studies focus only on one group of organisms (Ruiz-Jaen and Mitchell Aide, 2005). Results of these studies were highly variable (Picaud and Petit, 2007; Wallner *et al.*, 2012).

We took an opportunity to study invertebrate abundance, richness and diversity at a project converting land use from agriculture to prairie within a new housing development. Conservation development is an alternative form of housing construction in which homes are located around a central area protected for conservation purposes. An approximately 36 ha prairie restoration followed an initial alteration of hydrology to add meanders, riffles and pools. Water quality was improved and fish abundance increased by 84.6% over the pre-restoration sample (Thomas 2012). Subsequent to the stream restoration, the area was seeded in three phases with prairie forbs and grasses to mimic pre-settlement vegetative conditions.

We were interested in the establishment of invertebrate assemblages after the earth-moving that occurred as part of the stream hydrology portion of the project. Our first hypothesis was that invertebrate abundance, richness and diversity would be positively correlated with the establishment of prairie vegetation.

Methods

Study Area. The study area is located in McLean County in the state of Illinois, USA (40°27’32.97”N, 88°52’36.59”W). This is part of the Grand Prairie Natural Division (Schwegman, 1973). The Grand Prairie was once a vast plain of mostly tallgrass prairie with fertile soils developed from glacial outwash, lakebed sediments and deposited loess. The topography is generally level to rolling. McLean County has a humid continental climate with hot summers and no dry period. The general environment within a 40 km radius is crops. Average temperatures range from 31° C in the summer to -9° C in the winter. Precipitation averages 940 mm per annum (Best Places, 2014).

The study site was part of a housing development near Bloomington, Illinois. The area was formerly row crop agriculture containing the headwaters of Kickapoo Creek. Sections of Kickapoo Creek are classified as a “Biologically Significant Stream” (Thomas 2009) a designation developed by the Illinois Department of Natural Resources (IDNR). Kickapoo Creek is located within the Sangamon River Basin.

Reconstruction of the stream contours was the first part of the project, after which the area surrounding the creek was restored to prairie vegetation. Construction of the restoration (Figures 1-4) and subsequent seeding (Appendix A) occurred in three phases over a four-year period (2008-2012). Phase I construction began in 2008 with the final seeding occurring in the spring of 2009. Phase II construction began in 2009 with final seeding occurring in the spring of 2010. Phase III was constructed in 2011 and had a fall dormant seeding, thus 2012 represented the first growing season of this phase. The construction of each phase involved total disturbance of the site within the phase area. The topsoil layer (A and B horizon) was removed and the new ground contours established in the parent material. Replacement of the A horizon topsoil layer (to provide substrate for seeding) occurred for each phase. B horizon soils were removed from the site. The earthwork resulted in removal of all invertebrate and small mammal populations within a given phase during construction. Additionally, management during 2012 and 2013 included a prescribed burn in Phase I, mowing with hay left in place in phase II and mowing with hay removed in Phase III.

Figure 1. Schematic diagram of the restoration phases: Phase I was constructed and seeded in 2008 but had to be reseeded in spring of 2009. Phase II construction started in 2009 and was finished and the area seeded in spring of 2010. Phase III had a dormant seeding in fall 2011 so the first growing season was spring 2012.

Figure 2. Phase I facing northeast taken July 3, 2013.

Figure 3. Phase II facing northwest taken July 3, 2013.

Figure 4. Phase III facing northwest taken July 3, 2013

Sampling. May 7-14, June 30-July 7, and September 17-24, 2013, invertebrates were sampled by pitfall trapping, sweep netting, and sticky boards. These methods were chosen to sample invertebrates with different modes of locomotion and structural occupation found in a prairie landscape. In each of the three construction phases, there were three transects of six sampling sites. Transects were placed parallel to the creek at 15.8 m average distance (range 7.6-24.1 m) as measured with a GPS (Garmin Oregon 450t). All samples were within the same soil type (Sawmill silty clay loam). Sticky boards and pitfall traps were placed ~10 m apart within each transect and transects were placed 20-40 m apart.

Each sample site had a pitfall and sticky board (Sensor ~ 8 cm x 13 cm Yellow Monitoring Cards, GrowSmart), attached to a flag (~ 6 cm X 9 cm X 76 cm LimeGlo, Forestry Suppliers). Boards were placed with a minimum of ½ the board above the vegetation on to a maximum height of 75 cm. Sticky boards were retrieved two days later and placed in a clear plastic cover for future identification. Pitfall traps were 150 ml plastic cups each with an aperture of 70 mm that were placed in the ground flush with the surface. Each trap was filled with a solution of water and vinegar and a few drops of soap added to break the surface tension of the water. Each pitfall trap was retrieved seven days after placement, strained and placed in a separate clear plastic bag containing 70% alcohol.

Sweep netting consisted of two 50 m linear sweeps (100 sweeps each) conducted 3 m on both sides of the sampling transects in each of the three construction phases. The sweep net was 38 cm in diameter with muslin netting (Forestry Suppliers). All samples were collected on sunny days between 10:00 and 14:00 with winds below 5.5 m/s as measured on the Beaufort scale. Invertebrates were placed in a "knockdown" jar (containing chloroform soaked cotton) for several minutes and then placed in a separate labeled clear plastic bag containing 70% alcohol.

Invertebrates larger than 2 mm were identified to lowest operational taxonomic unit (OTU) possible, which in most cases was family, using taxonomic keys (Triplehorn and Johnson, 2005) and reference collections housed at the Illinois State Museum Research and Collections Center (ISM RCC) (Oliver and Beattie, 1996). Ten percent of the samples were examined a second time as quality control. An expert was available to assist with difficult identifications. Numbers of arthropods smaller than 2 mm were estimated. The method of locomotion for each OTU was classified as mostly flying or mostly epigeic. The OTU's were categorized by functional guild of detritivores, herbivores, flower visitors, parasites or parasitoids, predators or omnivores.

Data Analysis. Our design was such that we sampled invertebrates repeatedly within each construction phase along three transects at fixed locations using three sampling methods. Our nested design regarded the locations as random locations within transects within phases. We regarded our sampling methods as a random selection of all possible sampling methods and our sampling date as randomly selected from all possible dates. As a result, in most of our analyses, we used a mixed linear model with location, date and method as random effect variables and phase, our treatment, as the fixed effect variable. By applying a mixed effects model, samples can be regarded as independent across space and time (Millar and Anderson, 2004; Lazic, 2010; Winter, 2013). In one instance, we tested whether invertebrate dispersal effected the abundance of the taxa. In that case we regarded the taxa we found as a random selection of all possible taxa and the phases as random selection of all possible phases.

All our models were maximum random effect models, i.e. including the effects on both the intercept and the regression coefficient (Barr *et al.*, 2013). Our dependent variables were abundance, taxonomic richness (TR), i.e., the number of OTUs, and taxonomic diversity (TD), the exponentially transformed Shannon Weaver H', making it Hill numbers of order 1 (Hill, 1973; Jost, 2007). Residuals were checked in all analyses. Normality was visually assessed. Abundance was not normally distributed; therefore, we applied a log transformation. TD was normally distributed. TR was checked with and without log transformation. Results were not significantly different so TR was treated as normally distributed. Capture methods were not merged: abundance and diversity were per sample. The effect of means of locomotion of the invertebrates on abundance w tested with LRT. Data are reported as ± sd.

In all analyses, we applied a Likelihood-Ratio Test (LRT). We performed the statistical analyses using R software 3.1.1 (R Development Core Team (2013). We used lmer () of the package lme4 (Bates 2014), version 1.1-7. The model with the factor of interest is compared to the model without that factor.

Results

In total, there were 105 OTUs sampled from the three restoration phases (Appendix B). There were 26,263 individuals sampled over the three months of the study period. Overall abundance averaged 76.8 ± 347.5 (Table 1). Abundance was greatest in Phase III (142.55 ± 207.7), followed by Phase II (46.62 ± 50.0) and Phase I (41.21 ± 49.8). The influence of phase on abundance was tested with Likelihood Ratio Test and was statistically significant (LRT: Chi Sq=820.78, df=22, *P*=0.0454; n=342. Airborne invertebrates had no difference in abundance than epigeic (LRT: Chi Sq=0.0547, df=1, *P*=0.8151; n=342). Both TR and TD were greatest in July (Table 2).

Table 1. Average taxonomic richness (TR) and diversity (TD) ± sd (range) per sample for Phase I, II, III and overall.

Phase	TR	TD
PI	8.35 ± 4.43 (2-32)	5.14 ± 2.11 (1.21-10.50)
PII	9.04 ± 4.56 (2-34)	5.17 ± 2.35 (1.54-11.68)
PIII	11.23 ± 4.74 (2-26)	5.15 ± 2.24 (1.25-10.70)
Overall	9.5 ± 4.97 (2-34)	5.1 ± 2.2 (1.2-11.7)

Taxonomic richness (TR) in the complete study area averaged 9.5 ± 4.97 (2-34) per sample and was highest in Phase III (Table 1). Phase of restoration on TR was not significant (LRT: Chi Sq=3.956, df=2, *P*=0.1383; n=342). Taxonomic diversity (TD) in the complete study area averaged 5.1 ± 2.1 (1.2-10.50) per sample (Table 1). Phase of restoration on TD was not significant (LRT: Chi Sq=0.3462, df=2, *P*=0.8411; n= 342).

Table 2. Average taxonomic richness (TR) and diversity (TD) ± sd (range) per sample in each of the sampling periods of May 7, July 7 and September 24.

	TR	TD
May	8.71 ± 3.6 (3-17)	4.69 ± 2.25 (1.28-10.2)
July	11.16 ± 5.93 (3-34)	5.91 ± 2.21 (1.25-11.68)
Sept	8.74 ± 4.74 (2-26)	4.83 ± 2.04 (1.21-10.7)

There was no significant difference in abundance within functional groups between the three phases, but in all groups, abundance was highest in Phase III (Table 3). Detritivores were most abundant (54.38 ± 87.96) followed by omnivores (18.27 ± 70.07), herbivores (12.5 ± 32.44), parasites and parasitoids (6.01 ± 10.72), predators (5.87 ± 8.65) and flower visitors (2.11 ± 5.32). Most abundant taxa were Aranae: Lycosidae (1.5%); Colembola (13.0%); Orthoptera: Acrididae (2.3%) and Gryllidae (2.8%); Hemiptera: Miridae (4.5%) and Cicadellidae (2.4%); Coleoptera: Carabidae (2.8%); Hymenoptera: Braconidae (2.1%) and Formicidae (7.6%); Diptera: Chironomidae (8.2%), Culicidae (5.0%), Mycetophilidae (19.7%), Syrphidae (1.5%) and Muscidae (5.2%). The remaining taxa were either < 1% or unidentified Diptera species (Appendix B).

Table 3. Average abundance ± sd within functional groups of each of the three project phases.

Treatment	PI	PII	PIII	Overall
Detritivores	38.85 ± 45.83	43.75 ± 44.26	80.54 ± 135.06	54.38 ± 87.96
Flower visitors	1.04 ± 2.65	2.57 ± 5.6	2.71 ± 6.73	2.11 ± 5.32
Herbivores	10.26 ± 26.79	9.7 ± 23.45	17.53 ± 43.25	12.5 ± 32.44
Omnivores	8.04 ± 13.86	12.32 ± 15.13	34.44 ± 118.28	18.27 ± 70.07
Parasites and Parasitoids	3.62 ± 5.55	5.18 ± 8.45	9.24 ± 15.09	6.01 ± 10.72
Predators	6.27 ± 9.31	4.28 ± 6.18	7.05 ± 9.83	5.87 ± 8.65

4. Discussion

We expected invertebrate diversity to increase along with plant diversity as the restoration became established with the greatest diversity and richness in Phase I – the oldest phase - and least in Phase III – the youngest phase (Young, 2000). However, we found no significant difference in TR or TD between phases, nor a difference in abundance of functional groups. Visually, Phase I seemed to meet the expected appearance of restored prairie (Fig. 2). As a direct result of vegetation management, Phases II and III had less structure and fewer blooming forbs (Fig. 3 & 4). Subjectively the restored prairie five years' post-construction met visual standard measures of success. Plants had matured and created a diverse vegetative structure. Vegetation management was provided to remove invasive species before they could become fully established and to allow the native grasses and forbs to establish an adequate root system.

Picaud and Petit (2007) suggest a progressive gain of colonizing species over several years, then a plateau and possibly decline in species number. The first species to settle in a new area are likely to be those present in nearby ecosystems. Hendrychova (2008) reported spontaneous succession of plants and animal from neighboring high quality natural areas to often be more species rich and diverse than planned reclamations.

Our study area had the expected populations of highly mobile generalist species. The most abundant species were the Mycetophilidae. Fungus gnats occur around damp decaying vegetation, algae and fungi. In general, they serve a beneficial role as decomposers and convert dead vegetation into nutrients for plant growth. They also serve as pollinators and as a food source for insect predators, reptiles and birds. Chironomidae (midges) and Culicidae (mosquitoes) are also common in wet areas and serve as an important food source in the food chain.

We observed numerous Collembola in each of the three phases. Collembola are wind dispersed in addition to actively migrating and available from the surrounding landscape. They reproduce several times year which allows them to increase abundance in a short time period.

Cicadellidae (leafhoppers) are part of a diverse group of Auchenorryncha, many of which are closely associated with tallgrass prairie. With close to 700 species in Illinois (DeLong, 1948) this taxonomic group has been proposed as an indicator of tallgrass prairie quality (Wallner *et al.*, 2012). They comprised 2.4% of the individuals in our study. Parmenter *et al.* (1991) showed early colonization of beetles and grasshoppers was similar in all stages of restoration. Our study had similar high numbers of carabid beetles and grasshoppers in each of the three phases.

Muscidae were plentiful and play an important role in breaking down dead organic material. There were numerous other Diptera (flies) that were not identified. Mostly these did not fit into the more common families that were identified or were smaller than 2 mm and could not be thoroughly examined on the sticky boards.

Invertebrates that inhabit the area below the surface generally move from undisturbed areas at the edges. Because mobility is limited, the repopulation is generally slow. Our study area showed the heaviest concentration of ants to be in Phase III. Majer (1998) reported the highest number of ant species 6 years after site rehabilitation in a sand quarry in Queensland Australia. It is our belief that the ants were moving from the closest undisturbed area which was cultivated agricultural fields. Areas closest to Phase I were residential areas.

We also expected to find taxa such as Olicochaeta (earthworms), Gastropoda (snails and slugs), Isopods (pillbugs), Coleoptera (beetles), and Lepidoptera (butterflies and moths). There were only six earthworms in all of the pitfall traps in contrast to other studies in which there were often more than this number at each sampling location (Evans *et al. unpublished data*). The same is true for isopods. It would appear that these taxa had not yet penetrated the restoration site. Our results are consistent with those of Hutson (1980) who measured colonization of industrial reclamation sites. Other than Carabid beetles there were few beetle individuals in our samples. Beetle larvae occupy the below ground strata and seemed not to be present. Adults of several species were present and the vegetation was appropriate so complete establishment of reproduction may take more time. Since butterflies are highly dependent on specific plants for reproductive success and they must come from non-agricultural habitats, they too may have been slow to establish reproduction. Our study area was surrounded by agriculture and quite distant from remnant prairies found elsewhere in the county.

It was noted that small mammals were frequently found in identical pitfall traps in other studies in Central Illinois (Evans *et al. unpublished data*). Associated with these samples were numerous carrion beetles. There were only 34 carrion beetles during this entire study and no traps had small mammals. Small mammals, earthworms, and carrion beetles all inhabit the soil, with beetles utilizing burrows created by earthworms and small mammals.

Lack of many of these organisms at the time of this study may indicate the invertebrate assemblage of the prairie is not yet restored. At least the functional group of soil inhabiting species seems missing. This restoration project seems to follow a pattern more closely related to surface mine reclamation rather than to prairie restoration. Removal of soil and reconstruction of geological contours with partial replacement of topsoil provided a novel vegetative substrate. Recovery of soils after mining often requires more than 15 years to achieve values approximating those found in reference sites (Chambers and McComb, 1994; Craft *et al.*, 2002). Soil quality has been proposed as an indicator of sustainable land management (Herrick, 2000). Soil formation is an ongoing process which requires ongoing measurements and increased costs which are seldom fit within the time-frames and budgets of most restoration projects.

Our data indicate that after the extreme disturbance created by topsoil removal and subsequent replacement, establishment of an invertebrate assemblage appropriate to the new vegetation may take time (Schramm, 1990) or not occur at all. The restoration phases of our study (which were only two, four and five years old) are apparently all characterized by early pioneer assemblages that do not differ significantly from each other. The restoration area was farmed for decades prior to the restoration. Species adapted to agricultural row crops can be supposed to have been available to repopulate the restoration. Mobile species are expected to populate the restoration eventually but for epigeic prairie specialist arthropods, this might take a very long time, or they may not reach the restoration site at all due to colonization problems. Our results indicate that a more long-term view is necessary with some prairie restoration projects and that visual inspection may be inadequate to assess complete ecological restoration.

Urban housing development offers an opportunity to create novel ecosystems that are a consequence of our changing environment. Climate change and anthropogenic alteration of species distributions will force human acceptance to conditions as they are, rather than as we would have them (Hobbs *et al.*, 2009). A hybrid system would accept that agricultural inputs have permanently altered the chemical and biotic composition of the soil. It would accept that various pollinators are no longer available to aid the reproduction of both common and rare plants; and that plants once common in a particular place are now out of their climactic tolerance range. Plants are the basis of the ecological food web and thus the succeeding trophic levels are altered along with the vegetation. While we are able to physically restore prairie flora, at least for a time, we may not be aware of or even able to translocate the invertebrate assemblages and soil microorganisms required for sustaining the vegetation and that may not arrive on their own. Hybrid ecosystems may be the best option for sustainability.

Further research is needed to learn about the time-scale that is needed for prairie restoration projects on former agricultural lands to create a sustainable and functional prairie ecosystem.

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Appendix A

Seed lists combined from Phase I, II, and III.

Scientific name	Common name
Acorus calamus	Sweet Flag
Agastache foeniculum	Hyssop
Alisima subcordatum	Water Plantain
Allium cernuum	Nodding Onion
Allium stellatum	Prairie Onion
Amorpha canescens	Lead Plant
Andropogon gerrardii	Big Blue
Anenome cylindrica	Meadow Anenome
Asclepias incarnata	Swamp Milkweed
Asclepias tuberosa	Butterfly Milkweed
Aster azureus	Sky-blue Aster
Aster ericoides	Heath Aster
Aster novae-angliae	New England Aster
Aster umbellatus	Flat-topped Aster
Baptisia leucantha	White Wild Indigo
Bidens cernua	Nodding Bur-Marigold
Boltonia asteroides	False Aster
Bouteloua curtipendula	Side Oat's Grama
Bromus kalmii	Prairie Brome
Cacalia plantaginea	Indian Plantain
Calamagrostis canadensis	Blue Joint Grass
Caltha palustris	Yellow Marsh-Marigold
Carex bebbii	Bebb's Sedge
Carex bicknelli	Bicknell's Sedge
Carex comosa	Longhair Sedge
Carex cristatella	Crested Sedge
Carex frankii	Frank's Sedge
Carex grayi	Gray's Sedge
Carex hirsutella	Hairy-leaved Sedge
Carex hystricina	Sedge
Carex lacustris	Sedge

Carex laeviconica	Sedge
Carex lupulina	Sedge
Carex lurida	Sedge
Carex scoparia	Broom Sedge
Carex stricta	Tussock Sedge
Carex tribuloides	Bristlebract Sedge
Carex vulpinioidea	Foxtail Sedge
Cassia fasciculata	Partridge Pea
Cassia hebecarpa	Wild Senna
Chelone glabra	White Turtlehead
Coreopsis palmata	Prairie Coreopsis
Dalea purpurea	Purple Prairie Clover
Desmanthus illinoensis	Bundle Flower
Dodectheon meadia	Shooting Star
Echinacea pallida	Pale Coneflower
Echinacea purpurea	Purple Coneflower
Eleocharis obtusa	Spikenard
Elymus canadense	Canada Wild Rye
Elymus hystrix (Hystrix patula)	Bottlebrush Grass
Elymus riparius	Riverbank Rye
Elymus virginiana	Virginia Wild Rye
Eragrostis spectabilis	Love Grass
Eryngium yuccifolium	Rattlesnake Master
Eupatorium maculatum	Joe-pye-weed
Eupatorium perfoliatum	Boneset
Eupatorium purpureum	Sweet Joe-pye-weed
Euphorbia corollata	Flowering Spurge
Eylmus virginicus	Virginia Rye
Filipendula rubra	Queen-of-the-Prairie
Gentiana andrewsii	Bottle Gentian
Gentiana flavida	Cream Gentian
Glyceria striata	Fowl Manna Grass
Helenium autumnale	Sneeze-weed
Heliopsis helianthoides	False Sunflower
Hibiscus laevis	Rose Mallow
Hibiscus moscheutos	Swamp Rose Mallow

Hyericum pyramidatum	St John's Wort
Iris shrevei	Blue Flag / Iris
Juncus dudleyi	Dudley's Rush
Juncus effusus	Soft Rush
Juncus interior	Lake Rush
Juncus tenuis	Path Rush
Juncus torreyi	Torrey's Rush
Justicia americana	American Water-willow
Koeleria macrantha	June Grass
Liatris pychnostachya	Prairie Blazing Star
Liatris spicata	Marsh Blazing Star
Liatris spicata	Prairie Blazing Star
Lobelia cardinalis	Cardinal Flower
Lobelia siphilitica	Great Blue Lobelia
Lythrum alatum	Winged Loosestrife
Mimulus ringens	Monkey Flower
Monarda fistulosa	Bergamot
Panicum virgatum	Switch grass
Parthenium integrifolium	Wild Quinine
Pedicularis canadensis	Wood Betony
Penstemon digitalis	Beardstongue
Penthorum sedoides	Ditch Stonecrop
Phlox maculata	Sweet William
Physostegia angustifolia	Narrow Leafed Obedient Plant
Physostegia virginiana	Obedient Plant
Pontederia cordata	Pickerel Weed
Potentilla arguta	Tall Cinquefoil
Pycnanthemum pilosum	Hairy Mountain Mint
Pycnanthemum virginianum	Mountain Mint
Ratibida pinnata	Yellow Coneflower
Rudbeckia hirta	Black-eyed Susan
Ruellia humilis	Petunia
Sagittaria latifolia	Arrowhead
Schzachyrium scoparium	Little Bluestem
Scirpus cyperinus	Wool-grass
Scutellaria laterifora	Blue Skullcap

Silene regia	Royal Catchfly
Silphium integrifolium	Rosinweed
Silphium laciniatum	Compass Plant
Silphium perfoliatum	Cup-plant
Silphium terebinthinaceum	Prairie Dock
Sisyrinchium angustifolium	Narrowleaf Blue-eyed Grass
Solidago rigida	Rigid Goldenrod
Solidago speciosa	Showy Goldenrod
Sorghastrum nutans	Indian Grass
Spartina pectinata	Cord Grass
Sporobolis asper	Rough Dropseed
Sporobolus heterolepsis	Northern Dropseed
Teucrium canadense	Germander
Tradescantia ohiensis	Ohio Spiderwort
Tridens flavus	Purpletop
Verbena hastata	Blue Vervain
Verbena stricta	Hoary Vervain
Vernonia fasciculata	Ironweed
Veronicastrum virginicum	Culver’s Root
Viola pedatifida	Prairie Violet
Zizia aurea	Golden Alexanders

Appendix B

Abundance of Operational Taxonomic Units (OTU) in each of the three phases of restoration. Guild associations are detritivores (D), flower visitors (F), herbivores (H), not feeding as adults (NA), omnivores (O), parasites and parasitoids (PA), and predators (PR).

Taxa	**Phase I**	**Phase II**	**Phase III**	**Guild**
Class Oligochaeta: Earthworms	4	2	0	D
Class Gastropoda				
Snails	6	1	0	H
Slugs	46	64	47	H
Order Araneae: Spiders				
Araneidae: Orb Weavers	4	0	0	PR
Acanthepeira stellate: Starbellied Orbweavers	0	0	1	PR
Tetragnathidae: Long-jawed Orb Weavers	4	10	1	PR
Linyphiidae: Sheet Web Spiders	91	36	39	PR
Pisauridae: Nursery-Web Spiders	0	0	2	PR
Lycosidae: Wolf Spiders	101	87	201	PR
Gnaphosidae: Parson Spiders	19	9	21	PR
Thomisidae: Crab Spiders	2	3	12	PR
Salticidae: Jumping Spiders	4	4	3	PR
Spider hatchlings	40	0	0	PR
Order Opiliones: Harvestmen	0	2	11	PR
Order Acari: Ticks	4	1	2	PA
Order Isopoda: Isopods				
Armadillidiidae: Common Pillbugs	21	5	2	O
Order Diplopoda: Millipedes	1	2	3	D
Order Chilopoda: Centipedes	0	4	14	PR
Order Collembola: Springtails	611	861	1934	D
Order Odonata: Damselflies				
Coenagrionidae: Damselflies	5	21	9	PR
Order Orthoptera				
Acrididae: Grasshoppers	109	311	197	H

Taxa	**Phase I**	**Phase II**	**Phase III**	**Guild**
Gryllidae: Crickets	180	41	504	H
Order Plecoptera: Stoneflies	0	0	1	NA
Order Hemiptera: True Bugs				
Miridae: Plant Bugs	292	199	697	H
Nabidae: Damsel Bugs	0	0	1	PR
Anthocoridae: Minute Pirate Bugs	3	20	43	PR
Reduviidae: Assassin Bugs	6	32	27	PR
Lygaeidae: Seed Bugs	2	1	1	H
Geocoridae: Big-Eyed Bugs	0	1	0	PR
Largidae: Plant Bugs	58	78	8	H
Alydidae: Broad-headed Bugs	2	0	0	H
Scutelleridae: Shield-Backed Bugs	0	0	4	H
Rhopalidae: Scentless Plant Bugs	1	0	0	H
Cydnidae: Burrower Bugs	0	0	1	H
Pentatomidae: Stink Bugs	1	7	0	H
Cicadidae: Cicadas	0	1	0	H
Membracidae: Treehoppers	1	2	0	H
Cicadellidae: Leafhoppers	276	171	184	H
Fulgoroidea: Planthopper	28	12	18	H
Aphidae: Aphids	42	76	123	H
Order Thysanoptera: Thrips	1	0	0	H
Order Coleoptera: Beetles				
Cicindelidae: Tiger Beetles	0	0	1	PR
Carabidae: Ground Beetles	218	178	331	PR
Histeridae: Hister Beetles	3	4	2	PR
Silphidae: Carrion Beetles	32	0	2	D
Scaphidiidae: Shining Fungus Beetles	2	4	7	D
Trogidae: Trox Beetles	11	4	4	D
Scarabaeidae: Scarab Beetles	80	9	9	H
Popillia japonica: Japanese Beetle	1	0	0	H
Elateridae: Click Beetles	12	16	15	H
Cantharidae: Soldier Beetles	7	5	2	PR
Cleridae: Checkered Beetles	108	44	36	PR

Taxa	Phase I	Phase II	Phase III	Guild
Erotylidae: Pleasing Fungus Beetles	0	1	3	D
Byturidae: Fruitworm Beetles	0	0	1	H
Coccinellidae: Lady Beetles	6	2	6	PR
Hippodamia parenthesis: Parenthesis Beetles	3	4	6	PR
Mordellidae: Tumbling Flower Beetles	15	19	16	F
Meloidae: Blister Beetles	1	7	7	H
Cerambycidae: Long-horned Beetles	0	1	1	H
Chrysomelidae: Leaf Beetles	42	31	26	H
Microhopala vittata: Goldenrod leaf miner	1	0	0	H
Curculionidae: Weevils	38	50	106	H
Coleoptera larva ssp	18	5	17	H
Order Neuroptera: Antlions, Lacewings	10	2	2	PR
Order Hymenoptera: Wasps, Bees, Ants				
Symphyta: Sawfly ssp	15	10	12	H
Ichneumonidae: Ichneumon Wasps	6	15	11	PA
Braconidae: Parasitic Wasps	229	144	178	PA
Chrysididae : Cuckoo Wasps	4	9	23	PA
Sphecidae: Thread-Waisted Wasps	6	6	8	F
Halictidae: Sweat Bees	8	16	7	F
Andrenidae: Mining Bees	5	23	54	F
Apidae: Honey Bees	6	14	42	F
Bombus pensylvanicus: Bumble Bee	0	1	4	F
Mutillidae: Velvet Ants	1	0	0	PA
Pompilidae: Spider Wasps	0	1	1	F
Vespidae: Hornets, Wasps	2	14	22	F
Dolichovespula maculate: Bald faced hornet	6	5	21	F
Formicidae: Ants	122	74	1799	O
Lepidopetera: Butterflies and Moths				
Micro-lepidoptera[1]	8	15	8	F
Hesperiidae: Skippers	1	1	1	F
Pieridae: Sulphers	2	7	7	F
Pieris rapae: Cabbage Butterfly	0	1	0	F
Geometridae: Geometer Moths	1	0	0	F

Taxa	Phase I	Phase II	Phase III	Guild
Noctuidae: Owlet Moths	0	3	3	F
Lepidoptera larva ssp	9	34	29	H
Order Diptera: Flies				
Tipulidae: Crane Flies	5	5	4	F
Chironomidae: Midges	412	422	1318	NA
Culicidae: Mosquitoes	147	381	774	PA
Mycetophilidae: Fungus Gnats	167	103	4863	D
Stratiomyidae: Soldier Flies	0	2	0	F
Rhagionidae: Snipe Flies	1	0	0	PR
Tabanidae: Horse Flies, Deer Flies	0	1	0	PA
Asilidae: Robber Flies	1	0	1	PR
Bombyliidae: Bee Flies	0	2	0	F
Dolichopodidae: Long-legged Flies	57	1	10	PR
Phoridae: Hump-backed Flies	4	25	22	O
Syrphidae: Flower Flies	61	185	144	F
Calliphoridae: Blow Flies	26	3	5	D
Tachinidae: Tachinid Flies	0	0	4	PA
Muscidae: House Flies	224	291	842	O
Ulidiidae: Picture-winged Flies	19	20	30	F
Diptera ssp	543	1012	1249	O
Diptera larva ssp	2	3	7	O

[1] Small Lepidoptera of the Super Families Gelechioidea, Pyraloidea, Tiniodea, Gracillarioidea, Incurvarioidea, and Families Tortricidae and Pterophoridae.

