

Einfluss von Landschaftsstruktur und Landnutzung auf Laufkäfergemeinschaften in der Agrarlandschaft

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Einleitung

Eine Vielzahl menschlicher Aktivitäten beeinflusst auf lokaler und globaler Ebene die Zusammensetzung von Artengemeinschaften. Einen entscheidenden Einfluss hat hierbei die Veränderung von Lebensräumen durch landwirtschaftliche Nutzung. So gelten der Landnutzungswandel und die Intensivierung der Landwirtschaft als die Hauptursachen für den Rückgang der Biodiversität (Sala et al. 2000; Tilman et al. 2001; Thomas et al. 2004). Die Änderungen der globalen Biodiversität gibt nicht nur aus ethischen und ästhetischen Gründen Anlass zur Sorge. Ökologische Experimente und Modelle haben nachgewiesen, dass die Eigenschaften von Ökosystemen hochgradig von ihrer Biodiversität abhängen (Hooper et al. 2005). Durch den Verlust von Biodiversität besteht daher auch die große Gefahr, Ökosysteme in ihren Eigenschaften zu verändern und damit deren ökosystemare Dienstleistungen zu beeinflussen.

Agrarlandschaften tragen in einem großen Maß zum Gesamtlandschaftsbild in Deutschland bei. Im Jahr 2007 waren annähernd 50% der Gesamtlandesfläche unter landwirtschaftlicher Nutzung, wobei etwa 70% der landwirtschaftlich genutzten Fläche auf Ackerland und fast 30% auf Dauergrünland fielen (Statistisches Bundesamt 2010). Naturgemäß beherbergen Agrarlandschaften in Deutschland damit einen hohen Anteil der Gesamt-Biodiversität. Die Landwirtschaft, als größter Landnutzer in Deutschland, hat daher eine Schlüsselfunktion im Schutz der biologischen Diversität (Fourth National CBD Report - Germany 2010). Historisch trug die durch die Landwirtschaft geschaffene, ursprünglich vielfältigere Kulturlandschaft entscheidend zur Steigerung der landschaftliche Heterogenität bei und gilt als eine der Hauptursachen für die Entwicklung der Biodiversität in Europa (Robinson & Sutherland 2002, Benton et al. 2003). Die landwirtschaftliche Intensivierung seit der Mitte des letzten Jahrhunderts dagegen führte unter anderem zu einer starken Mechanisierung in der landwirtschaftlichen Wirtschaftsweise, deren Folgen tiefgreifende landschaftliche Veränderungen, wie beispielsweise die Vergrößerung der Schlagflächen, die Reduktion unbewirtschafteter Randstreifen, die Entfernung von Hecken und die Umwandlung von Grünland zu Ackerflächen, aber auch die Aufgabe wirtschaftlich unrentabler Flächen sind (Stoate et al. 2001; Robinson & Sutherland 2002). Während der Einfluss von Bewirtschaftungsfaktoren wie Düngung und Pestizideinsatz auf die Flora und Fauna der Flächen schon sehr früh untersucht wurde (z.B. Atkins & Anderson 1954; Critchle 1972;

Vanhecke et al. 1981), sind viele Fragen zum Einfluss dieser landschaftliche Veränderungen auf die lokale Biodiversität noch offen geblieben (Wu & Hobbs 2002; Turner 2005). Als wichtige Forschungsschwerpunkte der Landschaftsökologie werden beispielsweise die Gründe, Prozesse und Auswirkungen von Landnutzung und Landnutzungswandel und der Zusammenhang zwischen Landschaftskenngrößen und ökologischen Prozessen genannt, sowie die zeitlichen und räumlichen Beziehungen ökologischer Muster und Prozesse (Wu & Hobbs 2002).