Chapter 4

Lepidoptera pest species response to mid-summer fire

Based on: Lepidoptera pest species response to mid-summer fire. Evans, T.R., C.J.M. Musters, E.D. Cashatt, and G.R. de Snoo. Submitted 5/25/2016. Fire Ecology, 9: 25-32.

Abstract

In the American Midwest, summer fires are infrequent and there is little information on their impact on ecosystems. After an accidental wildfire in a 20 ha grassland restoration, new growth provided effective substrate for the noctuid species corn earworm (*Helicoverpa zea* Boddie 1850) and tobacco budworm (*Heliothis virescens* Fabricius 1777). These agricultural pests feed on a number of important crop species and have been implicated in crop losses up to 50 %. Invertebrate collections were made at 16, 45, 70, and 101 days post fire. A comparison of burned and unburned areas at 70 days post fire show 18 times the number of Lepidoptera larvae collected in pitfall traps in the burned area compared to the adjacent unburned area of the grasslands. These findings demonstrate that a mid-summer fire can affect the abundance of economically important insects.

Keywords: agricultural pests, corn earworm, Lepidoptera larvae abundance, Midwest, prairie management, tobacco budworm, wildfire

Introduction

In prairie management in the United States, prescribed burning is a preferred technique used to achieve a variety of objectives; fuel load reduction (Fernandes and Botelho, 2003), mineral soil exposure (Choromanska and DeLuca, 2002), nutrient release (Boerner, 1982), seedbed preparation (Chapman, 1936), invertebrate pest control (Vermeire *et al.,* 2004), disease reduction (Hardison, 1976) and invasive species control (Pendergrass *et al.*, 1999). Most research has been conducted on the impacts of spring prescribed fire in specialized habitats (Panzer, 2002; Vogel *et al.*, 2007) while information on the consequences of summer fires is limited. Interestingly, summer fires may more accurately represent natural and historical processes (Gleason, 1913; Howe, 1995).

The ecology of important agricultural pest species and proximate factors influencing their abundance are incompletely understood. These factors may include management practices un-related to pest control. In Illinois, Conservation Reserve Program (CRP) management takes place within an agricultural landscape and requires consideration of unintended consequences in an agricultural context. After an accidental wildfire, we set pitfall traps in the burned and unburned areas within a 20 ha field to observe the invertebrate repopulation of the area. Here we show that a mid-summer burn may provide additional opportunities for breeding of important pest species.

Methods

Study Area. The study area is located in central Illinois (Figure 1, inset) in Sangamon County (39°45’09.18N, 89°28’16.98W, within the Grand Prairie Natural Division (Schwegman, 1973), a vast plain formerly of mostly tall-grass prairie. The research area was a 20 ha field enrolled in the CRP for 12 years and seeded in native warm season grasses and mixed forbs. This field was part of a larger area of CRP that included tree plantings. Management of the field included hand removal of brush and trees with cut stump herbicide treatment. Due to reduced precipitation and high ambient temperatures during the preceding 15 months, this region was considered to be in an extreme drought (National Oceanic and Atmospheric Administration, 2012).

An unplanned wildfire (27 July 2012) burned more than 100 ha including the 20 ha field which was later selected for study (Figure 1). The fire was reported to be intensely hot, in part due to the high fuel load resulting from the drought, and was allowed to burn uncontrolled while available fire crews were protecting neighboring homes. It consumed all of the above surface vegetation. This was followed by a flush of growth, closely resembling new growth in the spring. We used this unique opportunity to study post-fire invertebrates.

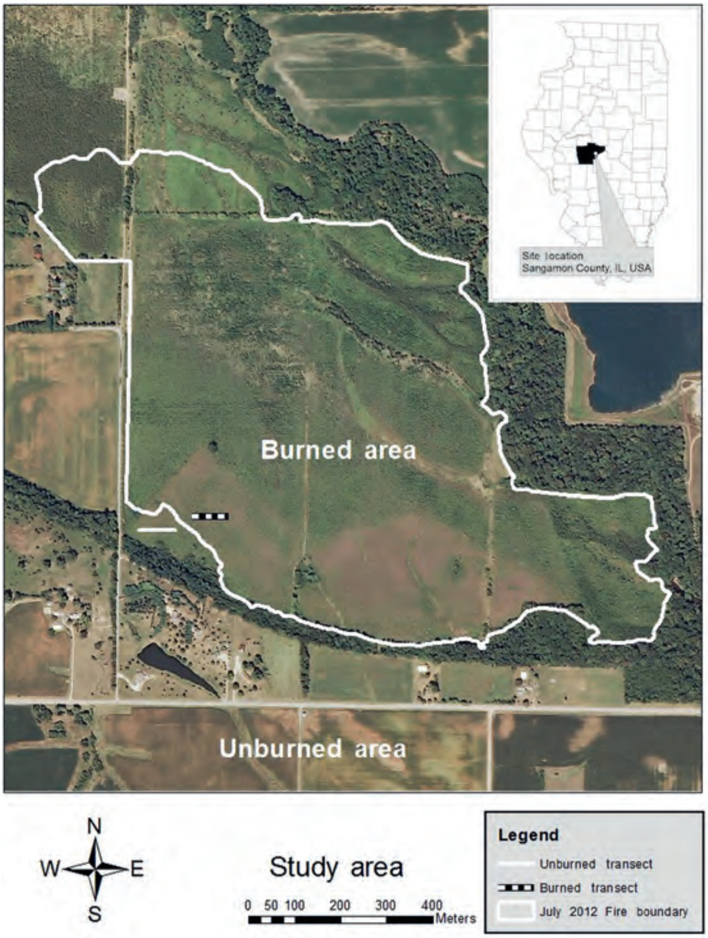

Figure 1. Site of wildfire (27 July 2012) showing the extent of the burned and unburned areas and the location of the transects. Inset shows the location of Sangamon County in Illinois.

Sampling. We sampled invertebrates using 18 pitfall traps placed on two 80 m transects in unburned and burned prairie restoration. There were nine pitfall samples 10 m apart on each transect. The end points of the transects were 50 m apart, 25 m from the burn boundary (Figure 1). Pitfall traps were 150 ml plastic cups with a water and vinegar solution and detergent added to break the surface tension of the water (Eymann *et al*., 2010). In a pilot study, Ethylene glycol was found to be a problem by attracting mammals to the traps. It was found to be a problem in similar studies and this disturbance can result in significant loss of data (Fassbender, 2002). For this reason, vinegar was used rather than ethylene glycol. The pitfall contents were retrieved 7 days after placement and stored in Isopropyl alcohol. We collected samples 11 August, 9 September, 5 October, and 4 November 2012 (16, 45, 70, and 101 days post-fire). The small area (2 ha) of unburned prairie limited the number of replicates (Figure 2). All specimens were counted and identified to family. Nomenclature follows Lafontaine and Schmidt (2010). The presence of large numbers of Lepidoptera larvae prompted a more thorough identification than study protocols indicated. Lepidoptera larvae were identified using keys and morphological characters from Crumb (1956), Neunzig (1964, 1969), and Stehr (1987).

Data Analysis. We performed statistical analysis using R software 2.14.1 applying a General Linear Model (GLM) assuming a quasipoisson distribution because of the non-normal data distribution. The model we used for the GLM analysis included all interactions between factors: Number ~ Burned * Month * Species. "Number" was the number of Lepidoptera larvae per pitfall, the response variable. "Burned" is a binomial variable indicating whether the pitfall was in the burned or unburned area and "Month" was the month of the observation. "Species" was either corn earworm (*Helicoverpa zea* Boddie 1850), or tobacco budworm (*Heliothis virescens* Fabricius 1777). The effect of separate factors was studied by applying an F-test.

Results

October (70 days post fire) the average number of Lepidoptera larvae in the burned area (n = 60) was over 18 times the number found in the unburned (n = 3) area. Noctuids, corn earworm and tobacco budworm (Neunzig, 1964; 1969), comprised 83 % (50 of 60) of the Lepidoptera larvae collected (Figure 2). Corn earworm was the most abundant (53 %) followed by tobacco budworm (30 %). The remaining larvae (17 %) were classified as Arctiidae and Noctuidae. They were categorized as "other" as they were clearly different from *H. zea* and *H. virescens* and were different from each other. Because of the low numbers of the other larvae, they were not identified to species nor included in further analyses.

Interaction effects were not significant (Table 1). Numbers of Lepidoptera larva differed in the burned and unburned areas of the field ($F = 91.776$, $P \leq 0.001$). The month in which the sample was taken also differed, with October having the most larvae ($F = 66.224$, $P \leq 0.001$). Numbers of corn earworm and tobacco budworm larvae differed from each other ($F = 6.127$, $P < 0.015$).

The observed increase in number of Lepidoptera larvae (Figure 2) corresponded to the time needed for vegetation to re-grow, adult moths to lay their eggs on new vegetation and larvae to go through several instars. The abrupt decline in numbers for November reflects a killing freeze (-3 °C) 4 November 2012 and autumn pupation.

Table 1. Analysis of the separate factors of the complete model. Factors significantly affecting larvae numbers are portion of the field that was burned or unburned (Burned), month of sampling post-fire (Month), and larval species of corn earworm or tobacco budworm (Species).

Complete Model	Df	Deviance	Residual df	Residual Deviance	F	Pr(>F)
Burned	1	59.511	142	205.481	91.778	< 2e-16 ***
Month	3	128.826	139	76.655	66.224	< 2e-16 ***
Specie	1	3.973	138	72.683	6.127	0.0146 *
Burned*Month	3	0.041	135	72.642	0.021	0.996
Species*Month	3	0.904	132	71.738	0.465	0.707
Burned*Species	1	.0928	131	70.810	1.431	0.234

Significance codes: '***' <0.001 '**' 0.01 '*' 0.05

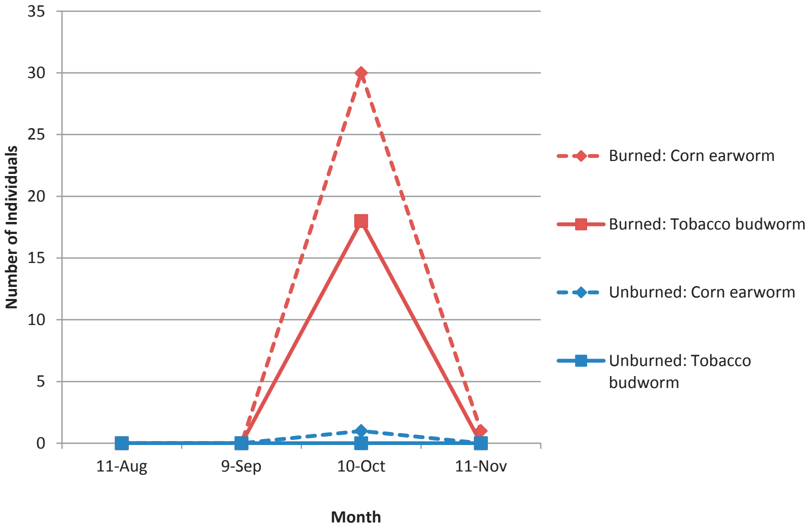

Figure 2. Numbers of Lepidoptera larvae (mean ± sd) in burned and unburned CRP field (Illinois, USA) during sampling at 16, 45, 70, and 101 days post-fire (27 July 2012).

Discussion

The key novel finding in this study is that a mid-summer burn can produce immediate major shifts in distribution of agriculturally-important insects, in the sense that it attracts adult moths to lay their eggs on tender re-growth after the fire. It is unlikely that the differences we found in the number of larvae were due to the change in vegetation density or movement of the larvae. In other studies (T.R. Evans, unpublished data), vegetation height and density had no significant impact on trapping probability.

In this study the predominant species collected were the noctuids corn earworm and tobacco budworm. Both species are polyphagous (Tietz, 1972) and significant agricultural pests because of their abundance and wide host range containing many agricultural crops (Neunzig, 1969). Host crops include corn, tomato, cotton, green beans, clover, vetch, lettuce, peppers, soybeans and sorghum. Estimated losses in field corn in the southern United States range from 1.5 to 16.7 %. In Illinois, major economic impact is limited to damage to sweet corn and seed corn with as much as 50 % loss (Cook and Weinzierl, 2004). The North Central Integrated Pest

Management Pest Information provides at least bi-weekly monitoring information in several Illinois counties for abundance of corn earworm adults.

Although the encountered noctuids usually die out during winter in most of the state, pupae survive winter in soil in far southern Illinois most years. Populations can also overwinter in other parts of the state during mild winters. Despite some local overwintering, populations of these insects in Illinois emigrate from southern states in late spring and early summer (Cook and Weinzierl 2004) with moths arriving on weather fronts and laying their eggs in susceptible crops. In Illinois, adults are usually found in June and can produce two full generations per season. At an average temperature of 25 °C it takes 49.3 days to complete development and burrow in the soil to pupate (Neunzig, 1969). Adults lay eggs on host vegetation; when larvae hatch they move away from light to moist shady areas. Population densities usually peak in late summer.

Dominant plants in the burn area and within 10 m of the trapping area were ground cherry (*Physalis spp.),* sunflower (*Helianthus* spp.), and goldenrod *(Solidago* spp.), known hosts of both larvae (Tietz, 1972). The encountered plant species are common in CRP restorations and provide host plants outside the agricultural crops.

Prescribed burning guidelines provide limits of fuel load, ambient temperature, wind speed and direction, and time of day (Bunting *et al.,* 1987). The accidental fire described in this study would not fall within limits found in prescribed burn guidelines. However, the flush of new growth occurs as part of the burning process, either planned or accidental. The newly emergent growth provides benefits for desired species (Baum and Sharber, 2012) as well as undesirable species.

The marked increase in number of Lepidoptera larvae we found in the newly established vegetation could indicate either that this type of young vegetation is a limiting factor for oviposition of the species concerned, or that the females of the species have strong preference for this type of vegetation for oviposition (Verdasca *et al*., 2011; Baum and Sharber, 2012). In the first case, mid-summer fire would strongly increase the number of eggs laid by the species in a certain area. In the latter case, assuming that the preference of the females is related to the survival of eggs and larvae, the mid-summer fire would increase the survival of the egg and larvae population in an area. In both cases, the mid-summer fire will increase the number of pupae in the soil during winter and in turn increase the probability of recruitment in the event of a mild winter. Only in the improbable case of no or a negative relationship between preference of females and egg and larvae survival, mid-summer fire would not increase the number of pupae in the soil. The abundance of available host plants allows early establishment of this pest species in those years where there are mild winters.

Grasslands evolved for millennia under conditions of natural summer and early fall fire started by lightning (Keeley and Rundel, 2005; Anderson, 2006; Pausas and Keeley, 2009). Historical frequency of fires is uncertain but available evidence indicates that fire occurrence varied from every 5-10 years to every 20-30 years (Wright and Bailey, 1982). The assumption that an individual ecosystem is adapted to fire is different than the assumption that a specific ecosystem is adapted to a specific fire regime (Pausas and Keeley, 2009). Application of a fire regime different from that to which species have evolved could produce negative results in (semi-) natural habitats (Howe, 1995). On the other hand, a regime that closely resembles natural fire events could be a risk for agricultural systems as our results would seem to suggest. How large the actual impact on agriculture of a mid-summer fire could be, both in terms of crops and area that would be affected, needs to be studied.

Both timing and frequency of fire as a management tool is an important facet of the planning process. Management goals should be clear with possible unintended consequences to the neighboring agricultural landscape taken into consideration. Fire has consequences and being aware of potential impacts lets us more wisely choose how to get the desired results.

Acknowledgements
We thank G.H. Godfrey and J. Wiker for confirming the identification of the *Noctuid* spp. We also thank R. Geroff for providing maps. We thank M.J. Mahoney for comments on a previous draft of this manuscript. We thank S. Ebbing for his instant response to all library requests.

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Chapter 5

Arthropod Recovery After a Wildfire: A Case Study

T.R. Evans, M.J. Mahoney, E.D. Cashatt , G. de Snoo and C.J.M. Musters. Arthropod Recovery After a Wildfire: A Case Study. Submitted to the International Journal of Wildland Fire

Abstract

Summer wildfires are infrequent and rarely documented in the American Midwest. Historically, fires were set by indigenous people for various reasons while today prescribed fire in the dormant season with carefully controlled conditions is most often used as a tool for vegetation management. Here we document the acute and chronic impacts of an accidental wildfire on invertebrate populations in a 20 ha grassland restoration in central Illinois, USA. Samples were collected in burned and nearby unburned areas using sticky boards and pitfall traps each month of the growing season immediately following the fire and the first and third growing seasons post-fire. Our study found that in the third growing season post-fire; some taxa did still not have the same taxonomic richness, diversity and abundance as the neighboring unburned area. Common measures of taxonomic richness, diversity and abundance did not represent the changes in invertebrate assemblages that occurred three growing seasons post-fire. We provide information for fire management decisions.

Keywords: wildfire, invertebrates, grassland, Conservation Reserve Program, CRP, mid-season fire, taxonomic richness, diversity, abundance

Introduction

Fire has long-term repercussions on invertebrates. Prescribed burns have been used for decades to mimic historic fires that were instrumental in the development of the tall-grass prairie ecosystem. It is believed that fire kept forests from encroaching on the grasslands. Current practice is to use prescribed burning, generally in the spring, for vegetation control. Increasingly, concern is being expressed about the impact of prescribed burns, their timing, interval, and intensity on other inhabitants of the prairie, specifically invertebrates (Jacobs *et al.,* 2015). Common population metrics may not tell the entire story.

Fire is frequently used a tool for gross vegetative control in grassland habitats in the Midwest (Knapp *et al.,* 2009). The benefits include fuel load reduction, seed release, and invasive species control (Warren *et al.*, 1987; Ryan *et al.,* 2013). Fires are usually conducted by trained personnel under narrowly prescribed conditions including relative humidity, wind speed and direction, soil moisture levels, and temperatures (Weir, 2009). Prescribed fire is usually conducted during the dormant season while many species are inactive and in a generally protected environment (Ryan *et al.,* 2013). There is a litter layer of dried vegetation to provide fuel for the fire (Knapp *et al.,* 2009). Often there is considerable soil moisture which keeps the soil and its plant and animal inhabitants from drying (Warren *et al.,* 1987; Gagnon *et al.,* 2015). Lack of canopy vegetation keeps the fire low on the ground and lessens impact on larger trees. Spring burns provide a flush of ash that acts as fertilizer (Sharrow and Wright, 1977). Removal of the litter layer allows increased insolation and early greening of the nascent vegetation (Sharrow and Wright, 1977; Swengel, 2001).

There are some negative aspects of dormant season burns. The window when all conditions are good is very small. Some species overwinter in the litter layer and are consumed by the fire (Ryan *et al.,* 2013). The effects of fire are additive and repeated dormant season burns may affect some species disproportionately. Consequently, there is an effort by some land managers to incorporate timing and interval of fires from historical data to mimic the evolutionary conditions of prehistoric prairies (Ryan *et al.,* 2013).

The acute and chronic impacts of fire on biodiversity can be divided into four phases: 1) fuel development phase; 2) combustion phase; 3) shock phase; and 4) recovery phase (Warren *et al.,* 1987). Acute impacts include mortality from the combustion and continue indirectly until new vegetative regrowth begins. Chronic impacts include immigration and emigration, changed botanical composition and physical structure, and altered invertebrate assemblages and trophic structures (Warren *et al.,* 1987). Invertebrate response is variable, dependent on which specific invertebrate group is being studied and the timing of the burn (Harper *et al.,* 2000; Swengel, 2001). Species below ground, protected by aboveground structure (e.g., unburned wood or rocks), or highly mobile species that can escape have little or no decline during the combustion or shock phases. For less mobile individuals, those in a flightless life stage or with slow dispersal propensity the impact is greater during each of the combustion, shock and recovery phases. There is also evidence that some species in a variety of families (mostly Coleoptera: Buprestidae, Cerambycidae, Silphidae; Diptera: Empididae, Platypezidae) are attracted to fire or smoke (Warren *et al.,* 1987; Reed, 1997; Schmitz *et al.,* 2016).

There are numerous studies focusing on the impact of fire on grasslands both short and long-term on single species (Morris, 1975; Bargmann *et al.,* 2015). There are also studies comparing impacts from a variety of vegetation control methods (Callaham *et al.,* 2003; Benson *et al.,* 2007). There are fewer studies looking at the long-term impacts on prescribed burns with various fire intervals (Evans, 1988; Enright *et al.,* 2015; Moore *et al.,* 2015). There is a lack of information about the impacts of fire that is not prescribed during the growing season in the Midwest agricultural landscape. Examination of these unusual conditions will allow us to develop general recommendations to benefit invertebrate assemblages rather than focus on survival of a single species of interest during the growing season.

In Illinois, wildfire is an uncommon event. In 2012, an unplanned wildfire burned a 100 ha area that included a 20 ha field enrolled as part of a larger area enrolled in the Conservation Reserve Program (CRP). A study of the invertebrate assemblage immediately following the wildfire found in increase in lepidopteran larva associated with the spring-like growth of vegetation 70 days post-fire (Evans *et al.,* 2013). This paper examines both acute and chronic impacts of the wildfire on invertebrate populations until new vegetation was established three growing seasons post-fire. Our study documented three population metrics, taxonomic richness, diversity, and abundance during the shock phase (ten days to the end of the vegetation growing season three months post-fire), the recovery phase (first complete vegetation growing season post-fire), and new vegetation establishment (third complete vegetation growing season post-fire).

In light of the ongoing discussions about the impact of fire on invertebrate communities, we took the unique opportunity of a mid-growing season wildfire to show long-term effects on the invertebrate assemblages. We used hypotheses testing with Kullback-Leibler information theory as a basis, to infer the impact of time post-fire through vegetation recovery phases on each of the population metrics (Warren *et al.,* 1987; Burnham and Anderson, 1998, Burnham and Anderson, 2001). After selecting the model that best fit our data, we then examined the impact on invertebrate abundance within taxonomic units and trophic guilds. We show how studies that report no change in population metrics such as taxonomic richness, diversity and abundance may be missing "the rest of the story" (Aurandt, 1977).

Methods

Study Area. The study area is located in Sangamon County, Illinois, USA (39°45'09.18N, 89°28'16.98W). This area was historically part of the tall-grass prairie within the Grand Prairie Natural Division (Schwegman, 1973) and more recently converted to agriculture. The research area was a 20 ha segment of a larger parcel of land enrolled in the Conservation Reserve Program (CRP). The field was seeded in native warm season grasses and mixed forbs in 2000. The landowners managed the field with hand removal of brush and trees and cut-stump herbicide applications.

Illinois climate is typically continental with cold winter temperatures (mean −3.8 °C), warm summers (24.6 °C), and frequently fluctuating temperature, humidity, cloudiness and wind conditions. Precipitation averages 895 mm per year and temperatures average 11.2°C. The growing season is ~185 days. During the first year of the study (2012) precipitation was 300-400 mm below average and ambient temperatures were 2.4 °C higher than average (Midwestern Regional Climate Center 2009; Springfield, Illinois http:/mrcc.isws.illinois.edu\CLIMATE –accessed December 4, 2015).

On July 27, 2012, an unplanned wildfire burned more than 100 ha which included the 20 ha field of study (Figure 1). Ambient weather conditions were extremely hot and dry with high winds. High fuel loads caused by the drought made the fire intensely hot. The fire was allowed to burn to the natural firebreak provided by a creek. The fire consumed most of the above ground vegetation that included young trees, grasses and litter layer. The fire was followed by new growth resembling spring conditions (Evans *et al.,* 2013). We used the opportunity to compare post-fire invertebrate populations with an unburned portion of the same field.

Sampling. We sampled invertebrates using sticky boards and pitfall traps placed on 80 m transects in the unburned and burned prairie restoration. We used nine sampling points 10 m apart on each transect. The ends of the transects were 50 m apart, 25 m from the burn boundary (Figure 1). Pitfall traps were 150 ml plastic cups with a water and vinegar solution and detergent added to break the surface tension of the water (Eymann, 2010). We retrieved pitfall contents seven days after placement, strained and stored in isopropyl alcohol.

We placed one sticky board (Sensor ~ 8 cm x 13 cm Yellow Monitoring Cards, GrowSmart), attached to a flag (~ 6 cm X 9 cm X 76 cm LimeGlo, Forestry Suppliers) adjacent to each pitfall trap. We placed sticky boards with a minimum of half the board above the vegetation. We retrieved sticky boards after two days, placed them in a clear plastic cover and saved them for future identification.

We conducted sampling to include the shock phase (ten days to the end of the vegetation growing season three months post-fire), the recovery phase (first complete vegetation growing season post-fire), and new vegetation establishment (third complete vegetation growing season post-fire) (Warren *et al.* 1987). In 2012, we collected invertebrate samples on 11 August, 9 September, and 5 October. In 2013 and 2015, collections were made on five dates, 1 May, 9 June, 9 July, 5 August, and 3 September 2013, and 12 May, 16 June, 21 July, 25 August, and 29 September 2015. We terminated the collections after the first hard freeze that seriously damaged or killed seasonal vegetation. The small area (~ 2 ha) of unburned prairie limited the number of replicates (Figure 1). A botanist characterized the vegetation, both in the burned unburned areas, on July 12, 2013 and again on August 26, 2015. Plant nomenclature follows Mohlenbrock (1986).

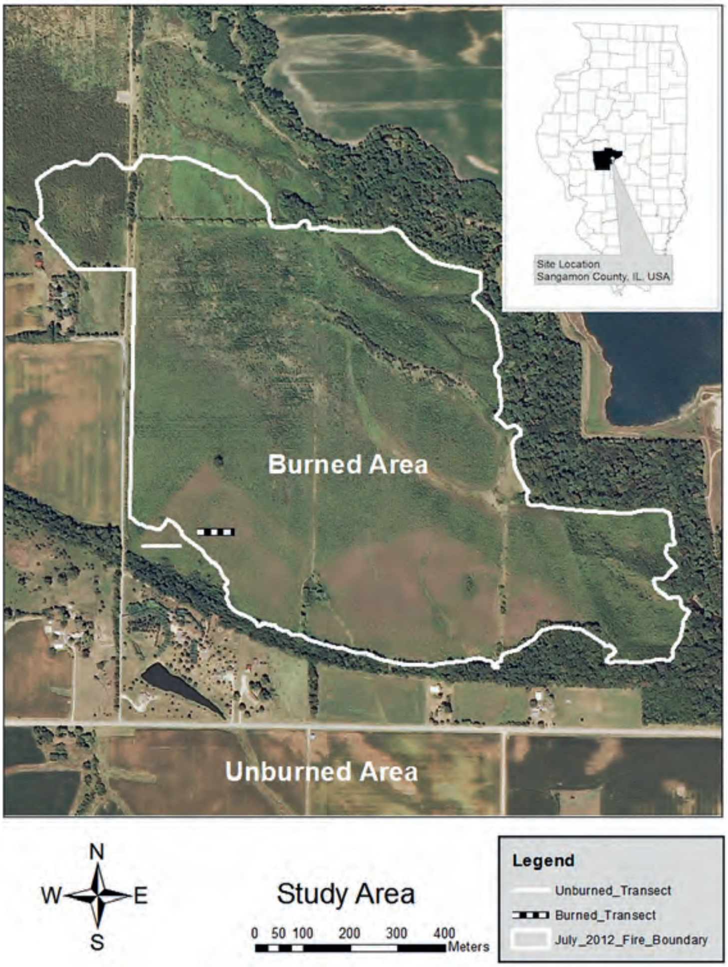


Figure 1. Map of study site and extent of wildfire 27 July, 2012.

We examined arthropods under a binocular microscope for identification. We re-examined ten percent of the samples as quality control. An independent expert adjudicated conflicting identifications. We estimated numbers of arthropods smaller than 2 mm. We used taxonomic keys (Triplehorn and Johnson, 2005) and reference collections housed at the Illinois State Museum Research and Collections Center (ISM RCC) to identify invertebrates larger than 2 mm. We made identifications to the lowest operational taxonomic unit (OTU) possible that in most cases was family. We characterized all OTUs to trophic guild, i.e., herbivores, detritivores, flower visitors, omnivores, predators, parasites and parasitoids, and non-feeding adults.

Data Analysis. We performed statistical analysis using R software 3.1.2 (R Development Core Team 2014). For analysis we used a Linear Mixed Model (LMM) [lmer () of the package lme4 (Bates *et al.* 2014). Treatment, month and year of collection, and method of collection were our independent variables that could also be used as random effect variables. All our models were maximum random effect models, i.e., including the effects on both the intercept and the regression coefficient in order to achieve conservative testing of the fixed effects (Barr *et al.* 2013). Our dependent variables were Taxonomic Richness (TR), i.e., the number of OTUs per sample, Taxonomic Diversity (TD) per sample, i.e., the exponentially transformed Shannon Wiener H', making it Hill numbers of order 1 (Hill, 1973; Spellerberg and Fedor, 2003; Jost, 2007), and Absolute Abundance (AA), i.e., the number of individuals per sample. TR is a measure giving equal weight to both rare and common species; TD as a measure of the evenness of distribution giving more weight to common species and less to rare species; and AA gives a measure of the difference in population size before and after the fire. Residuals were visually assessed in all analyses and were normally distributed for TR and TD. AA in the complete study area was not normally distributed and was log transformed for LRT analysis. Data is reported as $\bar{x} \pm$ SE. Impact of the fixed variables was tested with a Likelihood Ratio Test (LRT).

We used mathematical models to represent the various hypotheses of impact of fire on TR, TD, and AA (Burnham and Anderson, 1998; Burnham *et al.,* 2011). We developed four hypotheses about invertebrate assemblages being dependent on time post-fire. H_1 says that after 3 seasons, there is still an impact on the burned area; H_2 says that there was an impact the first two seasons but the burned area recovered in 2015; H_3 says there was an initial difference but had recovered in both 2013 and 2015; and H_4 says there was normal variation between years and no difference between burned and unburned areas after the fire. Each of the hypotheses was applied to TR, TD, and AA.

We used Akaike's information criterion corrected for sample size (AIC_c) to compare models (Burnham *et al.* 2011). Models having a difference in AIC_c scores within 1–2 of the best model have substantial support. Models within about 4–7 of the best model have considerably less support, while models with $\Delta AIC_c > 10$ have essentially no support.

We tested the impact of fire, year and month on AA within the trophic guilds (detritivores, flower visitors, herbivores, omnivores, parasites and parasitoids, and predators) with an LRT. While there are some species in each family that are exceptions, we classified each family as fitting a specific trophic guild. We then determined the percentage of individuals for each trophic guild as representative of energy transfer within the food chain. We tested the impact of fire and year on abundance within Orders that were greater than 4% of the total population with an LRT.

Results

Vegetative response. The pre-fire vegetation was rather homogenous, dominated by early successional native and non-native species typical of sites formerly in row crop agriculture. The dominant species was the highly rhizomaceous tall goldenrod (*Solidago altimissima*). The apparently lighter soils were dominated by annual species such as mule tail (*Erigeron canadensis*), daisy fleabane (*Erigeron strigosus*), pigweed (*Amaranthus* spp), as well as dense stands of Indian grass (*Sorghastrum nutans*) and big bluestem (*Andropogon gerardi*). Other grasses present in the unburned area were Hungarian brome (*Bromus inermis*) and Kentucky blue grass (*Poa pratensis).* Among invading woody species were cottonwood (*Populus deltoides*), mulberry (*Morus rubra),* Amur honeysuckle (*Lonicera maackii*), black cherry (*Prunus serotina*), and an abundance of blackberry (*Rubus alleghenensis*) in the sub-canopy.

Post-fire vegetation had a similar compositional matrix of big blue stem (*A. gerardii*) and Indian grass (*S. nutans*), and was also was dominated by Canada goldenrod (*S. altissima*). The burned area had more flowering stems and vegetative biomass with as well as less vigorous woody growth in the understory. The fire seemed to benefit the C_4 grasses and not the C_3 grasses. Effects of the fire on the vegetation species composition were still visually evident three years post-fire in large part by the absence of many of the annual and biennial species. Invading woody species had been top-killed in the fire but were beginning to re-grow.

Invertebrate response. There were 119 OTUs sampled from both the burned and unburned transects (Appendix) over the three sampling periods. The pattern of invertebrate richness, diversity and abundance in the unburned area and was used as a comparison to the area burned in the wildfire. In both areas combined there were 34018 individuals sampled over the 3-year study period. Taxonomic richness (TR) in the complete study area averaged 8.07 ± 0.17 (1-22) per sample. Overall TR did not differ in the burned and unburned areas (7.32 vs 8.82; LRT: $\chi^2 = 2.4054$; df = 1; $P = 0.1209$: random variables: month, year, and method, n = 468). Overall TD in the complete study area averaged 4.26 ± 0.08 (1-13.45) per sample and differed in the burned and unburned areas (3.95 vs. 4.57; LRT: $\chi^2 = 4.3654$; df = 1; $P = 0.03668$; random variables: month, year, and method, n = 468). Overall AA in the complete study area averaged 72.69 ± 4.53 (2 – 635) per sample and did not differ in the burned and unburned areas (60.29 vs. 85.09; LRT: $\chi^2 = 0.9604$; df = 1; $P = 0.3271$; random variables: month, year, and method, n = 468).

We used model-based inference based on Kullback-Leibler information using maximized log-likelihood to test the impact of the fire in each of three growing seasons post-fire for each of the population metrics: TR, TD, and AA (Burnham and Anderson, 1998; Anderson, 2007). For all three population metrics, the fire had an impact each growing season surveyed post-fire (Tables 1-2, Figures 2-4).

Table 1. Average taxonomic richness, diversity and abundance ± SE in the burned and unburned areas in each of the three growing seasons post fire.

Population metric	Location	2012	2013	2015
Taxonomic Richness	Burned	7.94 ± 0.49	6.54 ± 0.38	7.71 ± 0.26
	Unburned	6.76 ± 0.42	8.63 ± 0.47	10.23 ± 0.34
Taxonomic Diversity	Burned	3.49 ± 0.16	3.67 ± 0.16	4.51 ± 0.19
	Unburned	3.79 ± 0.17	3.94 ± 0.16	5.67 ± 0.23
Absolute Abundance	Burned	81.22 ± 10.82	52.39 ± 7.2	55.63 ± 7.45
	Unburned	61.09 ± 11.18	121.07 ± 16.31	63.50 ± 7.99

Table 2. Comparison of the four models for (a) taxonomic richness (TR), (b) diversity (TD) and (c) abundance (AA). H_1 says that after 3 seasons, there is still an impact on the burned area; H_2 says that there was an impact the first two seasons but the burned area recovered in 2015; H_3 says there was an initial difference but had recovered in both 2013 and 2015; and H_4 says there was normal variation between years and no difference between burned and unburned areas after the fire. Df: degrees of freedom of the model; AICc: corrected AIC; Delta AICc: difference in AICc between the model and the model with the smallest AICc; AICcWt: model weight according to delta AICc; Cum.Wt: cumulative model weights; LL: Log Likelihood.

(a) Comparison of the four models for TR.

Hypothesis	Df	AICc	Delta AICc	AICcWt	Cum.Wt	LL
H_1	51	2125.64	0	1	1	-1005.4
H_2	41	2143.65	18.01	0	1	-1026.8
H_3	31	2168.36	42.72	0	1	-1050.9
H_4	25	2175.11	49.48	0	1	-1061.1

(b) Comparison of the four models for TD

Hypothesis	Df	AICc	Delta AICc	AICcWt	Cum.Wt	LL
H_1	39	500.24	0	0.99	0.99	-207.48
H_2	29	508.77	8.53	0.01	1	-223.40
H_3	19	554.91	54.67	0	1	-257.61
H_4	13	557.14	56.90	0	1	-265.17

(c) Comparison of the four models for AA.

Hypothesis	Df	AICc	Delta AICc	AICcWt	Cum.Wt	LL
H_1	39	1009.54	0	1	1	-462.12
H_2	29	1081.28	71.74	0	1	-509.66
H_3	19	1139.90	130.36	0	1	-550.10
H_4	13	1202.70	193.16	0	1	-587.95

Invertebrates were identified to trophic guild. Although there are species with different feeding habits within families, we generalized from the most common species in our samples (Appendix). We tested abundance for each trophic guild with a LRT (Table 3). We analyzed invertebrate abundance as percentage of the total population in each of the trophic guilds to determine the ecological impact on population structure (Table 4, Figures 11-28). All trophic guilds differed between years, however, parasites did not differ between the burned and unburned areas. During the shock phase, the abundance of detritivores increased and flower visitors, omnivores, and predators declined in the burned area. During the recovery phase detritivores and predators decreased in the burned areas and flower visitors and omnivores increased. After the recovery phase omnivore abundance declined in the burned area while detritivores, flower visitors, and predators increased in the burned area.

Figure 2. Graphs showing taxonomic richness in 2012, 2013, and 2015.

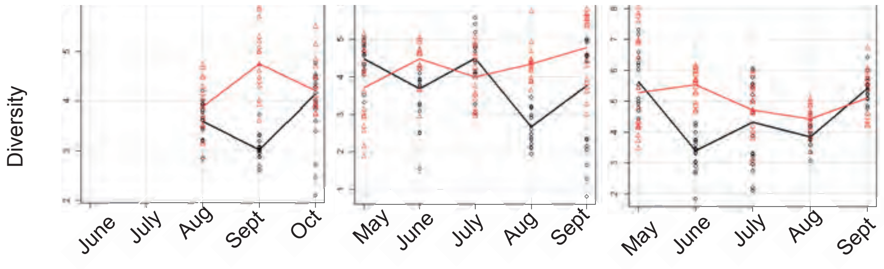


Figure 3. Graphs showing taxonomic diversity in 2012, 2013, and 2015.

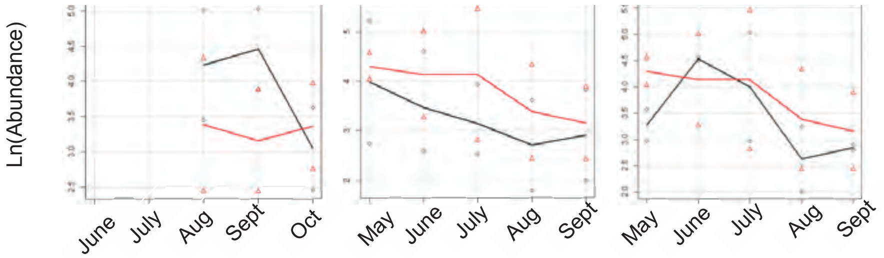


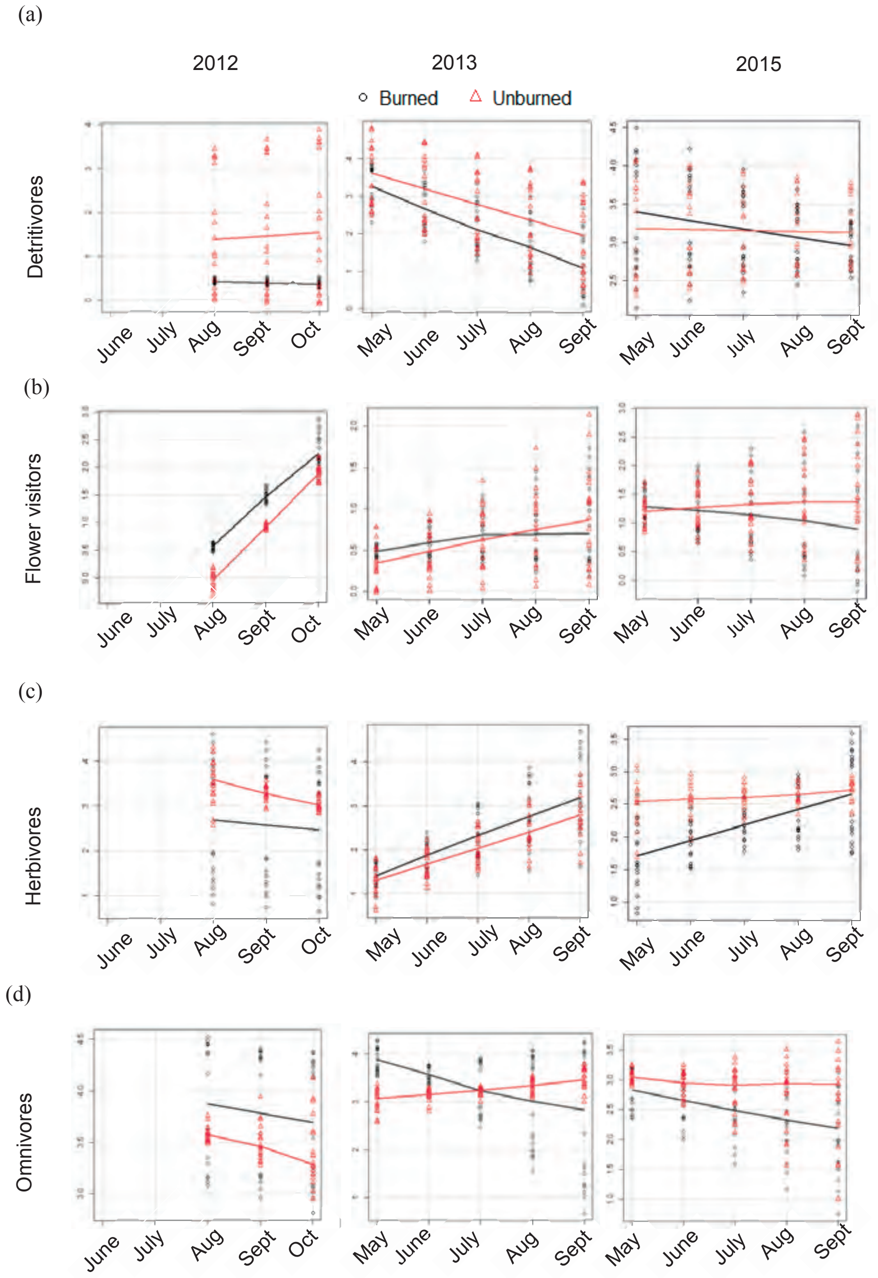
Figure 4. Graphs showing abundance in 2012, 2013, and 2015.

Table 3. Summary table of the impact of the fire on abundance within trophic guilds. Main Effects: T=Treatment (burned or unburned), M=Month of Collection; Y=Year of Collection; Interaction effects; T*M, T*Y, M*Y, T*M*Y; Det = Detritivores, Flower = Flower Visiting Insects, Herb = Herbivores, Omni = Omnivore, Par = Parasites and Parasitoids, Pred = Predators. Signif. Codes: “.”:$P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$); NS: not significant. Method of collection was a random variable.

Effect	Det	Flower	Herb	Omni	Par	Pred
T	.	*	NS	*	NS	**
M	***	*	***	NS	*	**
Y	***	*	*	***	**	**
T*M	NS	*	NS	NS	NS	***
T*Y	*	*	**	NS	NS	NS
M*Y	***	*	***	NS	*	NS
T*M*Y	NS	*	NS	NS	NS	NS

Table 4. Percentages of total abundance in each of the trophic guilds ± SE in the burned and unburned areas in each of the three years post-fire.

Guild	Treatment	2012	2013	2015
Detritivore	Burned	1.60 ± 0.88	21.58 ± 2.48	36.98 ± 3.15
	Unburned	17.82 ± 3.63	35.48 ± 3.32	33.60 ± 2.51
Flower	Burned	7.23 ± 1.24	3.36 ± 0.87	5.27 ± 0.93
	Unburned	3.12 ± 0.63	2.57 ± 0.60	5.24 ± 0.76
Herbivore	Burned	30.23 ± 4.16	20.52 ± 2.63	12.82 ± 1.52
	Unburned	34.03 ± 3.27	13.07 ± 1.58	15.00 ± 1.25
Omnivore	Burned	54.57 ± 4.44	39.56 ± 2.71	18.13 ± 1.73
	Unburned	39.46 ± 3.34	32.64 ± 2.24	24.03 ± 2.21
Parasite	Burned	4.02 ± 0.75	11.26 ± 1.97	11.81 ± 1.72
	Unburned	4.55 ± 1.01	11.22 ± 1.60	9.82 ± 1.06
Predator	Burned	2.34 ± 0.40	3.72 ± 0.52	14.99 ± 1.57
	Unburned	1.01 ± 0.32	5.01 ± 0.83	12.31 ± 1.59


(a)
2012
2013
2015
○ Burned
△ Unburned
Detritivores
June
July
Aug
Sept
Oct
May
(b)
Flower visitors
(c)
Herbivores
(d)
Omnivores

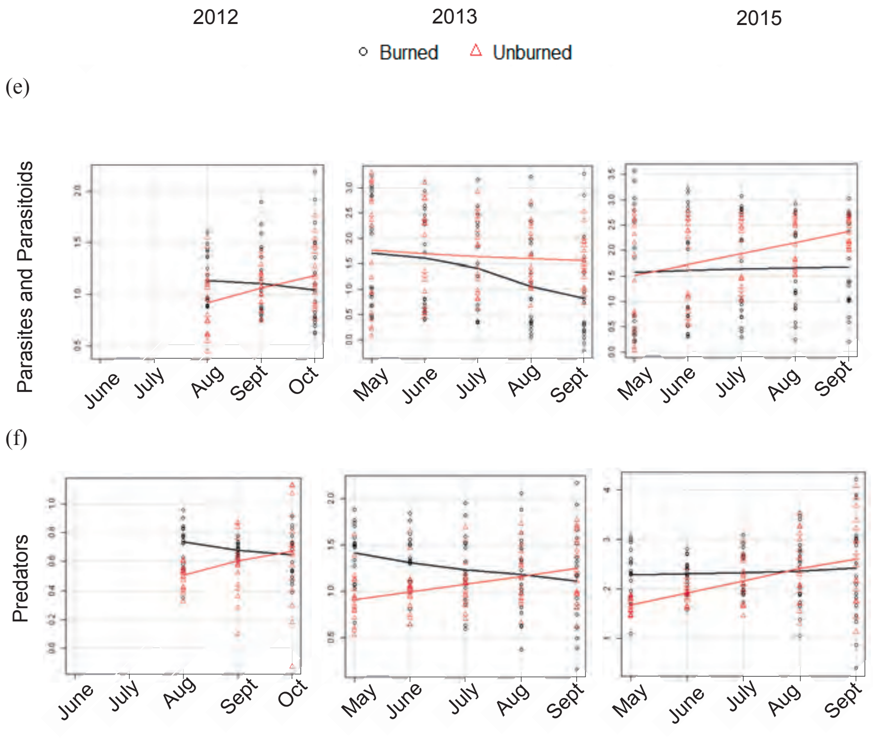


Figure 5. Graphs showing feeding guilds in 2012, 2013, and 2015.

Table 5. Summary of impacts on orders. Main Effects: Treatment (burned or unburned), Year of Collection; Interaction effects; treatment*year; Signif. Codes: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$); NS: not significant. Method of collection was a random variable.

	Treatment	Year	Interaction
Aranae	NS	***	NS
Coleoptera	**	***	**
Collembola	NS	***	NS
Diptera	**	**	**
Hemiptera	*	***	*
Hymenoptera	*	*	*
Isopod	**	**	***

Table 6. Percentages of total abundance in each of the orders ± SE in the burned and unburned areas in each of the three years of the study.

Order	Treatment	2012	2013	2015
Aranae	Burned	0.30 ± 0.17	3.26 ± 0.67	6.69 ± 1.04
	Unburned	0.75 ± 0.31	5.27 ± 0.94	4.73 ± 0.77
Coleoptera	Burned	5.47 ± 1.01	4.35 ± 0.85	7.75 ± 1.09
	Unburned	3.22 ± 0.77	4.65 ± 0.78	6.63 ± 0.75
Collembola	Burned	0.38 ± 0.17	3.26 ± 0.67	6.69 ± 1.04
	Unburned	0.75 ± 0.31	5.27 ± 0.94	4.73 ± 0.77
Diptera	Burned	39.59 ± 4.08	27.09 ± 3.33	17.7 ± 2.38
	Unburned	39.81 ± 3.63	35.59 ± 3.62	27.09 ± 3.63
Hemiptera	Burned	29.78 ± 4.35	19.27 ± 2.66	6.75 ± 0.97
	Unburned	39.01 ± 3.12	13.21 ± 1.62	11.87 ± 1.32
Hymenoptera	Burned	28.95 ± 3.96	34.28 ± 3.02	15.79 ± 1.78
	Unburned	17.38 ± 2.66	16.36 ± 1.82	14.22 ± 1.54
Isopod	Burned	13.52 ± 2.91	5.68 ± 1.42	4.69 ± 1.15
	Unburned	8.80 ± 2.36	13.81 ± 2.07	9.00 ± 1.72

We examined orders that represented more than 4 % of the total sample to see how composition changed taxonomically each year of the study. Significance of the burned area compared to the unburned area, natural variation in invertebrate abundance each year and their interactions are tested using LRT (Table 5). The abundance of Aranae, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, and Isopods all differed between years; however, Aranae, and Collembola did not differ between burned and unburned areas. During the shock phase Coleoptera, Hymenoptera, and Isopods were greater in the burned area and abundance was down in Diptera and Hemiptera. During the recovery phase, Hemiptera and Hymenoptera were more abundant in the burned area and abundance of Coleoptera, Diptera and Isopods were decreased in the burned area. After the recovery phase, abundance of Coleoptera, and Hymenoptera were greater in the burned area. The abundance of Diptera, Hemiptera and Isopods was down in the burned area compared to the unburned area. Mean percent of the total population ± SE in each of the burned and unburned areas in each year (Table 6).

Discussion

General Discussion. Invertebrate taxonomic richness and abundance in the burned area in the three growing seasons of our study appeared to completely recover (Table 1, Figures 2-4). These abundance measures are somewhat misleading in that they do not tell us how the composition of species has changed (Warren *et al.,* 1987). All trophic guilds except herbivores and parasites differed between the burned and unburned areas three vegetative growing season post-fire (Table 3). Abundance of all orders with more than 4% of the total except spiders and springtails differed between the burned and unburned area (Table 5). Taxonomic diversity tells us that the mix of taxa is not significantly different in the burned and unburned areas. However, the fluctuation in taxonomic diversity was greater and continued three growing seasons post-fire (Table 1, Figures 5-7).

New vegetation and lush spring-like growth drew invertebrates to the burned area in the shock phase post-fire. This is visible in the higher TR and AA in the burned area. This attraction may have applied to generalist species since it was not reflected in the TD. In the recovery phase, all three metrics TR, TD, and AA had lower levels in the burned than in the unburned area that continued within the third season. More nutritious vegetative growth and earlier emergence due to elevated post-burn soil temperature have been cited to account for increased metrics following the initial burn (Swengel, 2001; Evans *et al.,* 2013). Our two transects were relatively close. Differences were probably due to the local effects of burning such as changes in vegetation, litter layer, and topsoil, and not to different species pools or isolation. The close proximity of the unburned area provided a source of recolonization. However, the vegetation shift may have made the new habitat inappropriate for recolonization. Additionally, there may be cascade effects e.g., the increase in herbivores of the new vegetation may draw an increase in predators followed by an increase in parasites and parasitoids.

Detritivores largely disappeared in the burned areas during the shock phase of recovery (Table 3, Figures 11-13). They increased the following spring presumably in response to increased soil detritus which accompanied enhanced vegetation growth following the fire (Lussenhop, 1981). Springtails live in the soil and feed on decaying organic material. They are considered sensitive to soil moisture levels that could explain the difference found in the second growing season. It is not until there was a vegetative litter layer that the springtails approached abundances in the unburned area. This is consistent with other research in Illinois (Rice, 1932).

Flower visitors were trapped in the burned area but almost non-existent in the unburned area immediately post-fire (Table 3, Figures 14-16). Butterfly and moth larvae are phytophagous but the adults are beneficial plant pollinators. Adult butterflies and moths are strong fliers and responded to the flush of new growth for oviposition (Evans *et al,*. 2013). Adult Lepidoptera were not common in either the burned or unburned areas the second growing season post-fire. It was not surprising that early growth drew flower visitors as the vegetation first appeared immediately after the fire. The following spring, the charred soil allowed for early green-up and the fertilizing effect of the ash created good conditions for vegetative growth when the spring rains broke the drought. Differing responses between the final sampling period in the recovery phase and the following growing season may reflect a lack of overwinter survival as the litter layer began to accumulate.

Phytophagous invertebrates (herbivores) had a varied response to the fire. Beetles found in our study may have adaptations to fire conditions (Warren *et al.,* 1987; Reed, 1997; Schmitz *et al.,* 2016). Hemiptera in our study were dominated by Cicadellidae: leafhoppers, and Aphidae: aphids. The shift in leafhopper numbers may have been related to the shift in vegetation. There was a large difference in aphids that were possibly being drawn to the new vegetation. Abundance seems to have stabilized three growing seasons post-fire. Many phytophagous invertebrates fly well and were not impacted by the fire. Herbivores may have had difficulty overwintering in the burned area due to lack of a litter layer (Table 3, Figures 17-19).

Omnivores were initially drawn to the burned area but may have not responded well to the lack of litter layer and increased insolation of the recovery phase (Table 3, Figures 20-22). The most abundant Diptera taxa were not impacted by the fire. This is consistent with research following a winter fire in Illinois (Rice, 1932). Isopods (pillbugs) are moisture dependent. Because they are nocturnal and live mostly underground, they may have survived the combustion phase and migrated out of the burned area to the unburned area. Ants were more abundant in the burned than the unburned area. Their tolerance of dry soil makes them well adapted to arid conditions following a fire. They are known as rapid colonizers due to their social structure (Swengel, 2001).

Parasites and parasitoids were not different in abundance between burned and unburned areas (Table 3, Figures 23-25). Predators had greater abundance in the early part of each growing season and overall had a complex reaction to the fire with significant impacts of period of the growing season, phase post-fire, and impacts of the fire itself (Table 3, Figures 26-28). Carabid beetles increased in both the burned and unburned areas of our study. Other studies have documented an increase in numbers of predators following fire (e.g., (Rice 1932, Warren *et al.* 1987). Spiders make up a large proportion of predators. They survive the combustion phase by seeking refuge in the soil. Taxa active on the surface at the time of burning were probably eliminated, while those occupying subsurface burrows or sacs under rocks or in clumps of dense vegetation may have escaped thermal damage (Riechen and Reeder, 1972). Survival at this point is dependent on numerous factors. In addition, spiders are among the quickest invertebrates to colonize new sites due to their ballooning behavior (Weyman, 1995). Movement between the unburned and burned areas may have been dependent on prey availability.

Opportunism is widespread in fire ecology studies, with data on insects and other biota being obtained from wildfires or other unanticipated events contributing to the wider pool of knowledge and experience (Buddle *et al.,* 2006; Jackson *et al.,* 2012). While it might be considered desirable to study numerous mid-summer fires, it is our contention that every fire is unique. Studies of numerous fires bring with them the inevitable differences in weather, fuel load and other undetermined factors. A myriad of other factors includes the fire characteristics and timing of the burn related to phenology of the invertebrates being studied. Our study is limited but has the benefit of invertebrates being exposed to similar conditions at a single location. An interesting variable we were not able to study was the possibility that because of the severe drought conditions some invertebrates may have been in diapause similar to overwintering conditions. Thus, they may have survived the fire and not come out of diapause until the following year spring rains. This would explain why some groups did not differ between burned and unburned areas. An alternative explanation of the absence of some invertebrate groups in 2012 is life history. Some groups are active in the spring and less active late July and August. An additional limitation to our study and others is the introduction of sampling bias based on ease or difficulty of capture with the shift in vegetative cover.

Our study examines the response to fire through the four phase sequence of fire impact: fuel development, combustion, shock and ecosystem recovery (Warren *et al.,* 1987). The non-burned portion of the field represents the fuel development phase. The combustion phase was not documented due to the unplanned nature of the wildfire. Monitoring the shock and recovery phases began ten days post-fire and continued from the remainder of the season post-fire through the third complete growing season. The shock phase of this fire was complicated by the interaction of the fire with the effects of drought (Evans *et al.,* 2013). The vegetative response of spring-like growth was in distinct contrast to the dried dormant vegetation in the unburned area. The shock phase continued overwinter due to lack of litter layer, microclimate conditions, and continued drought. The first full growing season post-fire allowed the vegetation to shift composition based on the new soil and insolation conditions. During the growing season and following dormant period, a litter layer became established. The third growing season showed that vegetation in the burned area was well established and, as in other studies, fire seemed to simplify the plant community and favor warm-season C_4 grasses (Gibson *et al.,* 1993; Callaham *et al.,* 2003).