Grünlandflächen sind in einem besonderen Maße durch den Landnutzungswandel betroffen. Das Hauptziel der landwirtschaftlichen Entwicklung nach dem zweiten Weltkrieg war das Ersetzen von Dauergrünland durch produktivere Futterpflanzen (Gibon 2005). Auch aktuell sind bundesweit die Flächenanteile von Dauergrünland rückläufig, während die Flächen für Energiepflanzenanbau zunehmen (Statistisches Bundesamt 2011). Dabei zählen naturnahe Grünlandbiotope zu den artenreichsten Biotoptypen Mitteleuropas (Poschlod & WallisDeVries 2002; Isselstein et al. 2005; Lind et al. 2009). Grünland kann entweder als Lebensraum für spezialisierte Arten dienen, als Trittstein, oder temporär als Habitat für die Larvalentwicklung und den Reifungsfraß, die Überwinterung (Duelli & Obrist 2003) oder als Refugium bei ungünstigen Lebensbedingungen (Landis et al. 2000; Thorbek & Bilde 2004). Auch dem verhältnismäßig intensiv genutzten Wirtschaftsgrünland fällt durch seine im Vergleich zu Ackerflächen geringe Störungsintensität und durch seinen hohen Anteil in der Agrarlandschaft eine wichtige Bedeutung zu. Die unterschiedlichen Nutzungsintensitäten und Habitateigenschaften begünstigen vielfältige Artengemeinschaften und tragen damit entscheidend zur regionalen Artenvielfalt bei (Luff et al. 1992; Isselstein et al. 2005). Ziel zukünftiger Schutzmaßnahmen muss daher sein, sowohl dem gestiegenen Flächenanspruch der Landnutzer, als auch durch den Schutz geeigneter Grünlandflächen dem Erhalt einer hohen regionalen Biodiversität Rechnung zu tragen.

Durch die Flächenabnahme von Grünland einerseits und die Reduzierung verbindender Landschaftselemente wie Hecken und Randstreifen im Zuge der ackerbaulichen Intensivierung andererseits kommt es gerade in landwirtschaftlich intensiv genutzten Regionen immer mehr zur Isolierung von natürlichen und naturnahen Habitaten (Stoate et al. 2001; Benton et al. 2003; Burel et al. 2004; Burel & Baudry 2005; Tschardtke et al. 2005). Der durch die Isolation bedingte verminderte Austausch zwischen den Habitaten erhöht die Wahrscheinlichkeit lokaler Aussterbeereignisse (Connor et al. 2000; Keller & Largiadèr 2003; Hanski 1999) und vermindert die Wahrscheinlichkeit der Wiederbesiedelung (Fahrig &

Merriam 1985). Das Ausmaß, in dem Arten von der Verfügbarkeit natürlicher und naturnaher Landschaftselemente beeinflusst werden, ist von spezifischen Artmerkmalen abhängig. Auch die Fähigkeit, sich in einer Landschaft auszubreiten, hängt neben der Durchgängigkeit dieser Landschaft (Ricketts 2001) entscheidend vom Ausbreitungspotential der betrachteten Organismen ab (Diekötter et al. 2008).

Da die Eigenschaften von Ökosystemen von den funktionellen Merkmalen der dort lebenden Organismen und deren Verteilung und Häufigkeit in Raum und Zeit abhängig sind (Hooper et al. 2005), dient der Erhalt der Biodiversität gleichzeitig dem Erhalt der ökosystemaren Funktionen. Damit spielen neben dem reinen Naturschutz-Aspekt auch wirtschaftliche Interessen bei der Erhaltung von Biodiversität eine große Rolle. Die gesamten ökosystemaren Dienstleistungen, die von Flora und Fauna zur Verfügung gestellt werden, lassen sich häufig nur schwer beziffern (Chee 2004). Alleine jedoch die wirtschaftlichen Schäden z.B. bei Ausfall von Bestäuberfunktionen oder bei massenhaftem Befall von Schädlingen durch fehlende natürliche Antagonisten gehen in die Milliarden Dollar jährlich (Allsopp et al. 2008; Losey & Vaughan 2006). Das Verständnis der Zusammenhänge zwischen Landnutzung und Landnutzungswandel, ökologischen Prozessen und deren räumlicher und zeitlicher Abhängigkeit können helfen, zukünftige Landnutzungsstrategien zu entwickeln, die den Artenverlust minimieren und die ökosystemaren Dienstleistungen erhalten.