Management implications. The shift from positive taxonomic richness of that of the unburned area post-fire to negative in the first growing season post-fire indicates possible issues with overwintering or lack of appropriate habitat due to loss of the litter layer. We continued to see an overall 25% decrease in taxonomic richness the third growing season post-fire. At this time, the structure of the burned area was similar to the unburned areas and, therefore, reasons for the difference in taxonomic richness are probably not related to depletion of the litter layer (i.e., catchability of the invertebrates, increased insolation, lack of cover etc.). Reasons for this decrease are probably related to the change in vegetation. Vegetative changes in our study seemed to favor the C_4 grasses and prairie forbs. The suitable invertebrate assemblages for this mix of vegetation have to come from somewhere. Unless there is an appropriate habitat in the vicinity it may take some time, if ever, for the correctly matched invertebrates to populate the burned area. Historical burns would probably have been patchy with large spaces left unburned providing refugia for existing invertebrates to survive and repopulate the area. The burned area in our study did not have either refugia or nearby intact prairies to repopulate the site.

Fire is considered the most important tool in the management of vegetation in the Midwest (Kelly *et al.,* 2015). It is believed to be historically present and an important factor in the evolution of the American prairie (McClain and Elzinga, 1994). To land managers, it is a technique preferable to the use of chemical treatments, at the very least, used in conjunction with chemical application to undesirable vegetation (Warren *et al.,* 1987). The timing and intensity of the wildfire in our study was probably similar to conditions of fire before European settlement. We know that fire was responsible for keeping the forest from encroaching on the prairie (Briggs *et al.,* 1998). There is however, a degree of uncertainty about the interval and landscape scale of the burns. There is also some controversy about whether some prairie plants are fire dependent or fire tolerant.

The impacts of fire vary across taxa. Characteristics of the fire associated with invertebrate responses relate to the direct exposure to fire and amount of subsequent stress post-fire, suitability of post-fire vegetation to meet life history requirements, and availability of colonizing populations (Warren *et al.,* 1987; Swengel, 2001). It should also be noted that vegetation survival of fire is also dependent on the same fire characteristics (Frost, 1984). Information on invertebrate life history and ecology serve as a starting point and may allow one to predict their responses to fire. Yet the response of a species with a known life history and ecology may be confounded by the unknown effect of the fire on its predators, parasitoids, pathologies, and host plant (Harper *et al.,* 2000).

Prescribed fire has been proposed for control of insect pests (Vermeire *et al.,* 2004; Iglay *et al.* 2012). We suggest caution in implementing fire for manipulating arthropod populations for this purpose. While fire can control for some pests it may effectively open the door to other pests (McCullough *et al.,* 1998; Iglay *et al.,* 2012; Evans *et al.,* 2013). Moreover, this study shows that there may also be multi-year post-fire effects on invertebrates.

Here we show that while fire may be a desirable tool for vegetation management, it should be used with caution and an understanding that fire can have consequences with lasting effects for the invertebrate assemblages inhabiting the same space. Alternating timing or season of the burn may effectively decimate a species by destroying eggs, larva and adult forms. Burning on a short rotation may locally extirpate a species by not allowing a complete recovery. Using alternative forms of vegetation control such as mowing or grazing has a negative impact on invertebrates (Callaham *et al.,* 2003; Benson *et al.,* 2007). Alternating methods of vegetation control (grazing, mowing, and fire) also impacts invertebrates (Swengel, 2001). The argument that prairie dependent invertebrates evolved in tandem with fire dependent prairie vegetation is misleading because we may be mistaking fire tolerance for fire dependence (Anderson, 2006). We believe methods of vegetation control should be implemented to lengthen the fire rotation particularly in areas where we wish to maintain threatened species. To minimize the impact of prescribed fire on invertebrate taxa we recommend the use of fire exclosures, an extended fire rotation, and creating refugia that are representative of the entire grassland within the burn area. These management strategies add a layer of complication to an already intricate preparation period, but probably necessary to protect invertebrate assemblages.

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Appendix

Invertebrate taxa sampled post-fire during the remainder of the 2012 vegetation growing season, and the 2013 and 2015 growing seasons. Guilds: detritivores (D), flower visitors (F), herbivores (H), not feeding as an adult (NA), omnivores (O), parasites and parasitoids (PA), and predators (PR). B = burned area, U = unburned area.

Taxa	Guild	2012		2013		2015	
		B	U	B	U	B	U
Class Oligochaeta: Earthworms	D	1	17	19	133	8	26
Class Gastropoda							
Snails	H	0	5	1	45	11	30
Slugs	H	0	0	4	5	41	37
Order Araneae: Spiders							
Linyphiidae: Sheet Web Spiders	PR	6	7	19	24	17	31
Lycosidae: Wolf Spiders	PR	11	15	113	98	136	59
Gnaphosidae: Parson Spiders	PR	0	1	1	6	0	0
Thomisidae: Crab Spiders	PR	0	1	2	26	0	0
Salticidae: Jumping Spiders	PR	4	2	1	5	2	2
Spider hatchlings	PR	0	0	220	310	27	23
Spider ssp.	PR	0	0	0	72	0	2
Order Opiliones: Harvestmen	PR	6	4	7	40	10	11
Order Acari: Ticks	PA	0	0	4	14	1	3
Order Isopoda: Isopods							
Armadillidiidae: Common Pillbugs	O	1334	451	225	1126	104	768
Order Diplopoda: Millipedes	D	15	6	18	63	6	20
Order Chilopoda: Centipedes	PR	0	0	3	7	0	7
Order Collembola: Springtails	D	62	1253	1754	6367	2279	1847
Order Orthoptera							
Acrididae: Grasshoppers	H	28	23	40	34	65	62
Tettigoniidae: Katydids	H	0	0	0	0	0	1
Gryllidae: Crickets	H	4	3	27	7	27	23
Order Phasmatodea: Walkingsticks							
Heteronemiidae: Stick Bugs	H	0	0	0	0	1	0
Order Plecoptera: Stoneflies	NA	0	0	1	0	0	0
Order Blattaria: Cockroaches							
Blattidae: Cockroaches	O	0	0	0	0	0	3

Taxa	Guild	2012		2013		2015	
Order Hemiptera:True Bugs							
Gerridae: Water Striders	PR	0	0	0	2	0	0
Miridae: Plant Bugs	H	0	0	2	1	2	0
Nabidae: Damsel Bugs	PR						
Anthocoridae: Minute Pirate Bugs	PR	14	6	1	2	0	0
Reduviidae: Assassin Bugs	PR	2	0	1	1	0	1
Lygaeidae: Seed Bugs	H	6	0	0	1	0	1
Blissidae: Cinch Bugs	H	0	0	0	0	1	0
Coreidae: Leaf-footed Bugs	H	0	0	0	0	2	5
Cydnidae: Burrower Bugs	H	0	0	0	0	0	2
Thyreocoridae: Ebony Bugs	H	0	0	0	3	0	0
Pentatomidae: Stink Bugs	H	1	0	0	0	0	1
Membracidae: Treehoppers	H	0	0	0	1	1	3
Cercopidae: Spittlebugs	H	0	0	0	0	0	1
Cicadellidae: Leafhoppers	H	109	694	368	323	85	282
Fulgoroidea: Planthoppers	H	0	0	4	1	0	0
Aphidae: Aphids	H	507	77	67	17	130	135
Order Thysanoptera: Thrips	H	0	0	0	0	2	11
Order Coleoptera: Beetles							
Cicindelidae: Tiger Beetles	PR	12	0	11	0	9	2
Cicindela punctulata: Punctured Tiger Beetle	PR	0	0	9	0	0	0
Carabidae: Ground Beetles	PR	19	11	38	64	55	61
Carabidae: *Notiophilis ssp.*	PR	0	0	2	2	4	1
Calosoma sycophanta: Caterpillar hunter	PR	0	0	1	1	0	0
Histeridae: Hister Beetles	PR	0	0	4	5	0	0
Silphidae: Carrion Beetles	D	0	3	4	45	15	36
Scaphidiidae: Shining Fungus Beetles	H	0	0	0	0	0	1
Staphylinidae: Rove Beetles	PR	24	5	30	22	11	18
Trogidae: Trox Beetles	D	1	4	8	7	14	5
Scarabaeidae: Scarab Beetles	D	3	0	21	59	4	3
Popillia japonica: Japanese Beetle	H	1	0	0	0	0	0
Buprestidae: Jewel Beetles	D	1	0	0	2	0	0
Elateridae: Click Beetles	H	2	0	0	1	4	2
Lampyridae: Fireflies	PR	0	0	0	0	0	3
Cantharidae: Soldier Beetles	PR	2	0	2	0	4	7
Cleridae: Checkered Beetles	PR	10	3	0	1	2	3
Melyridae: Soft-winged Flower Beetles	D	0	0	0	0	0	1
Erotylidae: Pleasing Fungus Beetles	D	2	1	1	1	0	0
Coccinellidae: Lady Beetles	PR	0	0	1	1	1	0
Latridiidae: Minute Brown Scavenger Beetle	PR	0	0	0	0	2	3
Mordellidae: Tumbling Flower Beetles	F	35	12	16	20	30	66

Taxa	Guild	2012		2013		2015	
Tenebrionidae: Darkling Beetles	H	0	0	0	3	4	0
Meloidae: Blister Beetles	H	16	3	5	1	0	0
Chrysomelidae: Leaf Beetles	H	3	0	4	4	2	20
Microrhopala vittata: Goldenrod Leaf Miner	H	0	0	9	5	2	4
Curculionidae: Weevils	H	6	1	8	8	3	9
Coleoptera larva ssp	H	5	2	7	4	4	6
Order Neuroptera: Antlions, Lacewings	NA	1	0	3	0	2	1
Order Hymenoptera: Wasps, Bees, Ants							
Symphyta: Sawfly ssp	H	0	0	1	0	0	1
Siricidae: Horntails	H	0	0	0	3	0	0
Ichneumonidae: Ichneumon Wasps	PA	0	7	4	5	5	10
Ichneumonidae: *Ophion ssp*	PA	0	1	0	0	3	0
Braconidae: Parasitic Wasps	PA	28	36	75	64	45	38
Chrysididae : Cuckoo Wasps	PA	3	0	2	3	0	1
Megachilidae: Resin Bees	F	1	0	0	0	0	0
Sphecidae: Thread-Waisted Wasps	PR	4	3	2	2	0	1
Halictidae: Sweat Bees	PA	32	20	21	13	46	14
Andrenidae: Mining Bees	F	18	14	3	1	0	0
Apidae: Honey Bees	F	3	0	17	10	5	4
Bombus pensylvanicus: Bumble Bee	F	1	8	0	0	0	0
Tiphiidae: Flower Wasps	PA	1	4	0	0	0	0
Mutillidae: Velvet Ants	PA	1	0	0	1	0	0
Vespidae: Hornets, Wasps	PA	1	2	2	4	1	1
Formicidae: Ants	O	1677	402	1431	910	323	462
Trichoptera: Caddisflies	PR	0	0	0	1	0	4
Lepidoptera: Butterflies and Moths							
Micro-lepidoptera[1]	F	4	1	0	5	2	9
Hesperiidae: Skippers	F	7	6	0	0	2	5
Papilioninidae: Swallowtails	F	7	6	0	0	0	0
Papilio polyxenes anterius: Black Swallowtail	F	1	0	0	0	0	0
Pieridae: Sulfurs	F	6	5	3	0	0	1
Pieris rapae: Cabbage Butterfly	F	6	5	3	0	2	1
Nymphalidae: Brush-footed Butterflies	F	2	0	0	0	0	0
Geometridae: Geometer Moths	F	3	7	0	0	0	1
Noctuidae: Owlet Moths	F	0	0	0	1	7	3
Lepidoptera larva ssp	H	68	5	2	0	30	21

Taxa	Guild	2012		2013		2015	
Order Diptera: Flies							
Tipulidae: Crane Flies	D	1	10	1	2	2	5
Chironomidae: Midges	D	10	8	53	379	6	13
Culicidae: Mosquitoes	PA	22	2	47	144	209	240
Mycetophilidae: Fungus Gnats	D	3	0	9	44	640	390
Stratiomyidae: Soldier Flies	F	0	0	0	0	1	0
Tabanidae: Horse Flies, Deer Flies	PA	0	0	0	0	0	22
Apeioceridae: Flower-Loving Flies	PR	0	0	0	0	1	0
Bombyliidae: Bee Flies	F	0	0	0	0	0	2
Dolichopodidae: Long-legged Flies	PR	1	5	13	28	251	196
Phoridae: Hump-backed Flies	O	1	0	0	0	2	3
Pipunculidae: Big-headed Flies	PA	0	0	0	0	0	2
Syrphidae: Flower Flies	F	34	9	17	17	31	24
Calliphoridae: Blow Flies	D	0	0	0	0	1	1
Muscidae: House Flies	O	32	69	166	80	209	488
Sarcophagidae: Flesh Flies	O	66	75	0	0	0	0
Tephritidae: Fruit Flies	F	0	0	0	0	1	1
Ulidiidae: Picture-winged Flies	F	7	2	2	0	49	46
Diptera ssp	O	185	134	273	463	25	49
Diptera larva ssp	O	0	0	4	4	4	6

[1] Small Lepidoptera of the Super Families Gelechioidea, Pyraloidea, Tiniodea, Gracillarioidea, Incurvarioidea, and Families Tortricidae and Pterophoridae.

Guilds are mostly detritivores (D), flower visitors (F), herbivores (H), omnivores (O), parasites and parasitoids (PA), predators (PR), or not feeding as adults (NA)

- Other species not identified due to damage of features or difficulty in identification

Chapter 6

The impact of landscape complexity on invertebrate diversity in edges and fields in an agricultural area

Based on:
Evans, T. R., Mahoney, M. J., Cashatt, E. D., Noordijk, J., de Snoo, G., & Musters, C. J. M. (2016). The Impact of Landscape Complexity on Invertebrate Diversity in Edges and Fields in an Agricultural Area. *Insects*,*7*(1), 7.

Abstract

Invertebrate diversity is important for a multitude of ecosystem services and as a component of the larger ecological food web. A better understanding of the factors influencing invertebrate taxonomic richness and diversity at both local and landscape scales is important for conserving biodiversity within the agricultural landscape. The aim of this study was to determine if invertebrate richness and diversity in agricultural field interiors and edges in central Illinois, USA, were related to the complexity of the surrounding landscape. Our results show taxonomic richness and diversity in field edges is positively related to large scale landscape complexity, but the relationship is negative for field interiors. These unexpected results need further study.

Keywords: biodiversity; taxonomic richness; diversity index; landscape complexity; North American agriculture

Introduction

Agriculture is intensifying to meet the growing demand for food for the increasing numbers of people and livestock. Fields have increased in area resulting in the loss of non-crop field margins (Medley *et al.*, 1995; Tscharntke *et al.*, 2005; Kleijn *et al.*, 2011; Mineau and Whiteside, 2013). Chemical usage has increased, harvesting technologies have improved, and tillage frequency has increased. There is a known negative relationship between agricultural intensity and biodiversity (Stoate *et al.*, 2001; Geiger *et al.*, 2010; Martinuzzi *et al.*, 2013).

There are numerous benefits to conserving or restoring biodiversity in agricultural areas including provision of habitat for highly valued farmland birds (Herkert, 1995; Musters *et al.*, 2001; Geiger *et al.*, 2010), game species (Boatman, 1999) and economically relevant species of invertebrates (Gurr *et al.*, 2003). Habitat conservation and restoration support ecosystem services such as pollination (Gill, 1990), erosion control (Balvanera *et al.*, 2006) and natural pest control (Collins *et al.*, 2003; Gurr *et al.*, 2003; Geiger *et al.*, 2010). These practices enhance floral diversity within crops (Gabriel *et al.*, 2005) and serve as corridors to link protected areas for various species (Naiman *et al.*, 1993; Rosenberg *et al.*, 1997). Invertebrates provide ecosystem services such as pollination, and pest control although some species are agricultural pests (Kremen *et al.*, 2007; Zhang *et al.*, 2007). Habitat restoration in the USA is largely focused on large blocks of land. However, small narrow landscape elements like field edges, road sides, and ditch and creek banks may also play an important role in agricultural landscapes (Noordijk *et al.*, 2010). Being (literally) marginal, management of these vegetated elements to maximize biodiversity would not diminish agricultural production.

Previous work has shown that both local and landscape factors affect the biodiversity of semi-natural elements in agricultural areas and that the effectiveness of management for biodiversity depends on the landscape complexity (Tscharntke *et al.*, 2005; Kleijn *et al.*, 2011). Agricultural landscapes may be categorized as complex, simple or cleared (Tscharntke *et al.*, 2005). In general, as the complexity of the landscape increases, biodiversity increases, although some species groups are insensitive to it (Tscharntke *et al.*, 2005; Gonthier *et al.*, 2014).

Much research has been focused on typical European agricultural landscapes (Geiger *et al.*, 2010; Batáry *et al.*, 2011; Kleijn *et al.*, 2011) but other than utilization as corridors (Macfadyen and Muller, 2013), there has been little research on the biodiversity of agricultural field edges (area next to cultivated fields) in the USA. In this paper, we studied invertebrate diversity in and around agricultural fields in Illinois, Midwest USA. In this area, tall grass prairie has been largely displaced by intensive agriculture, making it important to conserve and restore remaining biodiversity. In addition, as financial incentives are provided to farmers to adopt environmentally friendly agricultural practices and take some tracts out of agricultural production (Mausbach and Dedrick, 2004), there is a need to study how and where biodiversity is best promoted to ensure funding is spent optimally. There is little baseline data on the relative importance of landscape factors affecting invertebrate taxonomic richness (TR) and diversity index (DI) in Midwestern field edges. (Marino and Landis, 1996; Menalled *et al.*, 2000). We hypothesize that the narrow elements (edges outside tilled area of fields) can be modified to enhance invertebrate diversity conservation and restoration in the Midwest. Invertebrate diversity in non-cultivated field edges (FE) might influence the richness and diversity of invertebrates in the cultivated field interiors (FI), which is important information for farmers given the ecosystem services these animals might provide (González *et al.*, 2015). We examined invertebrate diversity in and adjacent to 30 agricultural fields in three counties in central Illinois. Our central hypotheses were that, first, FE have a higher TR and DI than FI and, second, in both FE and FI, TR and DI would be greater as landscape complexity increased due to a larger regional species pool (Tscharntke *et al.*, 2012). We also examined local factors such as vegetative structure that could have affected TR and DI independently of landscape complexity.

Experimental Section

Study Area. The study was conducted in 2011 and 2012 in central Illinois in Cass, Christian and Sangamon counties (Figure 1). This is part of the Grand Prairie Natural Division, a vast plain of formerly tallgrass prairie (Schwegman, 1973). Soils are fertile and developed from glacial outwash, lakebed sediments and deposited loess. Natural drainage is poor but farmland drainage has been improved with the use of tile lines and ditches. The topography is generally level to rolling. Illinois climate is typically continental with cold winter temperatures (mean -3.8°C), warm summers (24.6°C) and frequently fluctuating temperature, humidity, cloud cover and wind conditions. Precipitation averages 1006 mm per annum and the growing season is ~185 days. In 2012 precipitation was much below normal (595.12 mm) (Midwestern Regional Climate Center, Springfield, Illinois: http:/mrcc.isws.illinois.edu\CLIMATE –accessed December 4, 2015). Due to the reduced precipitation and high ambient temperatures, the region was considered to be in an extreme drought (National Oceanic and Atmospheric Administration 2012).

Figure 1. Location of Cass, Sangamon and Christian counties in Illinois, USA.

We selected ten agricultural fields mostly seeded in a 2-3 year corn (*Zea mays*) and soybean (*Glycine max*) planting rotation in each of three counties for a total of 30 fields (Supporting Information, Table S1). Fields were visually selected for varied edge structure. The average field size was 28 ha with a range from 1-117 ha (Table S2). Fields differed in their surrounding structural complexity, ranging from simple landscapes with a relatively high percentage of arable land, to complex landscapes with a relatively low percentage of arable land and a large proportion of semi-natural land cover and other land use types (Table S3). The edge structure and vegetation ranged from closely mown grass monoculture to shrubby vegetation more than a meter in height (Table S2). Permission to access the fields was obtained from land managers and landowners (in many cases the landowner was different from the land manager). Vegetation in the FE was managed by various entities including the landowner, land manager, and township employees and consisted of a variety of mowing and herbicide regimes. Prior to the start of the study, FIs had been seeded with genetically modified (Roundup Ready) corn or soybeans by the landowners or managers (Table S1). Roundup Ready seeds are modified to be resistant to glyphosate type herbicides that are used to control weeds.

ArcView GIS 3.2 and ArcGIS Spatial Analyst (Environmental Systems Research Institute, Inc., Redlands, CA, USA) were used to determine field area (ha), field edge length (m), width of FE (m), distance to nearest large non-agricultural area (>1 ha), proportion of non-agricultural area at three different scales, and soil type. Field length was the length of the field adjacent to the FE where traps were placed. Complexity, i.e., proportion of non-agricultural area to agriculture, was determined using nested circular buffers (with radii of 500 m, 1000 m and 6000 m) around the center of each group of samples per field. We used existing landcover classifications from satellite imagery (Luman *et al.*, 2009). We defined agriculture as arable land sown in corn, soybean, winter wheat (*Triticum aestivum*) or other row crops. We defined non-agricultural areas as those classified as upland forest, savannah, coniferous forest, wet meadow, marsh, seasonally flooded, floodplain forest, swamp and shallow water. Other classifications such as clouds and cloud shadows were not included in calculating landscape complexity (Table S3).

Field locations were determined using a global positioning system (Garmin Oregon 450t). Each field was assigned a unique code to designate a specific sample. The crops grown in the sampled and adjacent fields were also recorded. Adjacent field was the nearest field without crossing a hard barrier such as a road. The height of both the crops and vegetative edges were measured at 30 points along a transect between the pitfall traps using a measuring stick (Table S2).

Sampling Methods. From late May to mid-June of 2011 and 2012, invertebrates were sampled with sticky boards, sweep netting, and pitfall trapping, from each field once each year. Sticky boards and pitfall traps were positioned May 28, June 1, and June 4 2011 and May 26, May 27, and May 28 of 2012, moving from south to north. Sticky boards and pitfall traps were placed at six locations per field, grouped equidistant from the ends of the field and adjacent to the FE; three in the FI and three on the FE spaced at 10 m intervals. Sampling sites in the FI were 10-15 m from the edge in the second equipment row (adjacent passage of the planter) and not in the turning row. Sites on the edge were 1-2 m from the FE within the vegetated edge. Sweep netting was conducted only in the FE to avoid damage to the crops.

Pitfall traps were 150 ml plastic cups with an aperture of 70 mm placed into the ground so that the mouths were flush with the ground and there was no discontinuity between the edge of the trap and the ground surface. Each trap was filled to ~ 2.5

cm with a solution of water and vinegar and a few drops of dish soap added to break the surface tension of the water. Ethylene glycol was not used because it attracted mammals to the traps during a pilot study. Pitfall traps were retrieved seven days after placement and contents placed in a labeled clear Ziploc bag containing 70% isopropyl alcohol and kept for future identification.

One sticky board (Sensor ~ 8 cm x 13 cm Yellow Monitoring Cards, GrowSmart), attached to a flag (~ 6 cm X 9 cm flag attached to a 76 cm long wire LimeGlo, Forestry Suppliers) was placed adjacent to each pitfall trap. Boards were placed with a minimum of ½ the board above the vegetation. Boards were retrieved after two days, placed in a clear plastic cover and saved for future identification.

Sweep net sampling was conducted between the date when samples were placed and when pitfall samples were retrieved. A sweep net sample consisted of 30 strokes, 360° around the sweep netter in the FE near each of the pitfall traps for three samples total per field. The net was 38 cm in diameter with muslin netting (Forestry Suppliers). All sweep net samples were collected on sunny days between 10:00 and 14:00 with wind 0-3 as measured on the Beaufort scale. Invertebrates were placed in a "knockdown" jar containing chloroform soaked cotton for several minutes and then placed in a labeled clear plastic Ziploc bag containing 70% isopropyl alcohol and kept for future identification.

Invertebrates were examined using a binocular microscope. Ten percent of the samples were re-examined as quality control. An independent investigator adjudicated any conflicting identifications. Numbers of invertebrates smaller than 2 mm were estimated. Invertebrates larger than 2 mm were identified to lowest operational taxonomic unit (OTU) which in most cases was family, using taxonomic keys (Triplehorn and Johnson, 2005) and reference collections housed at the Illinois State Museum Research and Collections Center (ISM RCC). Some invertebrates were identified to order rather than family due to rarity, dominance of one family, or difficulty of identification.

Data Analysis. We used R and the package 'lme4' (Bates and Maechler, 2010; Team, 2012). We constructed six generalized linear mixed models (GLMM) assuming a Poisson error distribution for our global models. Response variables were either Taxonomic Richness (TR) or Diversity Index (DI). TR was the number of OTUs for each sample. DI was the exponentially transformed Shannon Wiener H' ($e^{H'}$), making it Hill numbers of order 1 (Hill, 1973; Jost, 2007). This transformation was done to ensure DI had the correct statistical characteristics for analysis (Jost, 2007). Because of this transformation, DI can be interpreted as the number of abundant or common taxa within the sample (Jost, 2010). We rounded DI to be able to apply a Poisson family GLMM. A sample is defined as one group of OTU's per sampling method in each of three locations in the FI or FE per field per county.

The predictor variables that were handled as fixed factors in the construction of the models were measures of complexity at three different scales (500, 1000 and 6000 m) and the sample location within the field (either FE or FI). We tested the differences in the three counties at each of the three scales using ANOVA and post-hoc Tukey HSD. Since the complexity at 6000 m, 1000 m and 500 m was not independent, we constructed separate models for each scale. All other fixed variables were regarded as confounding variables and put in the models to correct for potential sources of bias due to the unequal spatial distribution of these variables. The confounding variables were checked with a correlation matrix and did not have high correlations. Fixed confounding variables were either quantitative or categorical. Quantitative variables (Table S2) included average vegetation height (cm), variation of vegetation height sd (cm), distance to the nearest non-arable space > 1 ha (m), width of the FE (m), length of the FE (m), and area of FI (ha). Categorical variables included crop in the FI (soybean or corn) and closest adjacent field (soybean, corn, grassland or developed). Developed included single homes, farm structures and parking areas. Since the 500 m, 1000 m and 6000 m buffers around the sample area that we used for measuring the complexity sometimes overlapped, introducing a potentially correlated effect of complexity on TR and DI between neighboring fields, we included the TR of the nearest field weighted by the area of overlap as a cofounding variable in the models. To study the difference in effect of confounding variable on FE and FI, we included the interaction between sample location (FE or FI) and all confounding variables of our models. There is a known relationship between the total number of individuals per sample, the sample size, and TR (Gotelli and Colwell, 2001; Magurran, 2004). We applied a correction by including the log-transformed sample size, ln (abundance), in the models. We tested the importance of all predictor and confounding variables by applying a Likelihood Ratio Test (LRT) in which we removed each variable separately and tested the change in the likelihood of the models. The negative two times log likelihood ratio approaches a χ^2-distribution (Bolker *et al.*, 2009).

Random factors were method of collection (sticky board, pitfall trap, and sweep net), and field within county within year of sampling. For testing the difference between counties, we removed county from the random variables and made it a fixed variable in the best fitting model of TR (the model at 1000 m scale). We then tested the impact of county with LRT. We followed the same procedure to determine the difference between years and sampling methods. For the purpose of fitting the models of TR, we added the identity of the sample (ID) as a random factor to the model. This makes the models for TR quasi-Poisson models (Elston *et al.*, 2001). Residuals were visually checked in all analyses for normality and equality of variance.

To find the simplest model for TR and DI, we first reduced the number of confounding variables per model stepwise based on a significant contribution of the variable to the model. We stopped this procedure when none of the remaining confounding variables could be taken out of the model without changing it significantly at the p-level of 0.10, so that even weakly confounding variables were still in the model. This left us with a relatively small model per level of scale for TR and DI, i.e., with six separate parsimonious models. Then, using information theory (Anderson, 2007; Mazerolle, 2011), we selected the best fitting model for TR and DI. These two models will be presented in the results. Information on all six parsimonious models is presented in Supporting Information (Table S4 a-f).

Results and Discussion

General Results. There were 890 samples collected by either pitfall trap, sticky board or sweep netting. This is less than the expected 900 because ten samples were lost due to animal disturbance. These ten samples were randomly distributed over the fields. A total of 155,460 invertebrates were identified to 138 different operational taxonomic units (OTUs) in the course of our study (Table S5). The three counties were significantly different in their landscape complexity (Table 1). The range of complexity varied between 5 and 79% non-agricultural area.

Table 1. Average ± se of complexity for each of the 3 counties expressed as the percentage non-agricultural area of the area in a radius of 500, 1000, and 6000 m around the sampling location. Minimum and maximum percentages are between brackets. Results of the F-test on the difference between counties are given on the bottom line;*: p<0.05; ***: p<0.001. Results of Tukey HSD are given in Table S6.

County	500 m	1000 m	6000 m
Cass	48.3 ± 7.46 (5-78)	46.9 ± 7.47 (12-79)	33.8 ± 3.47 (19-49)
Christian	33.0 ± 3.70 (16-50)	27.9 ± 2.26 (15-37)	21.9 ± 1.54 (16-27)
Sangamon	39.7 ± 5.13 (17-63)	43.9 ± 1.34 (37-50)	36.0 ± 0.47 (32-37)
$F_{(2,27)}$	1.85	4.99^{*}	11.80^{***}

The stepwise reduction of the number of confounding variables per model resulted in different models for the three levels of scale of complexity (Table 2). Only field length and ln (abundance) remain present in all models. The interaction between complexity and location is significant in all models, but the main effects of location and complexity are only significant in the models for 1000 and 6000 m.

The three simplest models for TR were compared by applying information theory (Anderson, 2007). The TR model for the 1000 m and the 6000 m level of scale did not differ (Table 3). The same was done for DI and here the model for the 1000 m level of scale was clearly the best fitting (Table 4). The estimated fixed effects of all six models are given in Table S4 a-f. We will use the 1000 m level models for further describing our results on TR and DI.

Table 2. Summary of the impact of the fixed effects on taxonomic richness and diversity index at the different spatial scales. Pred. variables = predictor variables; Conf. variables = confounding variables. Confounding variables included crop in the field interior (FI; soybean or corn), closest adjacent field (soybean, corn, grassland or developed), area of FI (m^2), width of the field edge (FE; m), length of the FE (m), distance to nearest non-arable (green) space > 1 ha, average vegetation height in both FI and FE (cm), variation of vegetation height (sd), correction factors for TR in the nearest sampling field weighted by buffer overlap and ln of abundance. For the predictor variables, * means that the estimated parameter is significantly different from zero. For the confounding variables it means that the variable could not be excluded from the model based on the LRT test, which means that either the main effect, the interaction effect with location or both effects are significant.

	Taxonomic Richness			Diversity Index		
	500 m	1000 m	6000 m	500 m	1000 m	6000 m
Pred. Variables						
Complexity	-	*	*	-	*	*
Location (FE or FI)	-	*	*	-	*	*
Interaction	*	*	*	*	*	*
Conf. Variables						
Crop	-	*	*	*	*	-
Adjacent field	*	*	-	-	*	*
Field area	-	-	-	-	-	-
Field length	*	*	*	*	*	*
With of FE	-	-	-	-	-	-
Distance to green sp	*	*	-	-	-	-
Height avg	-	-	-	-	-	-
Height variability	-	-	-	-	-	-
TR nearest	-	-	-	-	-	-
Ln(abundance)	*	*	*	*	*	*

Table 3. Comparison of the three simplest models for taxonomic richness. Df: degrees of freedom of the model; AICc: corrected AIC; Delta AICc: difference in AICc between the model and the model with the smallest AICc; AICcWt: model weight according to delta AICc; Cum. Wt: cumulative model weights; LL: Log Likelihood.

	Df	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Model 1000	22	4749.85	0	0.56	0.56	-2352.34
Model 6000	14	4750.30	0.45	0.44	1	-2360.91
Model 500	18	4763.42	13.57	0	1	-2363.32

Table 4. Comparison of the three simplest models for diversity index. Df: degrees of freedom of the model; AICc: corrected AIC; Delta AICc: difference in AICc between the model and the model with the smallest AICc; AICcWt: model weight according to delta AICc; Cum. Wt: cumulative model weights; LL: Log Likelihood.

	Df	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Model 1000	19	3545.72	0	0.98	0.98	-1753.42
Model 6000	15	3554.83	9.11	0.01	0.99	-1762.14
Model 500	13	3555.22	9.50	0.01	1	-1764.40

Taxonomic Richness and Diversity

Taxonomic richness (TR) and Diversity (DI) was highest in Sangamon, followed by Cass and Christian counties (Table 5). TR and DI were higher in 2011 than 2012 (Table 6). Pitfalls sampled the most taxa, followed by sweep net samples (Table 7).

Table 5. Average ± se taxonomic richness (TR) and diversity index (DI) per sample in Sangamon (n=298), Cass (n=298), and Christian Counties (n=294). LRT based on complete model (Table S7 a-b); **: p<0.01; ***: p<0.001.

County	TR	DI
Cass	9.87 ± 0.25	4.01 ± 0.17
Christian	9.30 ± 0.33	3.40 ± 0.12
Sangamon	11.86 ± 0.28	4.21 ± 0.15
LRT (Chi-sq, df=3)	16.42**	19.433 ***

Table 6. Average ± se taxonomic richness (TR) and diversity index (DI) per sample in 2011 and 2012. LRT based on complete model (Table S7 c-d); ***: p<0.001.

Year	TR	DI
2011	12.27 ± 0.23	4.16 ± 0.13
2012	8.43 ± 0.23	3.59 ± 0.11
LRT(Chi-sq, df=2)	81.00***	30.285***

Table 7. Average ± se, taxonomic richness (TR) and diversity index (DI) per sampling method. LRT based on complete model (Table S7 e-f); ***: p<0.001.

Method	TR	DI
Pitfall	12.52 ± 0.26	5.06 ± 0.14
Sticky board	8.15 ± 0.23	2.21 ± 0.07
Sweeping net	10.47 ± 0.41	4.88 ± 0.20
LRT (Chi-sq, df=3)	404.20***	347.29 ***

TR was higher in the FE (overall average 11.08 ± 0.24) than in the FI (9.24 ± 0.24), and the model results show this difference is significant (Table S4 b). Also, TR is positively correlated with landscape complexity (Table S4 b). But most striking is the strong interaction between location (either FE or FI) and complexity: TR decreases with increased landscape complexity in FI, while in contrast clearly it increases in FE (Figure 2, Table S4 b). DI was higher in the FE (overall average 3.92 ± 0.11) than in the FI (3.80 ± 0.13). Although these differences appear small, they are significant (Table S4 e). DI increases with complexity in FE and decreases in FI following the same pattern as TR (Figure 3, Table S4 e).

Table 8. The best fitting model for TR (Model 1000, Table 3; model estimates in Table S5 b). Variables included Location (FE or FI), Complexity at 1000 m, crop in the FI (soybean or corn), closest adjacent field (soybean, corn, grassland or developed), length of the FE (m), distance to nearest non-arable (green) space > 1 ha, and sample size (ln abundance). The importance of the separate fixed factors were tested with a LRT. Df: degrees of freedom; LL: Log Likelihood: Chi-sq: Chi-square (*: p<0.05; **: p<0.01; ***: p<0.001).

TR	Df model	AIC	LL	Chi-sq	Df chi	
Complete model	22	4748.7	-2352.3			
Location(FE or FI)	13	4783.0	-2378.5	52.278	9	***
Complexity	20	4765.7	-2362.8	20.988	2	***
Crop	18	4751.5	-2357.8	10.857	4	*
Adjacent field	16	4752.4	-2360.2	15.718	6	*
Field length	20	4756.0	-2358.0	11.302	2	**
Distance to non-arable sp	20	4751.7	-2355.9	7.0544	2	*
Ln(abundance)	21	5132.2	-2545.1	385.52	1	***

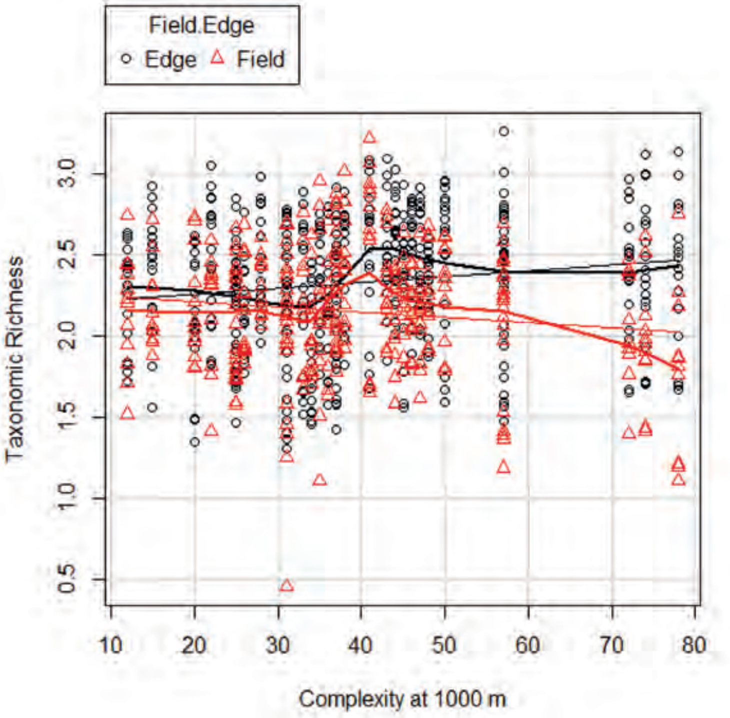

Figure 2. Taxonomic richness predicted by the best model for TR, Model 1000 (table 8) in FE and FI as related to complexity at 1000 m. Thin line: linear regression line; thick line: non-linear regression line (LOESS curve). The x-axis is percent complexity; y-axis is ln(TR).

As field length increased TR decreased in FI, but slightly increased in FE (Table S4 b), while DI decreased both in FI and FE (Table S4 e). TR and DI were influenced by the crops sown in the fields, with soybeans having the lowest TR and DI in FI and corn having the lowest TR and DI in FE (Table S4 b and e). Crop in adjacent fields affected also TR and DI, with developed land having the lowest TR and DI in FI, but soybeans having the lowest TR in FE and corn having the lowest DI in FE (Table S4 b and e). Soybeans in both the sampled FI and the adjacent field yielded the greatest TR: (Crop: 10.8 vs 10.0; Adjacent Field: 11.3 vs 10.5) and DI (Crop: 1.2 vs 1.1; Adjacent Field: 1.2 vs 1.1). Nearest non-arable space > 1 ha had a positive impact on the TR of FI and negative impact on FE but no impact on DI (Table S4 b and e).

Table 9. The best fitting model for DI (Model 1000, Table 4; model estimates in Table S4 d-f). Variables included Location (FE or FI), Complexity at 1000 m, crop in the FI (soybean or corn), closest adjacent field (soybean, corn, grassland or developed), area of FI (ha), width of the FE (m), length of the FE (m), and sample size (ln abundance). The importance of the separate fixed factors were tested with a LRT (*: p<0.05; **: p<0.01; ***: p<0.001).

DI	Df model	AIC	LL	Chi-sq	Df chi	
Complete model	22	3540.8	-1753.4			
Location (FE or FI)	12	3589.8	-1782.6	58.412	8	***
Complexity	18	3566.3	-1765.1	23.437	2	***
Crop	16	3547.9	-1757.9	9.0295	4	*
Adjacent field	14	3548.2	-1760.1	13.388	6	*
Field length	18	3550.5	-1757.2	7.65	2	**
Ln(abundance)	19	3556.6	-1759.3	11.72	1	***

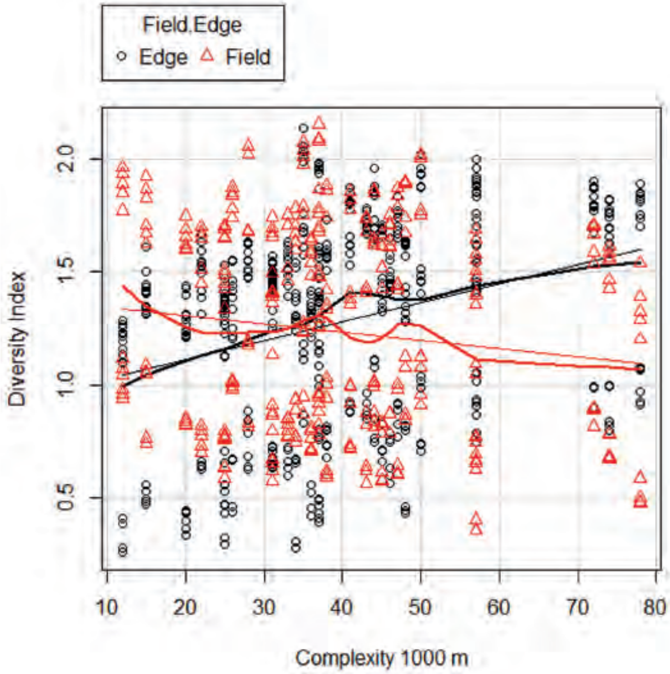

Figure 3. Diversity index predicted by the best model for DI, Model 1000 (table 9) in FE and FI as related to complexity at 1000 m. Thin line: linear regression line; thick line: non-linear regression line (LOESS curve). The x-axis is percent complexity; y-axis is the diversity index (DI).

Discussion. Based on our analysis we developed a snapshot of invertebrate communities early in the growing season. We uncovered significant differences between fields and edges in the way these communities were affected by landscape complexity. We found that TR was affected by complexity at the landscape scale of 1000 m and 6000 m. DI was affected by complexity at 1000 m. Both TR and DI increased with increasing complexity in FE and surprisingly decreased with increasing complexity in FI. Here we showed that the patterns of both TR and DI in fields and edges were identical as far as the relationship with landscape complexity was concerned.

We proposed several hypotheses that guided our study design and data collection:

- TR and DI would be greater in the edges than the fields.
- TR and DI would be greater as landscape complexity is greater, i.e. the relative non-agricultural area is greater. This degree of increase could be different for TR and DI.

- Local factors, which we addressed as confounding variables, may have a significant effect on TR and DI independent of landscape complexity.

Difference between FE and FI

The difference in TR between edges (FE) and fields (FI) seems small, however was statistically significant. Greater differences have been reported in a south African study in corn fields (Botha *et al.*, 2015) and in European studies that examined a large variety of field edges as they relate to organic farming (Holzschuh *et al.*, 2010), ecological compensation meadows (Albrecht *et al.*, 2010) and ditch banks (Noordijk *et al.*, 2010).

Boundaries between “habitat” and “non-habitat” are often clearly identifiable to the human eye and presumably also to invertebrates (Fahrig, 2001). The landscapes in our study had a large percentage of areas that would be considered usable habitat (forests, grassland, etc.) for invertebrates with the agricultural FI presumably at the lower end of any habitat ranking (Table 1). It is therefore not surprising that FE had more invertebrates than FI. Agricultural FI recently disturbed by planting would appear to be even more lacking in habitat value. Our results, however, are consistent with the positive values of soil loosened by planting, warmed by exposure to sunlight, and drained of heavy spring rains. Many invertebrates deposit eggs into the soil; larvae feed on underground roots and detritus; they pupate and emerge as adults to mate. Ants and the larvae of some beetles, moths, flies and worms transport below ground materials to above ground consumers (Polis *et al.*, 1997). The agricultural FI thus have habitat value and are not “non-habitat”. Invertebrates that occupy the FI are obviously ‘adapted’ to high disturbance levels and monoculture vegetation. They are frequently generalists that have a small body size and short life-cycle (Lang, 2003). These generalists are successful and likely account for TR in the FI. Species requiring pristine environments, undisturbed habitats or that have limited dispersal ranges can be expected to be rare in the FI, but could find conditions in the FE that provide a great range of possible habitable environments with varied vegetation type, height, edge width, etc.

TR and DI are highly correlated but give different information. TR gives equal weight to rare taxa as common taxa; DI gives more emphasis on common taxa with little contribution from rare taxa. DI is a relative measure of evenness (Jost, 2010). This is an important component of biodiversity. Having great numbers of a single pest species and few predator species may result in the same TR as having balanced numbers of predator and prey. Knowing that the same patterns persist with TR and DI for FE and FI allows us to address important ecological food webs without harming agricultural yields.

Vegetation in the FE and non-arable areas was not classified as native or non-native in our study. Presumably the non-arable areas had mostly native species, while the FE had varying amounts of native plants. Native invertebrates have evolved in step with the native plants and would optimize interactions. The crops in the FI are non-native. Providing a complex native habitat should provide opportunities for native invertebrate species. Future studies should assess the relationship of invertebrate diversity to native vegetation in the FE.

Differences in agricultural practices may account for divergence from European studies. Studies of FI and FE in Europe deal with a vastly different agricultural system than we studied in central Illinois. Researchers of European agricultural systems have studied cereal crops, peas, potatoes, and sugar beets with small scale crop rotation (Booij and Noorlander, 1992; Batáry *et al.*, 2011). GMO crops are infrequently sown and are prohibited in some nations (Levidow, 2001) while they are the norm for Illinois (Steffey *et al.*, 2004). Some FI are quite large in our study area (e.g.117 ha) while many European study field interiors are considerably smaller e.g. 22-30 ha (e.g. (Kragten and de Snoo, 2004)). Field edges in Europe are relatively stable and consistent temporally (Noordijk *et al.*, 2010). In our study area, FE are frequently mown, treated with herbicide, exposed to de-icing chemicals and burned, and therefore show little contrast from FI in our study or in field edges in Europe.

Our study was conducted during a two-week period in early summer, not long after crops had been sown. The period before our study included major disturbance of the soil from cultivation in the FI and potential movement of invertebrates between FI and FE. Invertebrates vary in their timing of emergence from diapause. The crops were growing rapidly but not yet shading the ground between plants as occurs later in the growing season. Patterns observed at this time may not be the same as patterns later in the growing season. Future studies should look at TR and DI across the growing season.

Agricultural areas in many parts of Europe have been active for many centuries if not millennia and in Illinois somewhat less than two centuries (Williamson, 1986; Warner, 1994). Data from European studies may not be transferable to studies in Illinois and vice versa. That does not mean, however, that the management techniques that are shown to be effective in Europe would not be equally effective in Illinois. Practices that might be beneficial in Illinois include "beetle banks" (Collins *et al.*, 2003), reduction of chemical applications in conservation headlands and field margins (de Snoo *et al.*, 1998), and Ecological Conservation Area wildflower strips (Kleijn *et al.*, 2006).

Landscape Complexity

Most of the fields of our study (n=30) were located in an area (6000 m scale) of high non-agricultural complexity of 16-30% (n=14), 30-40% (n=13) and > 40% (n=3). This is unexpected in an area known as the "corn desert" (Shepard *et al.*, 2008) and may be related to our selection of structurally diverse FE in proximity to natural areas. Assuming that the intermediate landscape complexity hypothesis (Tscharntke *et al.*, 2005) is also applicable in the agricultural areas of the Midwest, this would mean that agri-environmental measures to increase biodiversity would have little effect in our study area: the TR and DI are already optimal for an agricultural area. This idea is supported by the fact that the TR we found in the FI is relatively high and close to the TR in the FE (ca. 9 versus ca. 11 taxa per sample on average). However, it should be noted that our study areas may not be representative of the rest of the Midwest.

Local communities are firstly dependent on the regional pool of species (MacArthur, 1967). Local TR is expected to be larger within areas of greater landscape complexity (Batáry *et al.*, 2011), because increased complexity increases the regional pool from which to draw local communities (Tscharntke *et al.*, 2012). Therefore, the higher TR that we found in the FE in more complex landscapes fits this species pool hypothesis.

However, according to the species pool hypothesis, we would also expect higher TR in the FI. The pattern that emerges in our data shows that as TR in the FE increases, the TR in the FI decreases. There are several possible explanations of this deviation from expectation, which could be examined in further studies. First, because of the higher TR in the more complex landscapes, the predation pressure on invertebrates could be higher, either by other invertebrates or by vertebrates that were not measured by us (Warner, 1994; Nemec *et al.*, 2014). In the FE more invertebrate species would be able to escape this increased pressure because of the higher vegetation density, while in the fields the invertebrates are more vulnerable to predation. This would fit Tscharntke et al.'s (Tscharntke *et al.*, 2002) hypothesis that landscape complexity provides spatial and temporal insurance, which would mean in this case a more efficient regulation of pest species populations in the FI.

Second, another explanation is that invertebrates prefer the FE habitat and non-agricultural landscape elements even when they are able to occupy the FI niche. In this case, the data may reflect species moving into the FI only when they have no other option, e.g. when individual numbers are high in the FE or resources are depleted, but no escape to other landscape elements than FI is possible. When there is other, more suitable habitat available, that is where invertebrates will occur.

Third, it is intriguing to consider that plant-to-plant interactions in more complex areas may provide a defense for the FI (Heil and Karban, 2010; Kumar *et al.*, 2014). This might involve a signal sent by plants in the edge in response to herbivory being received by the crops in the FI (Karban *et al.*, 2000). Because the FI are a monoculture, the response spreads through the entire FI providing protection against the herbivores either repelling the herbivores or calling predators or perhaps both (Dudley *et al.*, 2013; Karban *et al.*, 2013). This effect could be masked in the FE by the dense vegetation.

We tested whether the study areas within the three counties varied significantly in their complexity (Table 1). The study areas were not randomly selected; they were selected because of their proximity to non-arable land within the agricultural landscape and did not include urban areas within the buffer circles. The three counties were typical of the Illinois landscape, but the study areas selected were probably more complex than the remainder of the land in the counties. These areas were not necessarily representative of either the rest of county, state or even Midwest.

Confounding Variables

A drought period began in the summer of 2011 and continued through 2012 with higher than normal temperatures and lower than normal rainfall. We tested if the difference in TR and DI was significantly different between years (Table 6). We do not know if the highly significant difference between years was typical of the normal variability of invertebrate populations or a product of the drought conditions.

We measured a number of confounding variables that we felt might impact TR and DI. Crops in the study areas were GM soybean and corn. Corn is usually the first crop to be sown when the fields dry out and start to warm. Soybeans are planted later. The planting dates and subsequent plant growth and shading may have influenced colonization by invertebrates. Price (Price, 1976) found that herbivores colonized the soybeans first with no appreciable increase in parasites and predators until the canopy had developed. Botha (Botha *et al.*, 2015) found that biodiversity loss was apparent if corn fields were within 30 m of the field margins being sampled. Therefore, it was no surprise that crop had an effect in our study.

All FI were tilled before planting and may or may not have been recently treated with glyphosate (broad spectrum herbicide). Herbicides vary in their impact on invertebrates and the impact often depends on the timing and context of the application (Freemark and Boutin, 1995; Pleasants and Oberhauser, 2013). Invertebrates vary greatly in their mobility and dispersal ability. In agricultural landscapes with high disturbance particularly in the planting and harvesting phases the dispersal technique is crucial for survival (Tscharntke *et al.*, 2005). In addition, crossing hard barriers, such as roadways, limits the mobility of arthropods (Mader *et al.*, 1990). These issues are outside the scope of this study but should be acknowledged as having an impact.

As the length of the FE increased, the TR and DI decreased. The edge along the fields may serve as a corridor for migration as well as a refuge during episodes of disturbance. The distance to additional field edges increases vulnerability of invertebrates with low mobility.

The distance to the nearest non-arable space > 1 ha was important to TR but had no significant impact on DI. We did not collect from the nearest non-arable space and cannot say how the TR and DI compared to our study fields. Gonzalez (González *et al.*, 2015) found both forest cover and proximity affected arthropod assemblages in soybean fields in central Argentina.

We measured a number of other factors which did not significantly contribute to our findings (Table 2). These included the size of the agricultural field, the width of the FE, the average vegetation height, vegetation sd and soil type. These were local factors within the agricultural landscape that affect other groups of organisms such as birds (Warner, 1992; Walk, 2001), and mammals (Duggan, 2011; Mulligan *et al.*, 2013), but not some reptiles (Williams *et al.*, 2012).

Conclusions

Our data indicate that invertebrate diversity responds to characteristics operating at both field and landscape levels. For FI and FE, habitat quality (in our analyses shown as the significance of confounding variables) had multiple effects. Research that considers the agricultural landscape strictly as a mosaic of habitat and non-habitat fails to recognize the utilization and possible enhancement of biodiversity provided by the managed FE since these may have considerable TR and DI of invertebrates. Knowing that landscape complexity is relatively high in some areas of central Illinois as compared to European landscapes, additional investigation is needed to determine whether there are special opportunities to enhance biodiversity in the agricultural landscape of central Illinois. Agri-environment schemes of the European Union have sometimes been shown to be effective in improving biodiversity (Kleijn and Sutherland, 2003; Scheper *et al.*, 2013). Keeping the large-scale complexity of the landscape that currently exists is clearly an important conservation strategy to preserve invertebrate populations. There seems to be no detrimental effects from an agriculture point of view, because a more complex landscape does not result in higher TR in FI. Planting FE with native plants is an easy step in providing habitat for native insects that could be tested.

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Chapter 7

Enhancement of Linear Agricultural Areas for Invertebrates and Breeding Birds

Based on:
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Abstract

Birds are an important part of the agricultural landscape, as having nature value, but also as pest control agents and bio-indicators for the health of the environment. Here we look at linear non-crop elements in agricultural areas as an opportunity to provide food for nestlings of avian species. We measured invertebrate availability as it relates to structural complexity at the local and landscape levels in three counties in central Illinois. Invertebrate availability was measured with taxonomic diversity and estimated biomass during spring of 2012 and 2013. Our study shows that field edge characteristics have the greatest impact on invertebrate diversity and abundance, as compared to field and landscape features. This finding shows that the availability of bird food, both in diversity and biomass, may be easily enhanced without changes to agricultural practices.

Keywords: agricultural landscape, birds, nestlings, taxonomic diversity, biomass, invertebrates

Introduction

In Illinois, as elsewhere, bird populations are changing with an overall decline in many species (Walk and Warwick, 2010), which has been related to loss of habitat due to agricultural intensification and increased urbanization of the landscape (Walk and Warwick, 2010). The use of pesticides may also play a role in avian declines (Geiger *et al.*, 2010). Agricultural intensification has the admirable goal of increasing production of food, feed, and fuel which is necessary to human life. At the same time, the loss of biodiversity and ecosystem services is a concern. In the United States, management for biodiversity has been with a focus on land sparing" (Phalan *et al.*, 2011; Grau *et al.*, 2013). This leaves isolated tracts to be managed for biodiversity and other areas focused on housing or agriculture. Many countries in Europe use a land sharing approach. This tactic uses a combination of landscape complexity and agricultural practices with a conservation approach to maximize biodiversity and ecosystem services and subsidize farmers for the subsequent loss in yield (Vickery *et al.*, 2004; Donald and Evans, 2006; Carvell *et al.*, 2007).

The landscape of Illinois has altered dramatically since initial settlement over two centuries ago. The General Land Office Survey (~1820) reported about two thirds of the landcover as prairie with the remainder forested (Anderson, 1970). Very little of the land was developed or cultivated. Settlement occurred moving from the south to the north with settlers coming from Tennessee and Kentucky. By 1920, 90% of Illinois was farmed with much of the population living in rural areas (Walk and Warwick, 2010). Cultivated ground was dominated by corn, and the remaining farmland a diverse mixture of hay, pasture and small grains (mostly oats). Most farms were small by today's standards, averaging 52 ha in size and most (> 90%) had both cattle and horses. Today farms have grown in size to an average of 149 ha (Walk and Warwick, 2010) with the fastest growing landuse type as developed (areas used for industrial, commercial, and residential purposes) (Walk and Warwick, 2010). The number of cattle and horses have dropped and with it the need for hay, pasture, and small grains. Row crops are dominated by corn and soy in a two to three-year rotation. Field size increased > 80% while the number of fields was about halved. Landuse will continue to shift in response to human needs and climate change.

Avian populations shifted along with the landuse. Idle grasslands, defined as not having been grazed, hayed or mowed in the year of the survey, declined from 1.8

million acres in the early 1900s to 1.2 million acres in the 2000s. Surprisingly the absolute abundance and species richness of birds in grasslands have increased during this time period (Walk and Warwick, 2010). What is less surprising is that the relative abundance of the species has undergone a major shift since the surveys conducted in the early 1900's with some species dropping from dominance while other species prospered with changing habitat availability. As field size increased and the amount of edge decreased, surveys of linear grasslands taken in the 2000s show a decline in both the absolute abundance and the number of species from surveys taken in the 1950s (Walk and Warwick, 2010).

Edges, i.e. the area between habitat patches, and their role as habitat for birds have been studied for decades (Ries *et al.*, 2004). Birds inhabiting this habitat are often generalists that can use the heavily disturbed areas (Walk and Warwick, 2010). Little is known about the distribution of invertebrates in agricultural field margins in the Midwest. The neglect of this ecologically important group is somewhat surprising considering the importance of invertebrates as food items for breeding birds and their nestlings. During the breeding season, the diet of many avian species shifts to include insects as a protein source (Bell, 1990; Cavitt and Thompson, 1997) and later to feed rapidly developing nestlings.