Die Gruppe der Laufkäfer eignet sich aufgrund ihrer spezifischen Eigenschaften sehr gut dazu, Forschungen zu diesen Schwerpunkten in der Agrarlandschaft durchzuführen. Sie sind in der Agrarlandschaft mit großer Artenvielfalt vertreten (Thiele 1977) und gehören zu den am besten sowohl taxonomisch als auch ökologisch untersuchten Arthropoden der nördlichen Hemisphäre (Rainio & Niemelä 2003). Laufkäfer sind über einen weiten geographischen Raum verteilt und in fast allen Habitaten zu finden (Thiele 1977; Desender et al. 1994; Lövei & Sunderland 1996; Niemelä 2000). Sie reagieren sensitiv auf abiotische Habitat- und Managementfaktoren (Niemelä 2000) und viele wurden daher als Charakterarten bestimmter Habitate beschrieben, z.B. für Moore, trockene Heiden, Auwälder und andere charakteristische Waldstandorte, aber auch für Äcker oder Grünland (Thiele 1977). Die Zusammensetzung und Struktur der Laufkäfergemeinschaft unterscheidet sich auch in diesen Offenlandstandorten der Kulturlandschaft deutlich (Thiele 1977; Luff 1996; Purtauf et al. 2004a). Viele dieser Laufkäferarten sind jedoch stärker generalistisch und auf einer Vielzahl von Äckern, Wiesen und Brachen nachzuweisen (Thiele 1977; Purtauf et al. 2004b). Daher

sind sie häufig weniger empfindlich gegen Änderungen der Umweltbedingungen als spezialisierte Arten (Rainio & Niemelä 2003). Da die Auswirkungen beispielsweise verschiedener Managementfaktoren bei Arten mit unterschiedlichen funktionellen Eigenschaften variieren können, sind aufgrund ihrer ökologischen Merkmale eingeteilte funktionelle Gruppen besser geeignet den Einfluss anthropogenen Störungen abzubilden, als der reine Artenreichtum oder die taxonomische Diversität (Purtauf et al. 2005a; Gobbi & Fontaneto 2008).

Neben den lokalen Habitat- und Managementfaktoren beeinflusst auch die umgebende Landschaft die Artengemeinschaft der Flächen. Hierbei wird neben der Landschaftsdiversität (z.B. Weibull et al. 2003; Maisonhaute et al. 2010; Woodcock et al. 2010) die Komposition und Konfiguration bestimmter Landnutzungsformen genannt (z.B. Batary et al. 2007; Werling & Gratton 2008; Gardiner et al. 2010; Maisonhaute et al. 2010). Es wird insbesondere auch auf den positiven Einfluss natürlicher und naturnaher Landschaftselemente wie Hecken, Waldflächen, Randstreifen, Uferstreifen und Grünlandflächen hingewiesen, die für eine Vielzahl von Laufkäferarten der Agrarlandschaft von essenzieller Bedeutung sind (Duelli & Obrist 2003; Billeter et al. 2008).

Die mit der landwirtschaftlichen Intensivierung einhergehende Reduzierung naturnaher Randstrukturen und Grünlandflächen führt zu einer stärkeren Isolierung der verbleibenden Flächen. Während viele Autoren sich mit dem Einfluss der Isolierung von Waldstandorten (z.B. Davies & Margules 1998; Magura et al. 2001) oder Heiden und Mooren beschäftigen (z.B. Bauer 1989; DeVries et al. 1996), ist nur wenig über den Einfluss der Habitatisolierung von Wirtschaftsgrünland auf die Laufkäfergemeinschaften und ihre unterschiedlichen funktionellen Gruppen bekannt. Auch auf den umliegenden Ackerflächen führt die Reduzierung naturnaher Landschaftselemente zu einer Veränderung der Lebensbedingungen. Während diese Flächen zwar den höchsten Artenreichtum an Laufkäfern in der Agrarlandschaft aufweisen können (z. B. Cole et al. 2005; Dauber et al. 2005; Vanbergen et al. 2005), sind viele Ackerarten jedoch zumindest in bestimmten Lebensphasen auf natürliche und naturnahe permanente Lebensräume angewiesen, da sie, beispielsweise zur Überwinterung oder zur Fortpflanzung, zwischen bewirtschafteten und naturnahen Habitaten wechseln (Wissinger 1997; Kromp 1999; Ekbom 2000; Lee & Landis 2002). Die Verfügbarkeit dieser Habitate sollte daher zumindest teilweise durch den Einfluss auf saisonale Besiedlungsprozesse die Artengemeinschaft der Äcker beeinflussen, was auf eine zeitliche Abhängigkeit dieser Beziehung schließen lässt.