We looked at linear, non-crop elements in agricultural areas early in the avian breeding season to provide invertebrates to feed nestlings. We examined edge and field features and landscape characteristics to determine which had the greatest impact on invertebrate diversity and estimated biomass with the goal of providing guidance to improving invertebrate biodiversity and food availability for bird nestlings within the agricultural landscape. Studies have shown that invertebrate richness and abundance are influenced by complexity at the landscape scale (Steffan-Dewenter and Tscharntke, 2002; Batáry *et al.*, 2007), field characteristics (Westerman *et al.*, 2003; Marvier *et al.*, 2007) and edge characteristics (Stinner and House, 1990; Wilson *et al.*, 1999). We examined the hypotheses that invertebrates were dependent on these features independently or in combination or not dependent on any of these characteristics.

Methods

Study Area. The study was conducted in central Illinois in Cass, Christian and Sangamon Counties (Fig. 1). This is part of the Grand Prairie Natural Division, a vast plain of formerly tallgrass prairie (Schwegman, 1973). Soils are fertile and well drained with the use of tile lines and ditches. The topography is generally level to rolling. Illinois climate is typically continental with cold winter temperatures (mean -3.8°C), warm summers (24.6°C) and frequently fluctuating temperature, humidity, cloudiness and wind conditions. Precipitation averages 895 mm per year and the growing season is ~185 days (Midwestern Regional Climate Center 2009; Springfield, Illinois http:/mcc.sws.uiuc.edu). During both years of the study period, precipitation was much below normal. Due to the reduced precipitation and high ambient temperatures, the region was considered to be in an extreme drought (National Oceanic and Atmospheric Administration 2012).

Figure 1. Location of Cass, Sangamon and Christian counties in Illinois, USA.

We selected 30 agricultural fields, ten in each of three Illinois counties, mostly seeded in a two to three-year corn (*Zea mays*) and soybean (*Glycine max*) rotation. The average field size was 28 ha varying between 1 and 117 ha. Structural complexity in the areas around the fields ranged from simple landscapes with a relatively high percentage of arable land, to complex landscapes with a relatively low percentage of arable land and a large proportion of semi-natural land cover and other land use types. We selected fields with varying degrees of edge structure ranging from closely mown monoculture through shrubby vegetation several m in height. Roadsides were managed with a variety of mowing regimes and some areas were impacted by drift of herbicides. We obtained permission to access the fields from either the land managers or landowners. Landowners or managers seeded field interiors with genetically modified corn or soybeans, prior to the start of the study.

Sampling Methods. From late May 26 to June 13 in 2011 and 2012, invertebrates were sampled with sticky boards, sweep netting, and pitfall trapping (Eymann, 2010). We selected this time period early in the breeding season to be comparable to other studies (Graber and Graber, 1963; Hendron, 2010) Sampling methods were chosen to sample varied invertebrate feeding styles (flying, gleaning, and epigeic). Sticky boards and pitfall traps were placed at six locations per field, grouped equidistant from the ends of the field and adjacent to the road or field edge; three in the cultivated field interior (FI) and three on the edge (FE) outside the tilled area and spaced at 10 m intervals. Sampling sites in the FI were 10-15 m from the edge in the second equipment row and not in the field head. Sites on the FE were 1-2 m from the FI and within the vegetated edge. Sweep netting was conducted only in the FE to avoid damage to the crops.

Pitfall traps were 150 ml plastic cups with an aperture of 70 mm placed into the ground so that the mouths were flush with the ground and was level with the ground surface. Each trap was filled to ~ 2.5 cm with a solution of water and vinegar and a few drops of dish soap added to break the surface tension of the water. Ethylene glycol was not used because it attracted mammals to the traps during a pilot study. Pitfall traps were retrieved seven days after placement and contents placed in a labeled clear Ziploc bag containing 70% isopropyl alcohol and kept for future identification.

One sticky board (Sensor ~ 8 cm x 13 cm Yellow Monitoring Cards, GrowSmart), attached to a flag (~ 6 cm X 9 cm X 76 cm LimeGlo, Forestry Suppliers) was placed adjacent to each pitfall trap. Boards were placed with a minimum of half the board above the vegetation. Boards were retrieved after two days and placed in a clear plastic cover and saved for future identification.

A sweep net sample consisted of 30 strokes, 360° around the sweep netter in the field edge near each of the pitfall traps for three samples total per field. The net was 15” in diameter with muslin netting (Forestry Suppliers). All sweep net samples were collected on sunny days between 10:00 am and 14:00 pm with wind 0-19 km/

hr as measured on the Beaufort scale. Invertebrates were placed in a "knockdown" jar containing chloroform soaked cotton for several minutes and then placed in a labeled clear plastic Ziploc bag containing 70% isopropyl alcohol and kept for future identification.

ArcView GIS 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) was used on The Illinois Critical Trends Assessment landcover database (Luman *et al.*, 2009) to determine field area (ha), field edge length (m), average depth of edge (m), distance to nearest large non-agricultural area >1 ha (m), proportion of non-agricultural area at three different scales, and soil type. Field edge length was the length of the field edge adjacent to the sampling area. Complexity, i.e., proportion of non-agricultural area, was determined within a 1000 m circular plot around each sampling location. Arable land included corn, soybeans, other miscellaneous row crops, and winter wheat (*Triticum aestivum*). Non-arable land was defined as upland forest, savannah, coniferous forest, wet meadow, marsh, seasonally flooded, floodplain forest, swamp and shallow water.

Field locations were determined using a global positioning system (Garmin Oregon 450t). Each field was assigned a number designating specific sample location. Dates of trap placement, sample retrieval and sweep netting were recorded. Vegetation of the edge, field, and nearest neighboring field was also recorded. The height of vegetative edge was measured at 30 points along a transect between pitfall traps using a measuring stick.

Characteristics of the edges included the height and variability of the vegetation within the edge; the treatment of the edge: whether it had been mown since the start of the growing season or effected by herbicide drift; the depth and length of the edge; and the amount of bare ground (Kennedy *et al.*, 2009) around the sample location. Field characteristics included the crop in both the study field and adjacent field not separated by a hard surface, field size and length, and crop height and variation. Landscape features included soil type, the distance to the nearest non-arable space > than 1 ha; and the proportion of non-arable land to arable land within a 1000 m circle.

Identifications. A general overview of the bird species present was generated by noting species seen or heard during the period of time the investigators were in the field either preparing or retrieving invertebrate samples, around 20 minutes per location May 26 to June 13 in 2011 and 2012.

Invertebrates were examined using a binocular microscope. Ten percent of the samples were examined a second time as quality control. An independent investigator adjudicated any conflicting identifications. Numbers of invertebrates smaller than 2 mm were estimated. Invertebrates larger than 2 mm were identified to lowest operational taxonomic unit (OTU) which in most cases was family, using taxonomic keys (Triplehorn and Johnson, 2005) and reference collections housed at the Illinois State Museum Research and Collections Center (ISM RCC). Some invertebrates were identified to orders rather than family due to rarity, dominance of one family, or difficulty of identification. We used the reference collections to measure a random sample of ten invertebrates in each family, of the mostly commonly collected taxa in Illinois, to determine average length.

Data Analysis. All statistical analyses were performed using the package 'lme4' in R (version 3.0.2; The R Foundation for Statistical Computing 2013). We applied a generalized linear mixed models (GLMM) assuming a Poisson distribution. Response variables were taxonomic diversity (TD), and estimated biomass (WT). TD was the exponentially transformed Shannon Wiener H' ($e^{H'}$), making it Hill numbers of order 1 (Hill, 1973; Jost, 2007). This transformation was made to ensure TD had the correct statistical characteristics for analysis (Jost, 2007). WT was an estimate of dry weight (mg) based on average length (mm) (Rogers *et al.*, 1976).

Mathematical models were used to represent the various hypotheses of response variables and model fit used as a method of choosing the best hypothesis (or best working model) (Burnham and Anderson, 1998). The model-selection approach can help select among the numerous hypothesis that could not be tested using a single model approach. For the purpose of developing the models, we classified the predictor variables into three groups: 1) *edge*: edge vegetation height and variation, edge length and depth, amount of bare ground, and whether vegetation had been recently mown or exposed to herbicide drift; 2) *field*: crop in the field and adjacent field, area and length of the field, and height and variation of the crop; and 3) *landscape*: soil type, distance to the nearest non-arable land > 1 ha, and percent of non-arable land within a 1000 m circle around the sampling site.

We developed eight hypotheses regarding the response variable X, either TD or WT, being dependent on a combination of these three groups of predictor variables. The eight hypotheses are as follows: H_1: X dependent on edges; H_2: X dependent on fields; H_3: X dependent on landscape; H_4: X dependent on edges and fields; H_5: X dependent on edges and landscape; H_6: X dependent on fields and landscape; H_7: Global Model: X dependent on edges, fields and landscape; and H_8: Null Model: X not dependent on either edges, fields or landscape.

Akaike's information criterion corrected for sample size (AICc) was used to compare models (Burnham *et al.*, 2011). Burnham and Anderson (1998) suggest that models having ΔAICc (difference in AICc scores) within 1–2 of the best model have substantial support. Models within about 4–7 of the best model have considerably less support, while models with ΔAICc > 10 have essentially no support.

Random factors were method of collection (sticky board, pitfall trap, and sweep net), and field within county within year of sampling. TD was rounded to be able to apply a Poisson family GLMM. In case of fitting the models of TD, we needed to add the identity of the sample (ID) as a random factor to the model in order to get a solution for the models. Although the variance component of ID was small, this could indicate that the error of the models was not completely Poisson distributed without the ID (Elston *et al.*, 2001). In these cases the actual distribution can be assumed to be a quasi-Poisson distribution. Data is reported as $\bar{x}$± SE.

Results

There were 890 samples collected by pitfall trap, sticky boards or sweep netting. We identified 155,460 specimens to 138 operational taxonomic units (OTUs). General invertebrate sampling results have been reported elsewhere (Evans *et al.*, 2016). Taxonomic diversity averaged 2.2 (1.0-15.3) ± 0.09. Biomass averaged 1155.0 mg (0.9-35720) ± 74.30.

For both TD and WT, our first hypothesis had the best fit: TD and WT dependent on edge features which included edge vegetation height and variation, edge length and depth, amount of bare ground, and whether vegetation had been recently mown or exposed to herbicide drift (Table 1). In edges, diversity remains almost constant as edge height increases. It increases as vegetation height variability, edge depth and percent of bare ground increases. It decreases as field length increases. In fields, as edge height and variability and percent of bare ground increase, diversity increases. As field length increases, diversity in the field increases. As edge depth increases, diversity in the fields decreases. In both fields and edges, as edge height and variability and percent of bare ground increased, biomass increased. As field length increased, biomass in the edges showed a slight decline and an increase in fields. As edge depth increased, biomass in the fields declined and in the edges increased. TD was slightly greater in the edges where there was no mowing or evident herbicide drift and treatment of the edges had no impact on the fields. WT was greatest in edges impacted by herbicide drift and least in areas that had been mown (Tables 2 and S1, Figures 2 and 3).

There were 19 bird species identified during sampling (Table 3). All birds were seen or heard at least five times in each of the counties in each year of sampling. We also report population trends, residence status, nest placement, number of broods per year, feeding habits and habitat preferences based on literature (Ehrlich *et al.*, 1988; Kleen *et al.*, 2004; Walk and Warwick, 2010).

Table 1. Comparison of the models for (a) taxonomic diversity (TD) and (b) estimated biomass (WT). $H_{1:}$ X dependent on local edges; H_2: X dependent on local agriculture; H_3: X dependent on landscape complexity; H_4: X dependent on local edge and local; agriculture; H_5: X dependent on local edge and landscape complexity; H_6: X dependent on local agriculture and landscape complexity; H_7: Global Model; H_8: Null Model. Df: degrees of freedom of the model; AICc: corrected AIC; Delta AICc: difference in AICc between the model and the model with the smallest AICc; AICcWt: model weight according to delta AICc; Cum. Wt: cumulative model weights; LL: Log Likelihood.

(a) TD

TD	Df	AICc	Delta AICc	AICcWt	Cum.Wt	LL
H_1	19	3571.09	0.00	0.98	0.98	-1766.11
H_3	31	3580.65	9.56	0.01	0.99	-1758.17
H_2	23	3581.28	10.19	0.01	1.00	-1767.00
H_5	45	3583.73	12.64	0.00	1.00	-1744.41
H_4	34	3586.77	15.68	0.00	1.00	-1757.99
H_6	49	3589.04	17.95	0.00	1.00	-1742.60
H_7	60	3598.09	27.00	0.00	1.00	-1734.63
H_8	4	3602.48	31.39	0.00	1.00	-1797.22

(b) WT

WT	Df	AICc	Delta AICc	AICcWt	Cum.Wt	LL
H_1	19	2928.34	0.00	1	1	-1444.73
H_3	31	2947.35	19.01	0	1	-1441.52
H_4	34	2948.13	19.79	0	1	-1438.67
H_8	4	2950.93	22.59	0	1	-1471.44
H_5	45	2956.96	28.62	0	1	-1431.03
H_2	23	2957.24	28.91	0	1	-1454.98
H_6	49	2976.58	48.24	0	1	-1436.37
H_7	60	2980.81	52.47	0	1	-1425.99

Table 2. Impact of individual variables in the fields and edges. Taxonomic diversity = (TD) and biomass = (WT).

Variable Increase	TD Edge	TD Field	WT Edge	WT Field
Edge Height	Decreased	Increased	Increased	Increased
Edge Variation	Increased	Increased	Increased	Increased
Edge Length	Decreased	Increased	Decreased	Increased
Edge Depth	Increased	Decreased	Increased	Decreased
Bare ground %	Increased	Increased	Increased	Increased
Treatment	Mown (least)	No Impact	Mown (least)	No Impact

Table 3. Birds seen or heard during sampling; population trends and life history compiled from literature. P/M: permanent or migratory; ag: agriculture. Nest location, number of broods, feeding habits, diet, and habitat (Ehrlich 1988), residence status and trend per year over the past 50 years (Kleen 2004); trends, diet and habitat (Walk 2011).

Species	*Latin name*	Trend per year	P/M	Nest location	Broods	Feeding habits	Diet	Habitat
Ring-necked pheasant	*Phasianus colchicus*	-2.0%	P	ground nest	1	ground glean	terrestrial and aquatic invertebrates, small vertebrates, seeds, grain, fruit	edge, ag, open country, woodlands
Northern bobwhite	*Colinus virginianus*	-1.9%	P	ground nest	1	ground glean	leaves, fruit, buds, tubers, spiders, snails, small vertebrates 85%veg 15% animals more insects in summer	hedgerows, tall grassland, old fields, woodlands, ag
Killdeer	*Charadrius vociferus*	8.1%	M	ground nest	1	ground glean	75% insects, remainder wide variety of invertebrates 2% weed seeds	gravel
Mourning dove	*Zenaida macroura*	0.5%	M	usually tree 0’-40’	multiple (2-6)	ground, foliage glean	seeds, including waste grain from cultivated fields > 99% of diet.	edge, ag
House wren	*Troglodytes aedon*	1.6%	M	cavity (snag) 0’-20’	2-3	ground, foliage glean	insects, including millipedes, spiders, snails	open woodland, shrubland, ag
American robin	*Turdus migratorius*	2.9%	M	tree or shrub 10-20’	2	ground, foliage, glean	insects, fruit	forest, woodland, gardens parks
Gray catbird	*Dumetella carolinensis*	0.7%	M	dense brush shrubland, edge 2’-10’	2	ground, foliage glean	insects, fruit, spiders, berries	dense brush
Brown thrasher	*Toxostoma rufum*	-0.9%	M	low shrub 0’-10’	2-3	ground, foliage glean	omnivore: insects invertebrates, small vertebrates, berries, fruit	dense brush, shrubland, edge
White-eyed vireo	*Vireo griseus*	-1.8%	M	dense brush 1’-8’	1-2	Foliage glean	insects during breeding season, 20-30% berries in winter	edge, ag, brushy moist areas near streams, old fields, scrub
Field sparrow	*Spizella pusilla*	-3.0%	M	sapling, shrub 0-2.5’	2-3	ground, foliage	insects, seeds, incl few spiders, seeds of forbs and grass	old fields, brush, edge, thorn scrub
Northern cardinal	*Cardinalis cardinalis*	0.6%	P	dense brush, sapling 1’-15’	multiple 2-4	ground glean	insects, seeds, fruit	dense shrubs, brush, thickets, riparian thickets
Blue grosbeak	*Guiraca caerulea*	1.7%	M	shrub 3’-12’	2	ground, foliage glean	insects, seeds, including snails, grain occasional fruit	dense brush
Indigo bunting	*Passerina cyanea*	-1.0%	M	tree, tangle 1.5-4’	2-3	foliage, ground glean	insects, seeds, fruit, including grain, berries	forest edge, woodland, old fields, shrub, orchards

American goldfinch	*Carduelis tristis*	-0.5%	M	shrub, forb 2'-40'	1-2	foliage, ground glean	seeds, insects, including seeds of deciduous trees, forbs, grass, floral buds, berries	weedy and cultivated fields, woodland, riparian edge
Song sparrow	*Melospiza melodia*	0.1%	M	shrub 0-3'	2-4	ground, foliage glean	insects, seeds, including grass and forb seeds, some berries, crustaceans and mollusks	early succession, dense veg riparian, forest edge
Red-winged blackbird	*Agelaius phoeniceus*	-0.3%	M	brush (wet), reeds	2-3	ground, foliage glean, hawks	insects, seeds, spiders, grass and forb seeds, rarely fruit	fresh water marshes, riparian edge, fields
Eastern meadowlark	*Sturnella magna*	-2.3%	M	ground nest	2	ground glean	insects, seeds, spiders, grass and forb seeds, some fruit	edge, ag, grassland savanna
Brown-Headed cowbird	*Molothrus ater*	1.1%	M	parasitic, shrub and ground	1-80 eggs	ground glean	insects, seeds, spiders, few snails, grain, grass and forb seeds	edge, ag, woodland forest edge, grassland
Dickcissel	*Spiza americana*	-3.5%	M	shrub, herbs 0-2'	1	ground glean	insects, seeds, younger birds 70% grain grass and forb seeds, 30% insects: adults is reverse	early succession, grasslands, meadows, savanna, cultivated and abandoned fields

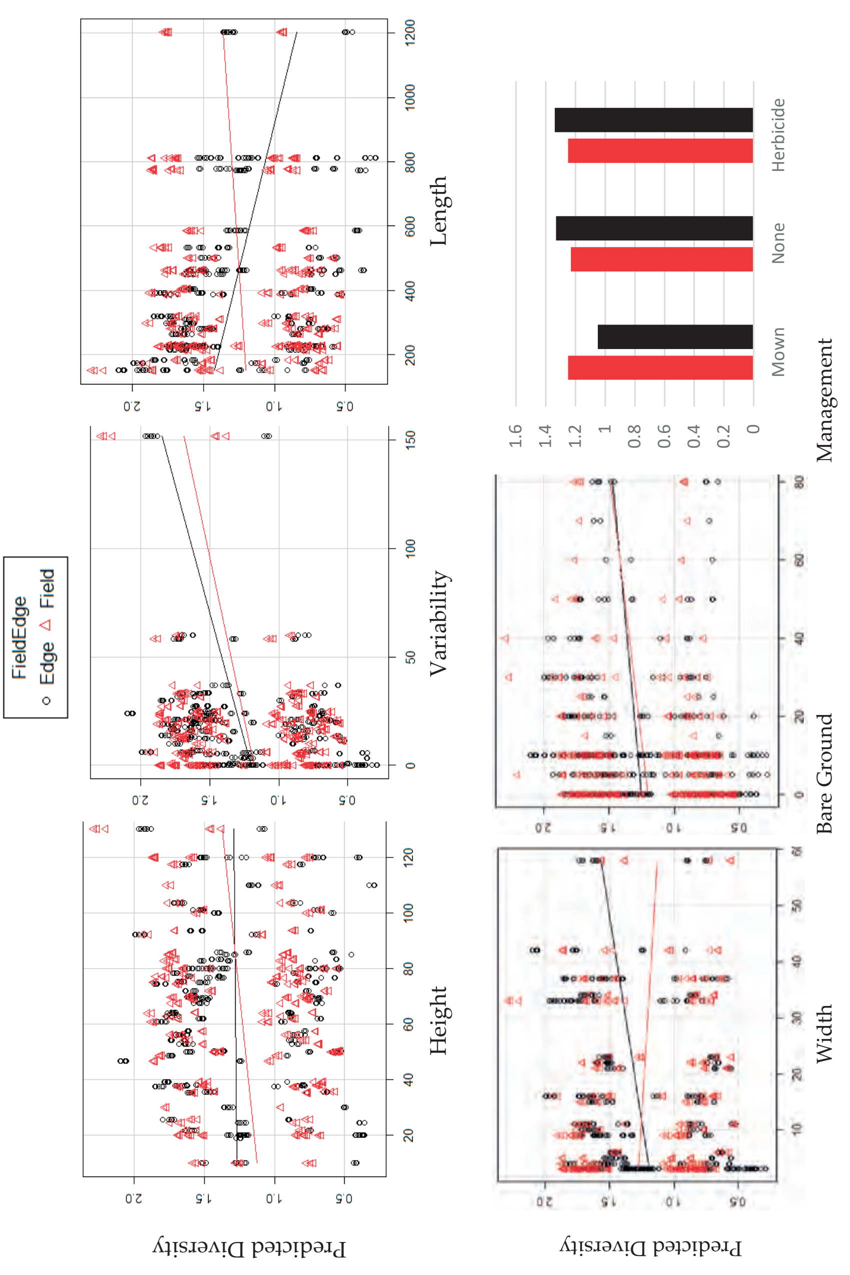

Figure 2. Diversity in fields and edges as predicted by each of the edge variables.

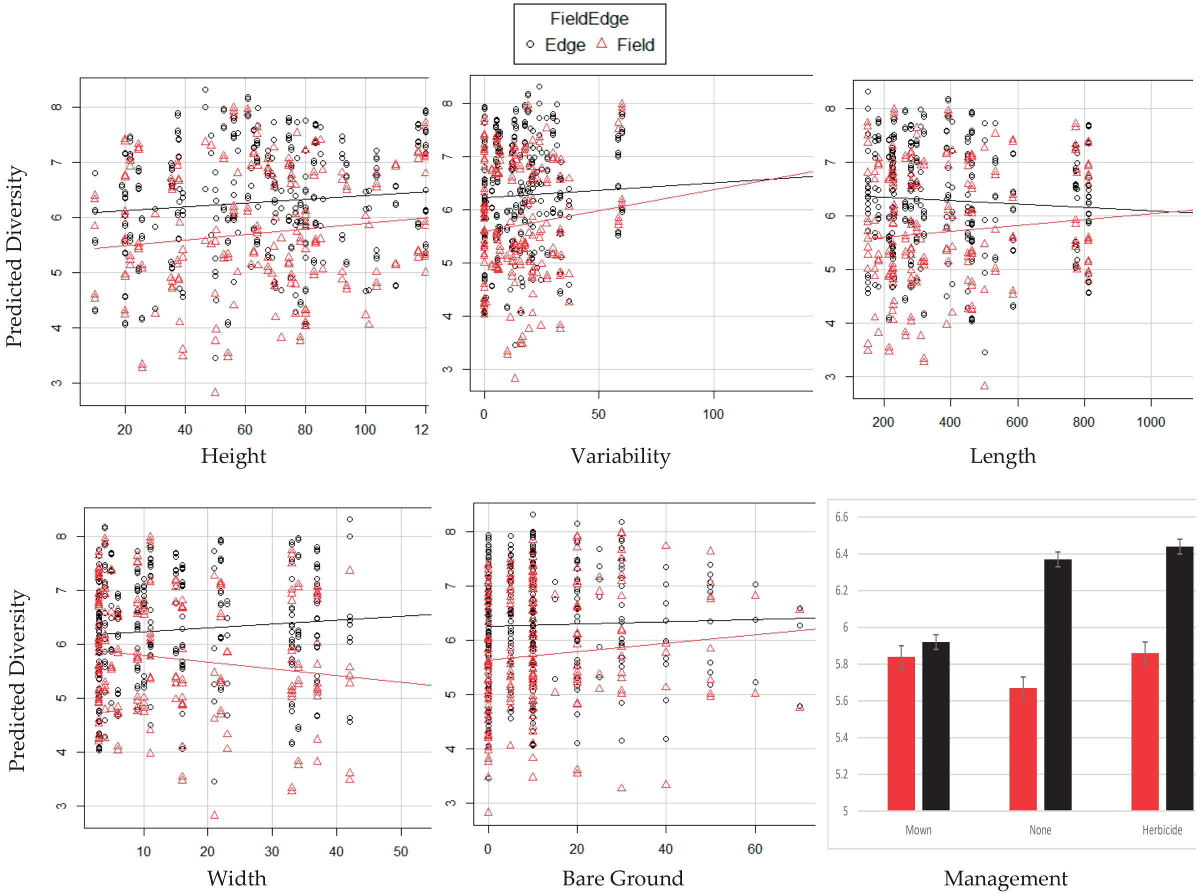

Figure 3. Biomass in fields and edges as predicted by each of the edge variables.

Discussion

Our study shows that TD and WT are most impacted by features in the edges. The height and variability of the vegetation is a reflection of the vegetation diversity of the edge. It provides a number of niches for invertebrates to occupy (Noordijk *et al.*, 2010a; Kang *et al.*, 2013). Many edges in our study were planted in grasses and mown at some time either recently or possibly the end of the last growing season. In these cases, the vegetation was monoculture of uniform height. More varied vegetation height was generally found in edges that were not managed. Similar to other studies, as the biodiversity of the vegetation in the edges increased the biodiversity and biomass of the invertebrates increased as well (Scheffer *et al.*, 1984; Healy, 1985).

The length of the edges is related to field size and has been increasing over time. As the field length increases the TD and WT decline. As the length of the field increases so does the distance to the nearest non-tilled areas that serve as refugia or source populations in recovery after adverse events (Pryke and Samways, 2012).

As the depth of the edge increases TD and WT in the edges both increase. This could be from the lack of pesticide drift further from the agricultural field (de Snoo *et al.*, 1998; Frampton and Dorne, 2007) as well as less exposure to road pollutants (Muskett and Jones, 1980; Forman, 1998). This increases the area for occupation by invertebrates as well as provide more area for escape from predators.

The amount of bare ground has been shown to be directly related to TD as it was in our study. Mowing and removing clippings allows greater insolation and access to vegetation (Morris, 1981; Parr and Way, 1988; Noordijk *et al.*, 2010b).

Edges planted in grasses were sometimes managed with mowing. We noted if they had been mown since the start of the growing season. If the edges were mown, there was less WT in the fields. It is possible that they were more exposed to predation by having little to no place to hide or they moved to refugia immediately after the mowing event and had not repopulated the sampling site. Many invertebrates are susceptible to desiccation and might have left the sampling site if it was too hot and dry after mowing. The response to herbicide drift was interesting. Impact of herbicide drift mostly evident in areas with tall grass. The structure of the grasses remained in place with new growth under the upper layer of dead vegetation. This allowed for refugia from predation, access to the soil surface, and protection from excessive drying.

While the effects on invertebrate assemblages were predictable based on other research, it was interesting to note the effects on the fields did not parallel the effects in the edges. Invertebrates in the fields had a less strong reaction to the characteristics of the edge (Table 3).

Birds are an important part of the agricultural ecosystem. They consume many insects such as mosquitoes, Japanese beetles and European corn borer moths. Without birds, many of these insects would do considerably more damage to crops and spread diseases such as West Nile Virus. Birds are also bio-indicators of environmental pollution with DDT contamination being an extreme example (Temple and Wiens, 1989; Furness, 1993; Padoa-Schioppa *et al.*, 2006). The birds in our study are generally considered common with some species increasing and others decreasing over time (Table 4). Our bird observations were somewhat limited because the time of day we conducted our sampling for invertebrates was a time of day birds were not very active. The birds noted in our study is an indication of what birds might benefit from enhancing the agricultural edges.

A limiting factor of our study is that when measuring the availability of bird food during the breeding season the sampling is concurrent with bird predation. When insects are at low densities, the impact of bird predation is proportionately greater (Holmes *et al.*, 1979). We have looked at insect availability defined as abundance of potential prey items within the agricultural edge that has the potential for being used by a bird searching for food. Whether an available insect is actually eaten depends on factors outside the scope of this study such as its probability of being detected, its acceptability and its chances of being caught and eaten.

Our study supports the theory that increasing ecological contrast has the potential for the enhancement of both invertebrate and avian taxa (Hammers *et al.*, 2015). Birds use a variety of habitat components and the best configuration would be a matrix that had all needed components to fill life history needs (Leopold, 1970; Smith *et al.*, 2011). Here we show that edges features effect the diversity and biomass of potential food. Our study shows that the area outside the cultivated field has the potential for improving invertebrate diversity and abundance with minimal impact to the cultivated fields, and irrespective to factors in the surroundings. The characteristics of the field edges are such that they can be achieved by the simple act of not mowing. This has the advantage of not requiring monetary expenditures or additional effort by the landowners.

While management of linear agricultural areas to enhance local structure is easy to apply, there are some disadvantages. There is often social resistance to management of this type. Farmers like their fields to look manicured from the roads. There can be visibility issues from a traffic standpoint. There can also be increased bird fatalities from impact with vehicles. However, there are also side benefits such as reduced soil erosion, creation of pollinator habitats, and enhanced visual experience for the public. Land sharing with enhanced local edge structure has the potential of lessening the decline of those bird species that use the agricultural landscape. More study is needed to determine the impacts of edge management and how to overcome social resistance.

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Appendix

Models and summary tables for taxonomic diversity (TD) and biomass (WT). Variables included Location (FI or FE); average vegetation height (EdgeHt), variation in the vegetation height (EdgeSD), length of the field (Length), depth of the area between tilled area and roadway or next field (EdgeDepth), percentage of bare ground (Bareground), treatment of the edge (none, herbicide drift, mowing), and a correction factor for sample size (ln Abundance). Our random factors were method of collection (sticky board, pitfall trap, or sweep net) and field within county within year (RegionYearField).

a) TD~(FieldEdge * (EdgeHt + EdgeSD + Length + EdgeDepth + Bareground + Treatment)) + ln.Abundance + (1|RegionYearField) + (1|Method)

Taxonomic Diversity	Estimate	Std. Error	z value
Intercept (FI)	1.21E+00	2.73E-01	4.412
Location FE	4.65E-02	1.67E-01	0.278
EdgeHt	-3.89E-05	1.04E-03	-0.037
EdgeSD	9.90E-04	1.35E-03	0.736
Length	-3.01E-04	1.50E-04	-2.001
EdgeDepth	2.05E-03	2.31E-03	0.887
Bareground	1.13E-03	1.75E-03	0.645
TreatmentNone	2.54E-01	8.29E-02	3.062
TreatmentRU	1.89E-01	1.05E-01	1.804
ln.Abundance	-1.48E-02	1.67E-02	-0.888
FieldEdgeField:EdgeHt	1.80E-03	1.31E-03	1.372
FieldEdgeField:EdgeSD	2.74E-03	1.58E-03	1.735
FieldEdgeField:Length	4.88E-04	1.78E-04	2.740
FieldEdgeField:EdgeDepth	-4.48E-03	2.92E-03	-1.533
FieldEdgeField:Bareground	1.15E-03	2.36E-03	0.489
FieldEdgeField:TreatmentNone	-3.03E-01	1.06E-01	-2.863
FieldEdgeField:TreatmentRU	-2.24E-01	1.45E-01	-1.540

b) Wt ~ (FieldEdge * (EdgeHt + EdgeSD + Length + EdgeDepth + Bareground + Treatment)) + (1|RegionYearField) + (1|Method)

Weight	Estimate	Std. Error	z value
Intercept (FI)	5.77E+00	6.33E-01	9.120
Location FE	5.97E-02	3.64E-01	0.164
EdgeHt	3.68E-03	3.24E-03	1.136
EdgeSD	-6.84E-03	4.65E-03	-1.472
Length	-7.75E-05	5.12E-04	-0.151
EdgeDepth	6.47E-03	8.36E-03	0.773
Bareground	3.82E-03	4.78E-03	0.798
TreatmentNone	3.26E-01	2.45E-01	1.331
TreatmentRU	4.19E-01	3.12E-01	1.342
FieldEdgeField:EdgeHt	4.45E-04	2.90E-03	0.154
FieldEdgeField:EdgeSD	1.35E-02	4.10E-03	3.295
FieldEdgeField:Length	3.68E-04	3.97E-04	0.929
FieldEdgeField:EdgeDepth	-1.70E-02	6.49E-03	-2.622
FieldEdgeField:Bareground	2.82E-03	5.40E-03	0.523
FieldEdgeField:TreatmentNone	-7.27E-01	2.32E-01	-3.134
FieldEdgeField:TreatmentRU	-5.71E-01	3.25E-01	-1.754

Chapter 8

General Discussion

Introduction

The aim of this thesis was to look at common vegetation management techniques within the agricultural landscape and determine the impact on invertebrate assemblages and the associated food web. This discussion begins with an overview of the specific studies comprising this dissertation. I then relate our results to the established theories of biodiversity and management. Then I compare our results with the European experience on agri-environmental schemes and relate this to the discussion on sharing or sparing. I make management recommendations based on our results and discussions. Finally, I propose additional research questions.

Answers to Research Questions

Our research focused on answering the following questions:

1) **How does mowing regime of agricultural roadsides impact invertebrate assemblages (Table 1a)?**

The mowing experiment demonstrated that mowing and removing the clippings showed the greatest improvement in taxonomic richness as measured in the edges (Chapter 2). In the conservation set-aside (CRP) edge there was a +33% increase in taxonomic richness from the least effective treatment to mowing six times per growing season and removing clippings after mowing. In the agricultural edge, there was a +44% increase in taxonomic richness from the least effective treatment to mowing six times per season and removing clippings after mowing.

2) **How do extreme earth moving (removal of topsoil and re-contour of the land) and standard vegetation control treatments (mowing and prescribed fire) impact the invertebrate community in a newly created prairie restoration (Table 1b)?**

The prairie restoration in Bloomington Grove demonstrated that invertebrate assemblages do not necessarily follow the progress of vegetative prairie restoration (Chapter 3). A combination of vegetation controls was used after restructuring of the land contours. These included prescribed fire, mowing two times per growing season and leaving clippings and mowing two times per growing season and removing clippings. Invertebrate taxonomic richness declined as time post restoration increased. There was a 48% decline in taxonomic richness between two and five years post restoration.

3) How does a mid-summer wildfire affect a grassland invertebrate community (Table 1c)?

We had two studies, one showing the immediate impact on Lepidoptera larva and the second study showing the long-term impacts to invertebrate assemblages over three growing seasons. The immediate period post fire was beneficial to some Lepidoptera species (Chapter 4). The flush of spring-like vegetation provided a rich environment for newly hatched larvae. Not all invertebrates responded positively and after the wildfire taxonomic richness of invertebrate assemblages in our study did not completely recover three growing seasons post fire (Chapter 5). At 0-3 months, there was an increase of taxonomic richness in the burned area of +16% over that in the unburned area which shifted to a deficit of -24% in the first growing season and -25% in the third growing season.

4) How do the invertebrate assemblages in agricultural fields and edges relate to local and landscape complexity (Table 1d-e)?

The landscape complexity study demonstrated that including complexity at the level of 1000 m into the models resulted in the best fitting models for taxonomic richness, however, the difference in taxonomic richness between low and high levels of complexity at the three landscape levels is less than 15%. The landscape in our study was relatively complex in terms of crop and non-crop areas with a range of 5-78%. At 6000 m, the difference in taxonomic richness between low and high complexity landscapes is +15%, at 1000 m is + 4% and at 500 m is + 2%. More interesting than the overall shift in complexity are the different responses to complexity in the edges and in the fields (Chapter 6). In the edges the difference in taxonomic richness from low to high complexity at 500 m is + 6%, at 1000 m is 15% and 6000 m + 34%. In the fields the difference from low to high complexity at 500 m is - 3%, at 1000 m is - 2% and at 6000 m is + 8%.

5) How does the invertebrate population relate to food availability, particularly for birds during the breeding season (Table 1f)?

The study measuring food availability for breeding birds (as measured by invertebrate biomass) is dependent on local factors such as edge vegetation height and variability, length and depth of the edge and the amount of bare ground rather than characteristics of the agricultural fields and complexity at the landscape level (Chapter 7). The factor with the greatest increase in biomass was vegetation variability on the edge with a + 61% increase from the least to the most variable.

Table 1. Management implications for average taxonomic richness (TR) or abundance of our studies.

a) Mowing experiment (Chapter 2). M2 = mowing two times per growing season and leaving clippings; M6+R = mowing 6 times and removing clippings, and M6 = mowing 6 times and leaving clippings. Ag = agriculture; CRP = Conservation Reserve Program.

Location	M2	M6+R	M6
Ag Edge TR	10.2	12.4	8.6
CRP Edge TR	8.2	10.9	10.5

b) Prairie restoration in Bloomington Grove (Chapter 3).

Time post-restoration	+ 2 yr	+ 4 yr	+ 5 yr
Average TR	11.7	8.6	7.9

c) The long-term fire study (Chapter 5).

Treatment	TR 0-3 months post-fire	TR second growing season	TR fourth growing season
Burned	7.9	6.5	7.7
Unburned	6.8	8.6	10.2

d) Field Edge study (Chapter 6) overall TR.

Complexity	TR at 6000 m	TR at 1000 m	TR at 500 m
< 20 %	9.4	10.1	10.1
>30%	10.8	10.5	10.3

e) TR (model including landscape) in the fields (Chapter 6).

Complexity	TR at 6000 m	TR at 1000 m	TR at 500 m
< 20 %	8.8	9.5	9.5
>30%	9.5	9.3	9.2

f) TR (model including landscape) in the edges (Chapter 6).

Complexity	TR at 6000 m	TR at 1000 m	TR at 500 m
< 20 %	9.0	9.9	10.4
>30%	12.1	11.4	11.0

g) Bird food study (Chapter 7). Measure of abundance.

	Lower quartile	Upper quartile	% food availability
Increase edge depth	1082	1192	+10.2%
Decrease length of field	1273	1134	+12.3%
Decrease field size	1026	1174	+12.6%
Increase edge variability	843	1358	+61.1%
Increase edge height	1160	1111	- 4.2%

Methodological issues

Taxonomic resolution and species traits. Because our studies were focused on increasing biodiversity in agricultural areas, the most important response variables in all our studies except the one focused on bird food, were taxonomic richness and diversity of arthropods. We would like to discuss two methodological issues. The number of arthropod individuals sampled in the body of studies numbered in the hundreds of thousands and most of these were identified to the taxonomic level of family. However, pitfall traps inadvertently collected more than the targeted arthropods. The author felt that these non-insect invertebrates were of interest as part of the assemblage, but was unable to identify them to family. In these cases, identification was by morphospecies (Oliver and Beattie, 1996) with the lowest taxonomic unit identified named as the operational taxonomic unit (OTU). Many individuals were quite common and could be easily identified to family. Adult arachnids were identified to family; however, the juveniles were not. This level of coarse resolution has acknowledged problems, including lack of standardization between phyla. On the other hand, if we had discarded these data, we might not have identified the lack of soil dwelling invertebrates in the prairie restoration. Soil dwelling fauna create structure for water infiltration, decompose surface litter, and enhance nutrient flow (Whiles and Charlton, 2006; Zaitsev *et al.*, 2016). This information is important when planning prairie restoration or evaluating its success.

The distribution of the traits of the taxa within a sample or at a location are supposed to give information of the local ecosystem functioning (Webb *et al.* 2010; Violle *et al.*, 2007; Mouillot *et al.*, 2013). Species functional traits are most often used in aquatic ecosystems (Chevenet *et al.*, 1994; Townsend and Hildrew, 1994; Ieromina *et al.*, 2016). Functional traits have been proposed to act as filters to remove all species lacking a specific permutation of characteristics (Keddy, 1992). For this reason, some of our studies looked at the feeding guild of the sampled taxa (Chapters 2, 3 and 5). It enabled a more extended description of the results.

However, other traits might also have been informative as they relate to the agricultural environment and predict presence or absence after a specific management technique. Important traits to examine in relation to my study include, but are not limited to, dispersal ability and life stage. This type of research requires a priori determination of what characteristics are important in order to construct a trait matrix (Grime, 1974; Keddy, 1992). Placing the sampled individuals within a functional guild also presented problems though, and may not even be possible at the coarse taxonomic resolution of our studies. Additionally, functional traits within a family or even within a species is often dependent on life stage.

Lack of replicates. Because part of our study was done in given situations, as mentioned in the introduction, two of them had no replicates (the prairie restoration, Chapter 3, and the fire study, Chapters 4 & 5) and one had very limited replication (the mowing study, Chapter 2). This means that the effect of what in these studies are regarded as treatments (phases of prairie restoration, burned vs non-burned and mowing regimes) cannot be separated from the effect of the different locations of these treatments (Hurlbert, 1984). The results of these studies should therefore only be regarded as first indications of the effects of prairie restoration, burning and mowing on invertebrate assemblages.

Theoretical synthesis

We examined our empirical studies in light of the ecological theories presented in the introduction (Chapter 1). The theory of island biogeography applies most appropriately to natural areas surrounded by agriculture. To a lesser extent this theory could be applied to agricultural fields surrounded by urbanized areas and perhaps fragmented by roads. This theory was somewhat applicable to the prairie restoration examined in Chapter 3, where the prairie restoration site could be regarded as being an 'island' within an agricultural 'ocean'. The 'island' of prairie was created, as if a volcanic island, and in the process of awaiting arrival of appropriate species.

The general principles of metapopulation theory apply to individual species and their populations. Application of this theory is to spatially isolated members of the same species and includes both source-sink and patch dynamics. Our studies (except chapter 4) are focused at communities, not individual species. However, metapopulation theory, with its support of species occupation of unsuitable habitat, suggests that also the fields may play a role in the presence of viable populations of invertebrates in field edges, because they may be sinks that enable species to have a large populations size. The fact that we found relatively high taxonomic richness within the fields (Chapters 6 and 7) supports this idea.

Metacommunity paradigms do not necessarily require identification to species when taxonomic richness and diversity are the central focus of the study (Leibold *et al.*, 2004). The simple scheme of four key processes (selection, drift, speciation, and dispersal) presented by Vellend (2010) help us apply metacommunity theory to our studies. Coarse identification remains a limiting factor in all of our studies except the short-term fire study (Chapter 4). That being said, it is interesting to look at the patterns observed in our studies and try to use metacommunity theory for the interpretations of the results. Both selection and dispersal may be applicable to our studies with speciation and drift less applicable to the observed patterns.

Species composition and diversity are dependent on the regional pool of species. The importance of the surrounding landscape is most clearly confirmed in our study of the taxonomic richness and diversity of field edges and field interiors in different landscapes (Chapter 6). Most remarkable is that complexity seems to have a positive effect on field edges, but a negative on field interiors. If this can be supported by further study, it opens up possibilities for new management measures for conserving biodiversity at the landscape level. The actual effect of landscape complexity on taxonomic richness may not be large, but since it could be working in huge areas, the ultimate national effect could also be great. A consideration is that the complexity that exists in this landscape today is not original, but degraded from pre-settlement conditions. The complexity that exists in the agricultural areas of our study was in the form of forest. The prairie which once existed is no longer part of the landscape. However, for cultural reasons as well as traffic safety, the edges in our studies (Chapters 2, 6, and 7) may be more suitable to prairie vegetation rather than trees.

The importance of the surrounding landscape is not only shown in the studies of edges (Chapters 2, 6 and 7), but also in the Bloomington Grove study (Chapter 3). The substrate was taken to bedrock and the vegetation was restored. But the colonization of ground and soil invertebrates seems problematic and is in line with island theory that says that the size of the restoration patch and the distance from intact prairie may require a great deal of time if it ever occurs. In this study, the lack of a ground and soil dwelling species pool from which to draw appropriate assemblages may have had an important role.

Land managers continue in their belief that "if you build it, they will come" (modified quote from the film Field of Dreams). This rationale does not acknowledge the need for a source population. Our study of the prairie restoration is an example of this belief. "It" was built but there was no appropriate place from which "they" could come: the only place for soil invertebrates to emigrate from was agricultural fields. Prairies once covered 61% of the Illinois landscape (CTAP 2001). Only 930 ha of high quality prairie which is about 0.01% of the pre-settlement acreage remains (CTAP 2001). Remnant prairies are generally located in places inaccessible to farm implements or in pioneer cemeteries with minimal disturbance (Taylor et al. 2009). The nearest intact prairie to the Bloomington Grove site is a 2-ha cemetery prairie 40 km to the northeast (against prevailing winds). The vegetation is similar to the restoration site. Common grasses include big bluestem, little bluestem, prairie dropseed and Indian grass. Typical prairie forbs include shooting star, prairie gentian, compass plant and wood betony. Management practices on both sites are similar and include prescribed burning and exotic species control.

Dispersal and lack thereof are also extremely important within the agricultural landscape. Recent studies have shown that flying invertebrates may not always suffer from landscape fragmentation and isolation (Tscharntke et al., 2002; De Bie et al., 2012). This is confirmed in our study of the immediate effects of a wild fire (Chapter 4), where it was shown that some butterflies are capable of immediately finding new vegetation that can be eaten by their larvae. However, plants are known to have troubles with colonization (Blomqvist et al., 2003; Ozinga et al., 2009; Evju et al., 2015) so that vegetation recovers slowly, which might be the main reason for the slow recovery of the invertebrate community after the wild fire (Chapter 5).

Selection of species is dependent on adaptation to the specific characteristics of the landscape both at the local and regional scale. Local factors showed to be important in the mowing study (Chapter 2) and the study of bird food (Chapter 7). This relates to the hypothesis of "ecological contrast" (Kleijn et al., 2011). The effects of conservation or restoration efforts are expected to be greater as the ecological contrast increases (Batáry et al., 2015). In our studies of edges (Chapters 2, 6, and 7), the edges were generally narrow and there was small ecological contrast between edges but greater contrast between fields and edges. In addition, the "natural areas" in our study were not remnant habitats from pre-settlement times. Rather they were mostly converted from farmland. Based on this information, predictions made using the ecological contrast theory would be that improvement in biodiversity or bird food availability would be small, as we found in our studies. Increased arthropod richness is predicted where there is increased local structure (Evans, 1988; Tscharntke and Greiler, 1995; Dennis et al., 1998). Our bird food study (Chapter 7) demonstrates that edge structure is the best way to provide this life history requirement.

Biodiversity Conservation

The agricultural landscape provides food, fuel and fiber; regulates ecosystem processes; and it provides habitat and cultural services for human physical and mental wellbeing (Cardinale et al., 2012). Moreover, it provides opportunity for biodiversity conservation. It is important to separate conservation initiatives targeted at rare species and protection of high quality natural areas from initiatives focused on the agricultural landscape with its high human impact. Studies have repeatedly shown that conserving what is left is more effective than trying to retrieve what has been lost (Matson and Vitousek, 2006). Our studies are directed to the areas of high commodity production rather than pristine natural areas.

Many ecologists believe that preservation of biodiversity has the consequence of preserving ecosystem services as well (de Groot et al., 2014; Jax and Heink, 2015). However, the complex interactions of both biotic and abiotic factors in preserving ecosystem services thru biodiversity are not clearly understood (Van Oudenhoven et al., 2012; de Groot et al., 2014). Scales of observation range from microbes (Van Der Heijden et al., 2008; Fierer et al., 2013) to landscapes (Tscharntke et al., 2005) and milliseconds (Vincent et al., 2012) to epochs (Behrens et al., 2014). Research has shown mixed effects with response effects dependent on complexity and management of the surrounding landscape at various levels (Burel et al., 1998; Kleijn et al., 2009; Batáry et al., 2015; Cormont et al., 2016).

Conservation initiatives are most effective when targeted to specific taxonomic groups or ecosystem services (Cormont et al., 2016). Conservation initiatives within the American Midwest agricultural landscape should be focused on keeping landscape complexity and ecosystem services such as crop pollination (Kremen et al., 2007; Potts et al., 2010) or pest control (Bauer et al., 2015; Letourneau et al., 2015). In keeping with the above research, there are underutilized parts of the agricultural matrix that may be managed to enhance biodiversity (Chapters 2, 6, and 7). This does not necessarily mean restoration to an earlier vegetative state but could in fact be a "novel" ecosystems (Hobbs et al., 2009; Morse et al., 2014). Highly disturbed ecosystems respond with changes in species composition and ecosystem function (Chapters 4 and 5). Restoration of disturbed ecosystems to a past state may be very difficult (Chapter 3), if not impossible, as well as very expensive (Palmer et al., 2014). Ecosystems are dynamic and change naturally over time (Friend et al., 2014). Choosing a single reference point in time requires extensive documentation of both biotic and abiotic factors that may not exist (Higgs et al., 2014).

Often goals that favor conservation are in opposition to those that favor economic interests of the farmer. It is important to find a means of balancing these objectives. There is high potential for meeting the objectives of both interests utilizing financial incentives for providing ecological services on agricultural lands. The answer of what scale meets the requirement of the ecosystem service should determine how conservation initiatives should be distributed in order to safeguard the service. Building redundancy into the system will allow for different species performing the same function at differing scales to be protected, thus enhancing system resilience (Tscharntke et al., 2012). Our studies show a way to meet these objectives using existing management techniques with little to no impact on the agricultural fields.

Sharing or sparing; farming in the Midwest US and western Europe

There is a movement in the US that recognizes the need for an agricultural ecosystem that is more sustainable than at present (NRC, 1989). In general, this requires stepping back from intensification, or in other words 'land sharing'. Evaluation of which practices provide the most benefit for the least amount of money is part of this process. Encouraging practices that provide limited benefits and costly trade-offs are difficult to justify both in Europe and the US. This body of research did not look at in-field practices that are found in western Europe, although European research would allow us to apply the practices that have been found to work the best.

In the EU, the typical sharing approach of agri-environmental schemes (AES) has been in place for a sufficient period of time to determine effectiveness. Biodiversity continues to decline despite implementation of AES (Kleijn *et al.*, 2011). A meta-analysis of published studies concluded that conservation management should be adapted to the structure of the landscape and targeted taxa (Batáry *et al.*, 2016).

Ecological contrast may be an important factor in evaluation of effectiveness (Kleijn *et al.*, 2011). To justify conservation expenditures, the cost benefit ratio should be part of the practice evaluation (Ansel, 2016). The mixed results of the EU indicate that the EU does not yet have the answer to the question “How do we stop the trend of biodiversity decline?” It is imperative that we keep looking for the answer (Edwards and Abivardi, 1998).

It is important to note that the area of my study is among the top counties in agricultural yield in the state (USDA, 2015) and 33% higher than the national average (USDA, 2016). Specific research sites were in areas of high vegetative complexity mostly created by reclamation of previously farmed land. There were few, if any, untouched natural areas within my study area. The land sparing philosophy is most successful with intact ecosystems, rather than recovered/restored land (Law and Wilson, 2015). The area of our study is one of high yield within a degraded landscape with a small proportion of land ‘spared’. I suggest management actions could improve biodiversity with the addition of ‘sharing’ philosophies to the existing ‘sparing’ philosophy of the Midwest (Law and Wilson, 2015).

In a free market economy, as yield increases, prices of crops drop, forcing farmers to increase acreage farmed in order to maintain income. This loss of income, derived from economic markets is not generally subsidized. Thus, land that could be freed for restoration may continue to be farmed. Alternatively, this economic loss may provide the incentive to place marginally producing farmland into set-asides as a means of providing predictable income. The limitation of these programs is that the farmers often want assurances that they can withdraw from the programs when commodity prices rise.

There are several existing examples from the US of sharing oriented measures. Growing multiple crops in rotation is one of them and has multiple benefits such as slowing the development of weed and pest resistance and putting nitrogen back into the soil (Kremen and Miles, 2012). Whether or not this reduces yield in light of the future expense of remediation is in question (Kremen and Miles, 2012). Another example is genetically modified crops that are dominant in the US. Many protesters are concerned that ingesting GM products may be harmful to human health. Studies have not found any detrimental effects (James, 2003; Johnson et al., 2007). The benefits of increased yield and pest resistance are well documented (James 2003).

However, the impact of chemical inputs on the soil microbiota and surrounding environment is questionable (Sanchez-Bayo, 2014). Pollinator decline is an issue of great concern both in Europe and the US and may have different proximate causes on the two continents (Biesmeijer *et al.*, 2006; Cameron et al., 2011).

In Chapter 1, I indicated how agricultural history and practices in the US and Europe are different. They are similar with the push to increase productivity and efficiency and with opposing needs to preserve ecosystem function and biodiversity. Differences in prevalence of GM crops, livestock husbandry, landscape complexity with its associated matrix, and use of fire as a management tool, created the question of generalizability of research across continents. That being acknowledged, biological processes are obviously the same on both continents. In my view, it may be necessary for the US and EU to both "share" and "spare" whenever possible. My research points toward low cost measures to reduce the loss caused by management practices within the local landscape. However, my experiences while conducting this research, indicated that implementing any practice, will require active involvement of all of the stakeholders (Landis, 2016).

Recommendations for effective management

Continued loss of invertebrate abundance and diversity will eventually be detrimental to the agricultural ecosystem. Europe implemented a variety of practices with the hope and expectation of stemming the losses. Mixed results have caused the public and various governmental entities to question the expenditures. Yet the alternative of doing nothing is not viable. A suite of practices to improve invertebrate conservation dependent on acceptance by the local residents may help stem the losses. As studies in the EU have shown, gaining cultural acceptance is a large part of battle.

My studies show that practices should consider invertebrates as part of the planning process. Practitioners of pre-scribed fire are focused on the management of vegetation. Urban housing developments are focused on visual appeal as well as water catchment. Mowing is the concern of everyone. And of primary importance is the goal to keep the complexity that currently exists, because one it is gone, it is difficult to get it back.

My results are first indications and not strong enough to make policy recommendations. They will probably not grab the attention of the media. Implementation is unlikely at this point. However, getting my research published is a first step to drawing attention to management possibilities within the agricultural ecosystem.

Roadsides. The convenient access to roadsides makes a change in management regimes an easy ecological target. An increase in vegetation structural complexity creates habitat that meets the needs of both invertebrates and birds. The difficulties with this option are both political and cultural. During our studies, we found multiple jurisdictions responsible for mowing within the same field edge. Changes to roadside management would require voluntary changes to behavior of both farmers and managers of rural roadsides. One important rationale for mowing was visibility for traffic safety. In addition, the landowner frequently engaged in what is locally termed "recreational mowing". Many landowners enjoy seeing neatly mown edges. They explained that this demonstrates responsible farming practices; i.e. short vegetated edges and no weeds in the fields. Enhancing biodiversity is a motive unlikely to cause a shift in mowing regimes. Changing these viewpoints may be a challenge.

Recommendations:

- Landowners could be offered financial support for creating structure with wildlife friendly bushes and forbs. A simple mower or tractor attachment to catch clippings would allow removal of organic material. Mowing could be done as needed or in a more complex mosaic of mowing regimes. Setting the mower height high would keep the vegetation from scorching in hot dry periods during the summer.
- A management plan could be developed by those departments responsible for roadside management. It could allow for adaptive changes in response to the citizen feedback and safety considerations. A variety of mowing regimes could be considered to provide flexibility rather than a "one size fits all" approach.
- Non-native plants could be replaced with natives as funds or local sponsors become available. A priority list to get the most benefit to the

landscape context could be developed. Getting local environmental groups involved provides "buy-in" and assistance in maintenance. There are programs in many local areas that remove litter.

- An educational promotion of direct benefits to the farmer of enhancing pollinators and natural enemies of pest species would facilitate change of the social culture in the agricultural community.

Prairie Restoration. A return to prairie vegetation may be a more complicated transition than we realize. After decades of agricultural use the soils have changed in response to disturbance and chemical input. We can plant the appropriate prairie vegetation and have a visually perfect landscape. However, it is also important to have the correct soil structure. This is an essential component of the system which allows for uptake of water and nutrients. Research has shown the impact of earthworms on local ecology (Jones *et al.*, 1994; Edwards, 2004). In the Midwestern United States, earthworms disappeared during the last glacial episode 10,000 years ago (Reynolds and Wetzel, 2004). This would indicate that our prairie flora evolved in tandem with migration of soil fauna. The prairie restoration in our study seemed depauperate of soil inhabiting invertebrates.

Recently there has been an increased interest in pollinators with a focus on the decline of the European honeybee. We know that reproduction of some plant species depends on having appropriate pollinators which may be specialists specific to certain plants. Often, however, we do not know which pollinator is specific to the plant in question. In our study, we saw a decline in the taxonomic richness as the prairie vegetation became better established. This might indicate a mismatch between common invertebrates and the newly established prairie vegetation. Sustainability of the prairie vegetation may require specialist invertebrates that cannot reach the newly established prairie without human translocation efforts.

Recommendations:

- Fire and mowing are both excellent methods of getting prairie vegetation established. This allows an extensive root system to become established before the upper structure. The prairie restoration in our study used a combination of mowing and fire as vegetation management.

- Once vegetation is established, invertebrates could be inventoried with particular attention paid to the trophic guilds and available niches and translocated from existing grasslands if necessary.
- After vegetation establishment fire, could be low intensity and used sparely. Mowing or short term grazing could be used as a viable alternative. Refugia in the form of exclosures could always be provided.

Prescribed Fire. The wildfire on one of our study sites presented an opportunity to document invertebrate assemblages after a fire which may have mimicked historic conditions. A meta-analysis of wildfire research showed a lack of publication for reasons including study design flaws (Zaitsev *et al*., 2016). This study suffered from the same lack of replication as similar wildfire studies and may be a contributing factor to the "file drawer" effect (Zaitsev *et al*., 2016). We attempted to compensate for design flaws with robust statistical design (Winter, 2013; Anderson, 2007).

During the immediate period post fire, we documented an increase in Lepidoptera larva in response to the new lush vegetation (Chapter 4). Later collections documented a failure to reach the same diversity and abundance as in the unburned area (Chapter 5). This is similar to some other studies and contrary to others. We simply do not know enough about invertebrate assemblages and their responses to fire to continue as we have to burn without consideration of this important ecological group.

Changing the way, we conduct prescribed burns will require some effort. There are difficulties with changing attitudes fire management. Often prescribed fire is "sold" to governing entities as "fuel load reduction". Leaving fuel unburned is contrary to the state purpose of the fire. Some managers are paid by the "number of acres burned". Leaving areas unburned reduces the paycheck. Often the biologists requesting the fire are not part of the technical crew implementing the fire. Convincing non-biologists to leave areas unburned to save invertebrates may seem inane.

Recommendations:

- Fire could be prescribed to leave areas unburned either through exclosures or under such conditions that not all areas are burned. This could also be through a mosaic of fire rotation. Patch Mosaic

Burning should be carefully evaluated before instituting (Parr and Anderson, 2006)

- Fire interval could be increased with hand removal of undesirable plants during the interim.
- All fire plans could have built into them the concept of refugia for both plants and animals including invertebrates.

Spatial complexity at local or landscape scales. The overriding theme to all of our studies revolves around complexity at both the local and landscape scale. We examined specific vegetation management techniques in the context of how best to maintain or improve invertebrate taxonomic richness and abundance. Our studies support the proposition "land sparing" and preserving what complexity we have is important (Landis, 2016). But we have also shown the benefits of "land sharing". The land shared offers numerous opportunities for enhancement of invertebrate richness and abundance. Conservation initiatives are generally more effective with off-field practices (Batáry *et al.*, 2015). Off-field practices would probably have easier acceptance by the farming community. Gradually, the expansion of the area encompassed by off-field practices could be introduced. Unless there is a particular rare or endangered species conservation measures should be general, inexpensive and easy to implement.

Recommendations:

- Edges could be planted and maintained to enhance structurally complexity. Our studies show a benefit to both invertebrates and avian species. Presumably the structure would enhance habitat for other species as well.
- Existing waterways and riparian areas could also be planted and maintained to enhance structural complexity. Expansion of these practices could be inexpensive by allowing natural vegetative succession to occur which would allow associated fauna to follow.
- Ecosystem services could become the theme of conservation measures within the agricultural landscape. Reduction of chemical input and run-off, decreasing soil erosion, enhancement of wild pollinators are all services which would enhance invertebrate biodiversity.

Recommendations for further research

Needs for agricultural products will continue to grow as we provide food, fuel and fiber to a growing world population. The balancing act between increased production and reduced impact will remain important. Ecosystem services and biodiversity are central to maintaining health and life. There is much that is unknown about the agricultural landscape. Our studies were limited in scope and further research is needed. The most important conclusion of our research is that management takes place within the larger context of the ecosystem and is more nuanced than we understood. Research questions arising from our studies include 1) Does translocation of invertebrates with limited mobility help repopulate an area after habitat destruction caused by topsoil removal or fire?; 2) What are the long-term impacts on invertebrate assemblages in other areas and with fires at other seasons and fire intervals?; 3) What different roadside management regimes are not a hazard to traffic and culturally acceptable to the general public as well as the farming community?; and 4) How does bird use and reproductive success in the agricultural context change as edge structure changes naturally or is changed by the land managers?

It is necessary to examine the shortcomings and limitations of this body of research. Design flaws and lack of replicates created issues with inferences to the general population. This body of research (Chapters 2, 4 and 5) suffered heavily from "demonic intrusion" (Hurlbert, 1984) in the form of drought, wildfire and roadside 'neatniks'. Ideally studies would have been designed and executed with sufficient interspersion and replicates (Hurlbert, 1984). The isolated block layout of the mowing study was designed to minimize the impact of the landscape gradient as well as invertebrate dispersal. When it became clear non-independence of samples may be an issue we dealt with the problem statistically (Winter, 2013; Millar and Anderson, 2004). The course taxonomic resolution made it difficult to discuss specifics and about 'pest species' or functional guilds other than in general terms. There is a lack of reference sites for the Bloomington Grove study (Chapter 3). There is so little prairie remaining in the state that all existing sites are protected. It is possible, but highly unlikely to obtain permits to collect from these sites.

There are additional issues in the agricultural ecosystem outside the scope of this study that are important to invertebrate assemblages. These issues include the decline in pollinators, genetic modification of crops, and use of pesticides. Issues rising in importance are the food production and distribution issues, use of CRISPR technology to modify crops, antibiotic use in livestock and soil health. Additional research questions include 1) how do we restore habitat for native pollinators so we are less dependent on imported honey bees?; 2) how do we maintain effectiveness of existing pesticides as well as use lesser amounts?; 3) What are the unintended consequences of CRISPR (clustered regularly interspaced short palindromic repeats) technology not only at the species level but the ecosystem level?; 4) how do we address the social issues of food security and distribution; and 5) What are the impacts of chemicals on both micro and macro invertebrates that inhabit the soil?

There is a purported Chinese blessing/curse "May you live in interesting times". We do, indeed, live in interesting times. Technology presents us with both the threat and possibility of increased agricultural production through targeted application of fertilizers and pesticides, satellite monitoring of soil moisture and drought conditions, and crop modification through CRISPR. All these technological advances offer the promise of providing fuel, food and fiber on less land and with less impact thus "sparing" land for nature and associated biodiversity. I can only hope we take the high road and leave room for "the little things that rule the world".

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Publications

T.R. Evans, M. J. Mahoney, E.D. Cashatt, J. Noordijk, G.R. de Snoo and C.J.M. Musters. 2016. Comparing roadside mowing regimes to enhance invertebrate diversity. Submitted to Soil and Water Journal.

Tracy R. Evans, Meredith J. Mahoney, E.D. Cashatt, Bryon W. Cross, Geert R. de Snoo and C.J.M. Musters. Invertebrate communities associated with three early phases of a prairie restoration project. 2016 .*In Press* Great Lakes Entomologist

Evans, T.R., Musters, C.J.M., Cashatt, E.D. and de Snoo, G.R., 2013. Lepidoptera pest species response to mid-summer fire. *Fire Ecology*, *9*, 25-32.

T.R. Evans, M.J. Mahoney, E.D. Cashatt , G. de Snoo and C.J.M. Musters. Arthropod Recovery After a Wildfire: A Case Study Submitted to the International Journal of Wildland Fire

Evans, T.R., Mahoney, M.J., Cashatt, E.D., Noordijk, J., de Snoo, G. and Musters, C.J.M., 2016. The Impact of Landscape Complexity on Invertebrate Diversity in Edges and Fields in an Agricultural Area. *Insects*, *7*(1), p.7.

Evans, T.R., Mahoney, M.J., Cashatt, E.D., de Snoo, G. and Musters, C.J.M., 2016. Enhancement of Linear Agricultural Areas to Provide Invertebrates as Potential Food for Breeding Birds. *Land*, *5*(3), p.26.

Summary

Global population is growing ~ 1.1% per annum with projected populations reaching 9.6-12.3 billion by 2100. Extreme poverty has declined globally by more than half falling from 1.9 billion in 1990 to 836 million in 2015. Increased agricultural production of food, fuel and fiber will be necessary to meet the needs of the growing population. Goals to increase agricultural production are often in competition with other societal goals. Water used to increase food production leads to reduced availability for other purposes, including human consumption. Clearing forested land for use in growing agricultural products decreases biodiversity and carbon sequestration. The difficult and critically important challenge is to balance the multiple needs of society in the most sustainable way possible.

This thesis concentrates on how common vegetation management impacts invertebrate biodiversity, as a critical resource, in an area which is used for intensive agricultural production.

We focused on answering the following questions:

1) **How does mowing regime of agricultural roadsides impact invertebrate assemblages?**

2) **How does extreme earth-moving impact the invertebrate community in a newly created prairie restoration?**

3) **How does a mid-summer wildfire impact a grassland invertebrate community?**

4) **How do the invertebrate assemblages in agricultural fields and edges relate to local and landscape complexity?**

5) **How does the invertebrate population relate to food availability, particularly for birds during the breeding season?**

In chapter 1, I introduce general background information, terminology, and ecological theory. I provide an overview of agriculture in the United States and Europe. I also discuss the research questions and design.

In chapter 2 we looked at roadside edges as an important part of the rural landscape that have the potential to contribute habitat for enhancing biodiversity. Roadside edges are generally managed with a variety of mowing regimes based on non-ecological objectives such as traffic safety, expense and aesthetic perceptions. We conducted a pilot study in rural Sangamon County, Illinois USA to compare the influence of roadside management regime on biodiversity along a roadside with neighboring fields planted in no-till agriculture or Conservation Reserve Program (CRP). Three mowing regimes were applied to a roadside. Two of the management regimes are common in Illinois: mowing twice a year and regular mowing throughout the growing season, both leaving the clippings where they fall. The third regime was regular mowing and removing the clippings. Our study showed invertebrate richness was greatest in roadsides with regular mowing and clippings removed. When invertebrates were grouped as predators, parasites and parasitoids, omnivores, herbivores, flower visitors and detritivores, taxonomic richness remained highest in the area mowed with clippings removed, but abundance varied according to life history requirements of the invertebrates. Taxonomic diversity was not different between treatments.

In chapter 3 we took the opportunity offered by a restoration project associated with a large-scale housing development in central Illinois to survey invertebrates in three phases of plant restoration that were part of a larger project. This cross-sectional study of invertebrate recovery at two, four and five year's post-restoration showed that there was no overall difference in invertebrate taxa richness and diversity. Overall abundance was greatest in the most recently restored area. Richness, diversity and abundance of six functional groups did not differ. The restoration phases of our study were apparently all characterized by early pioneer assemblages that did not differ significantly from each other. The conclusion is that development to more diverse and richer assemblages might take more than five years in some prairie restoration projects. The new and unexpected finding was that the reestablishment of invertebrate assemblages was not closely tied to vegetation restoration.

In chapter 4 we looked at the impact of an accidental wildfire in a 20 ha grassland restoration. New growth provided effective substrate for the noctuid species corn earworm (*Helicoverpa zea* Boddie 1850) and tobacco budworm (*Heliothis virescens* Fabricius 1777). These agricultural pests feed on a number of important crop species and have been implicated in crop losses up to 50 %. Invertebrate collections were made at 16, 45, 70, and 101 days post fire. A comparison of burned and unburned areas at 70 days post fire show 18 times the number of Lepidoptera larvae collected in pitfall traps in the burned area compared to the adjacent unburned area of the grasslands. These findings demonstrate that a mid-summer fire can affect the abundance of economically important insects.

In chapter 5 we continued our study of the acute and chronic impacts of an accidental wildfire on invertebrate populations in a 20 ha grassland restoration in central Illinois, USA. Samples were collected in the burned and nearby unburned areas using sticky boards and pitfall traps each month of the growing season immediately following the fire and the first and third growing seasons post-fire. Our study found that in the third growing season post-fire, some taxa did still not have the same taxonomic richness, diversity and abundance as the neighboring unburned area. Summarizing measures of taxonomic richness, diversity and abundance did not represent the changes in invertebrate assemblages that occurred three growing seasons post-fire. This has implications for fire management decisions.

A better understanding of the factors influencing invertebrate taxonomic richness and diversity at both local and landscape scales is important for conserving biodiversity within the agricultural landscape. The aim of the study described in chapter 6 was to determine if invertebrate richness and diversity in agricultural field interiors and edges in central Illinois, USA, were related to the complexity of the surrounding landscape. Our results show taxonomic richness and diversity in field edges is positively related to large scale landscape complexity, but the relationship is negative for field interiors. These unexpected results need further study.

In chapter 7 we related the structural complexity at local and landscape levels of scale to invertebrate biomass and diversity as a food source. We looked at linear non-crop elements in agricultural areas as an opportunity to provide food for nestlings of avian species. We measured invertebrate availability as it relates to structural complexity at the local and landscape levels in three counties in central Illinois. Invertebrate availability was measured with estimated biomass and taxonomic diversity during spring of 2012 and 2013. Our study shows that field edge characteristics have the greatest impact on invertebrate biomass and diversity, as compared to field and landscape features. This finding shows that the availability of bird food, both in biomass and diversity, may be easily enhanced without changes to agricultural practices.

Finally, chapter 8 presents an overview of the most important results and discusses them in the context of ecological theory, management implications, and recommendations.

Samenvatting

Het aantal mensen op aarde groeit met ongeveer 1,1 % per jaar tot 9,6-12,3 miljard in 2100. Extreme armoede is tot minder dan de helft afgenomen van 1,9 miljard in 1990 tot 836 miljoen in 2015. Een toename in de landbouw productie van voedsel, brandstof en vezels zal noodzakelijk zijn om in de behoefte van de groeiende populatie te kunnen voorzien. De groei van de landbouwproductie concurreert vaak met andere maatschappelijke behoeften. Waterverbruik door de landbouw verkleint de beschikbaarheid van water voor andere doelen waaronder voor drinkwaterproductie. Het kappen van bossen voor uitbreiding van het landbouw areaal vermindert de biodiversiteit en de vastlegging van CO_2. De grote en vitale uitdaging voor de toekomst is de balans te vinden tussen onze maatschappelijke behoeften op de meest duurzame manier mogelijk.

Dit proefschrift richt zich op het beheer van niet-agrarische vegetaties in het agrarisch landschap en bestudeert wat de gevolgen ervan zijn voor de gemeenschap van ongewervelde dieren die een belangrijke voedselbron zijn voor andere dieren. We richten ons op het beantwoorden van de volgende vragen:

1) **Hoe beïnvloeden maairegiems van wegbermen in landbouwgebieden de gemeenschap van ongewervelde dieren?**

2) **Hoe beïnvloedt extreme grondverplaatsing de gemeenschap van ongewervelde dieren in een nieuw prairie herstel project?**

3) **Hoe beïnvloedt een spontane brand in de zomer de gemeenschap van ongewervelde dieren in een grasland?**

4) **Hoe wordt de gemeenschap van ongewervelde dieren in agrarische percelen en hun randen beïnvloedt door de lokale en landschappelijke complexiteit?**

5) **Hoe wordt de voedselbeschikbaarheid, in termen van ongewervelde dieren voor vogels tijdens het broedseizoen, in agrarische percelen en hun randen beïnvloedt door de lokale en landschappelijke complexiteit?**

In hoofdstuk 1 introduceer ik de algemene achtergrond van dit proefschrift, de gehanteerde terminologie en de ecologische theorie waarop het gebaseerd is. Ik geef een overzicht van de landbouw in de Verenigde Staten van America en van Europa. Ook bespreek ik de onderzoeksvragen en de onderzoeksopzet.

In hoofdstuk 2 worden wegbermen beschouwd als een belangrijk onderdeel van het landelijk gebied met de mogelijkheid bij te dragen aan het vergroten van de biodiversiteit ervan. Wegbermen worden over het algemeen onderhouden met een verscheidenheid aan maairegiems die gebaseerd zijn op niet-ecologische doelen, zoals verkeersveiligheid, minimale kosten en mooiheid. We voerden een pilotstudie uit landelijk Sangamon County, Illinois USA, om de invloed van beheer op de biodiversiteit van wegbermen te bestuderen. De bermen grensden aan landbouwvelden of natuurbehoud gebieden (Conservation Reserve Program). Drie maairegimes werden toegepast in de wegbermen. Twee ervan worden algemeen ingezet in Illinois: twee keer per jaar maaien en regelmatig (zes keer) maaien in het groeiseizoen, beiden zonder het weghalen van het maaisel. Het derde regiem was regelmatig maaien met weghalen van het maaisel. Onze studie liet zien dat de taxonomische rijkdom van de ongewervelde dieren het hoogst was bij dit derde regiem. Wanneer de ongewervelde dieren werden ingedeeld in functionele groepen, nl. predatoren, parasieten, omnivoren, herbivoren, bloembezoekers en detrivoren, dan bleef de taxonomische rijkdom het hoogste in het derde regiem, maar de abundantie van de groepen verschilden per groep tussen de regiems. De taxonomische diversiteit, waarbij rekening wordt gehouden met verschillen in abundantie tussen taxa, was niet verschillend tussen de maairegiems.

In hoofdstuk 3 wordt beschreven hoe we de kans kregen bij een prairie-herstel programma, dat gekoppeld was aan een de ontwikkeling van een woonwijk in midden Illinois, de ongewervelde dieren te bestuderen in drie fasen van het herstel van de vegetatie. Deze studie naar het herstel van de gemeenschap van ongewervelde dieren in vegetaties van twee, vier en vijf jaar na het begin van de restoratie liet zien dat er geen verschil bestond tussen de fasen in de taxonomische rijkdom of diversiteit. De totale abundantie was het hoogst in de laatst herstelde vegetatie, die van twee jaar geleden. Rijkdom, diversiteit en abundantie van zes functionele groepen verschilden niet tussen de fasen. De herstel fasen in onze studie bleken alle drie de kenmerken te dragen van vroege pionier gemeenschappen en verschilden onderling niet van elkaar. De conclusie is dat de ontwikkeling naar rijkere gemeenschappen met hogere diversiteit waarschijnlijk langer dan vijf jaar duurt bij prairie herstel projecten. Onverwacht en nieuw was de ontdekking dat de vestiging van gemeenschappen van ongewervelde dieren niet sterk verbonden is met de herstellende vegetatie.

In hoofdstuk 4 bestudeerden we het gevolg van een spontane, zomerse brand in een 20 ha groot hersteld grasland in centraal Illinois, USA. De hergroei na de brand voorzag de rupsen van twee mottensoorten (*Heliothis virescens* Fabricius 1777; *Helicoverpa zea* Boddie 1850) van een voedselbron. Dit zijn plaaginsecten van een aantal belangrijke gewassen en hebben soms geleid tot een verlies van 50 % van de opbrengst. Ongewervelde dieren werden in ons onderzoek verzameld op dag 16, 45, 70 en 101 na de brand. Een vergelijking van de vangsten in trapvallen liet op dag 70 een aantal mottenrupsen zien dat in het verbrande gebied 18 keer hoger was dan in het ernaast gelegen niet-verbrande gebied. Dit laat zien dat een brand in de zomer gevolgen kan hebben voor economische belangrijke insecten.

In hoofdstuk 5 vervolgden we ons onderzoek naar de directe en lange termijn gevolgen van een spontane brand in het herstelde grasland. Iedere maand van het groeiseizoen volgend op de brand en het eerste en derde seizoen daarop volgend werden ongewervelde dieren verzameld met plak- en trapvallen in het verbrande en niet-verbrande gebied. We vonden dat in het derde groeiseizoen na de brand bepaalde taxa nog steeds niet dezelfde taxonomische rijkdom, diversiteit en abundantie hadden als in het ernaast gelegen niet-verbrande gebied. Samenvattende maten voor de taxonomische rijkdom, diversiteit en abundantie bleken geen goed beeld te geven van de feitelijke veranderingen die plaatsvonden in de gemeenschap van ongewervelde dieren in de drie groeiseizoen na de brand. Dit heeft gevolgen voor het beheer dat gebruik maakt van branden.

Een beter begrip van de factoren die de taxonomische rijkdom en diversiteit van ongewervelde dieren bepalen, zowel op lokaal als landschapsniveau, is belangrijk voor het behoud van biodiversiteit in agrarische gebieden. Het doel van de studie die beschreven wordt in hoofdstuk 6 was om vast te stellen of de rijkdom en diversiteit van de ongewervelde dieren op agrarisch gebruikte velden en in hun randen in centraal Illinois, USA, gerelateerd was aan de complexiteit van het landschap eromheen. Onze resultaten laten zien dat de taxonomische rijkdom en diversiteit positief samenhangt met de complexiteit van het landschap, maar dat deze relatie negatief is voor de velden. Deze onverwachte resultaten behoeven verder onderzoek.

In hoofdstuk 7 leggen we een verband tussen structurele complexiteit op lokaal en landschapsniveau en de biomassa en diversiteit van ongewervelde dieren als voedselbron voor vogels. We kijken daarvoor naar de lineaire, niet-agrarische elementen in het agrarische landschap als mogelijkheid voor vogels om er het voedsel te verzamelen voor hun jongen. We maten de beschikbaarheid aan ongewervelde dieren en relateerde dat aan de structurele complexiteit op lokaal en landschapsniveau in drie regio's in centraal Illinois, USA. De beschikbaarheid aan gewervelde dieren werd gemeten als geschatte biomassa en taxonomische diversiteit in het voorjaar van 2012 en 2013. Onze studie liet zien dat kenmerken van de randen om de velden de grootste invloed hebben op de biomassa en diversiteit, in vergelijking met de kenmerken van de velden en het landschap. Dit laat zien dat de beschikbaarheid van voedsel voor vogels, zowel in termen van biomassa als diversiteit, gemakkelijk kan worden vergroot zonder dat veranderingen in de landbouw zelf nodig zijn.

Tot slot geeft hoofdstuk 8 een overzicht van de belangrijkste resultaten en bespreekt deze binnen het raamwerk van de ecologische theorie, worden de implicaties voor beheer besproken en worden aanbevelingen gedaan.

Curriculum vitae

Tracy Rene' Evans (nee Van Kampen) was born in Aurora, Illinois USA on the 21st of October in the year 1950. She attended High School in West Chicago, Illinois and received her diploma in 1968. She completed her Bachelor of Science Degree in 1972 at Blackburn College in Carlinville, Illinois with a major in Biology. She completed a Master of Science degree at Southern Illinois University in Edwardsville, Illinois (SIU-E) in 1975 with a major in Audiology. Her project was the design of a course to teach para-professionals aural rehabilitation skills. She obtained her Certificate of Clinical Competence - Audiology in 1976. She had a 20 year career as a clinical Audiologist in a medical setting. In 1993 she completed a Master of Science degree at Southern Illinois University in Carbondale, Illinois (SIU-C) with a major in Zoology. Her Master's thesis was measuring flight speeds of birds using Doppler radar under the supervision of Prof. L.C. Drickamer. She began working as a researcher at the Cooperative Wildlife Research Laboratory, SIU, Carbondale, IL. She then worked as a biologist for the Illinois Department of Natural Resources for 18 years. She occasionally taught general biology at several community colleges evenings throughout her 40-year career.

While on a sabbatical leave in Leiden, she worked on a project at the Institute of Environmental Sciences Leiden (CML) studying short-term exposure to electromagnetic fields on reproductive capacity of invertebrates in the field situation under the supervision of M.G. Vijver. A short time after returning to the US, Tracy started her PhD on Management Implications for Invertebrate Assemblages in the Midwest American Agricultural Landscape as part of the Sandwich Programme at CML, resulting in this thesis. She retired from her government position in 2013 and was appointed as Research Associate at the Illinois State Museum Research and Collections Center. Her research at the museum was supervised by Dr. E.D. Cashatt. During her PhD, she gave a number of scientific lectures and attended several symposia. Prof. Dr. de Snoo and Dr. Musters were her supervisors during this time.

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There are a great many people to thank. These people have either made my research possible or eased my path through the process. To go back to the beginning, I have to thank Rudi Westendorp, who at that time was at the Leyden Academy of Aging. Rudi invited my husband, to do a teaching sabbatical in Leiden and I was able to accompany him. While we were living in Leiden, I participated in a research project supervised by Martina Vijver at the Environmental Institute. By the end of our stay, we had made many friends and I was invited to participate in the "Sandwich" PhD program. I am so grateful to my promotor, Geert de Snoo for his gentle guidance into a more focused research project and to Kees Musters for his statistical expertise. Kees, you have become my friend and I hope that our Skype sessions don't end with the promotjie. I also wish to thank the members of my committee. Their expectations made me work harder and learn more, and contributed in a very important way to the improvements of my thesis. I truly am grateful.

My thanks to Jory Sjardijn and Jose' Brittijn who made an effort to keep the conversation in English when I joined the group for lunch. Esther Phillips always provided conversation about things other than research and was there to prop me up during various administrative issues. I worked on a project with Wil Tamis that introduced me to feral parrots around the world. Thank you, Wil. Maarten van 't Zelfde provided technical GIS support. And Martina, you are my Dutch soul sister. I value our friendship and professional relationship. You provided support and conversation and are a role model. Few women are successful at being role models and providing support to other women. You have a skill that will take you far. Thank you for sharing with me.

Back in the US with the idea for a project, I began planning. During the time I was writing proposals, I had lots of help with GIS from Will Hinsman and Lisa Beja, for which I am grateful. I worked evenings and weekends on my research studies for more than two years while being employed full-time. Before the first field season, my husband kept urging me to do a pilot study to see what problems that might crop up. He was right. The first problem was that the anti-freeze which was used in the pitfall traps drew various "critters". None of the pitfall traps in the pilot study made it through the night. There were possums, raccoons, mink, and coyotes.

This was not an issue in comparable Dutch studies and I had to find researchers closer to home to find a solution. And I had some difficulty obtaining permissions to access various properties. I discovered that the landowner and land managers were often different people and I had to obtain permissions from both. Thank you to the many land owners and managers who gave permission and the tolerant understanding I got when I was on property where I did not have permission because I had incorrectly read the map.

My next problem was to learn to identify invertebrates. The nearest University with an entomology department was at the University of Illinois, 90 minutes away by car. My dear friend, Kent Smith, suggested I talk to Tim Cashett at the Research and Collections Center (RCC) at the Illinois State Museum. Kent retired within a couple of months and moved out of the area, it came so close to not having the expert tutelage of Tim Cashett. Thank you, Kent, you are greatly missed. Which leads me to Tim, a.k.a. E.D. Cashett. I had four years of access to a renowned invertebrate taxonomist. I was provided an office and lab and definitive identification whenever it was needed. I cannot thank you enough. Support from Becky Dyer included typical office support and then this wonder woman would identify the invertebrates I was having difficulty with when Tim was unavailable. To these folks and all my museum colleagues, I am very grateful.

Midway through the second field season, a wildfire ripped through one of my study sites. My initial devastation was complete. My husband was out of the country and I was at a loss. I didn't have the "oomph" to start my study over. I bounced back with the idea of doing a new study about invertebrate recovery after a mid-summer wildfire. The fire study was limited due to the small area that remained unburned after the fire, but I had data (pitfalls with several Lepidoptera larva) in October, and was able to publish results of what I came to call my "lemonade" study (making something good from something sour). Folks at the Sangamon County Soil and Water District were very supportive and I would like to thank Terry Nichols (now deceased), Barb Mendenhall, and Ray Geroff.

I received specialized identification assistance from George Godfrey, Jim Wiker and Jim Steffen. The identification of noctuid larva required looking at the cusp of a molar on each of the larval specimens to determine species. George, Jim and Tim spent hours to ascertain the correct identity. Thank you, George and Jim. One

Friday evening while Tim was on annual leave, I was having difficulty identifying a spider. It was adorable but I could not find it in any of the books I had available. It should have been extremely easy to identify because it had a bright red chin. So I sent an e-mail to a colleague at the Morton Arboretum who was good with spiders. He responded "spiders don't have chins, red or otherwise"! A few days later he sent me a photo of *Habronatus coecatus* and video of the mating dance. What a joy, thank you Jim for that and your power point presentation on spider identification. My red-chin spider was only the second documented in the museum collections and has "joined" the state collections.

At the start of my second field season, I had to have two emergency abdominal surgeries, which effectively put a halt on completing my research. The flowers sent by CML touched me to the soul. Thank you. They came when needed. Museum colleague, Meredith Mahoney, volunteered to do all the manual work in each of the three ongoing studies. This was above and beyond the call of collegiality. She was wielding a pickaxe in record heat and drought conditions to dig pitfall traps. I am so grateful, again I could not have done this PhD without you. This graduate study was like all others and had its share of problems. Fire, emergency surgery, retirement of Tim Cashatt, and closure of the Illinois State Museum system due to state budget issues. When I complained about the fire to Geert, he said that as awful as it was, it was not the worst graduate student story he heard that year. One student had her study site trampled by a herd of elephants. It helped to put things in perspective. With that being said, I am extremely grateful to Leiden University for having a "sandwich" program and accepting me into it. My age was never an issue nor did anyone ask "what are you going to do with the degree once you have it"? I am also grateful to CML who sent Kees to Illinois to see my research sites which helped when we were comparing agricultural practices in Europe and the USA. Jinze Noordijk has been helpful with his research advice and for providing an additional sounding board when I needed to feel a bit less isolated across the water. And here in Illinois I received research advice from Brian Anderson and TJ Benson. Thank you both. Bonnie Styles, director emeritus of the Illinois State Museum system provided an appointment, office, laboratory, and support that was totally amazing. I am very grateful to have been part of the museum community for the past five years.

Last, but not least, I want to say thanks to my husband Andrzej. Andrzej, you have been at my back from the beginning, pushing, prodding, and propping me up. You edited, encouraged, and assisted in so many ways. You knew that this degree was something I needed to do for myself and made space for me to get it done. You never wavered in your belief that I was mentally up to the challenge of completing this PhD. Thank you so very much!

I am certain to have missed a number of people, and to all of you, please know how grateful I am for your support and encouragement. I would like to say thank you very much!