Neben einer möglichen zeitlichen Abhängigkeit auf die Ausbreitungsprozesse von Laufkäfern liegt eine räumliche Abhängigkeit der Landschaftseinflüsse nahe. Viele Laufkäferarten sind potentiell flugfähig und es können sogenannte Ausbreitungsflüge zu geeigneten Habitaten oder Spontanflüge bei Störung nachgewiesen werden, andere Arten sind hingegen generell flugunfähig (Thiele 1977; Den Boer 1977, 1990; Desender 1989; Matalin 2003). Das Ausbreitungspotential beeinflusst daher sowohl die Überlebensfähigkeit der Populationen auf isolierten Flächen (Den Boer 1990) als auch die räumliche Dynamik von Arten in Abhängigkeit ihrer saisonalen Habitatsprüche (Wissinger 1997). Eine Analyse der räumlichen und zeitlichen Variabilität der Landschaftseinflüsse auf die Diversität von funktionellen Laufkäfergruppen mit unterschiedlichem Ausbreitungspotential kann daher helfen, die Ausbreitungsprozesse der Laufkäfer in der Agrarlandschaft insgesamt besser zu verstehen. Damit können zukünftige regionale Managementstrategien besser auf die ökologischen Bedürfnisse der Artengemeinschaften ausgerichtet werden, um deren ökosystemare Funktion zu erhalten.

Laufkäfer können abhängig von ihren Artenmerkmalen unterschiedliche ökosystemare Dienstleistungen zur Verfügung stellen. Viele Untersuchungen haben gezeigt, dass räuberische Arten eine Rolle bei der Bekämpfung von Pflanzenschädlingen in der Landwirtschaft spielen können (Ekbohm et al. 1992; Östman et al. 2003; Schmidt et al. 2003; Bommarco et al. 2007). Ihre Rolle als Prädatoren von Ackerwildkrautsamen wurde erst in jüngerer Zeit publiziert (z.B. Honek et al. 2003; Hurst & Doherty 2003; Gallandt et al. 2005; Honek et al. 2006; Menalled et al. 2007; Koprdoва et al. 2008; Gaines & Gratton 2010) und lässt noch eine Reihe von Fragen offen. So unterscheiden sich die Ergebnisse zur Bedeutung von Samenfraß durch Invertebraten nicht nur zu unterschiedlichen Jahreszeiten, sondern auch für unterschiedliche Untersuchungsregionen erheblich (siehe z.B. Harrison et al. 2003; Westermann et al. 2003; Mauchline et al. 2005; Jacob et al. 2006; Honek et al. 2006). Einflüsse der Bewirtschaftungsweise und des landschaftlichen Kontextes auf die ökosystemare Dienstleistung könnten einen Teil dieser Diskrepanzen möglicherweise erklären.

Ein besseres Verständnis der vielfältigen Landschaftseinflüsse auf die Laufkäfer der Agrarlandschaft und ihre ökosystemaren Dienstleistungen ist essentiell, um mögliche Schutzmaßnahmen zu beurteilen. Im Rahmen der vorliegenden Arbeit wurden daher in den Jahre 2004 bis 2007 in drei verschiedenen Regionen in Deutschland 50 Grünlandflächen und 24 Ackerflächen beprobt. Es wurde Untersuchungen angestellt, um

- den Einfluss von Habitat- und Management-Faktoren sowie landschaftlicher Steuergrößen auf die Gemeinschaftszusammensetzung und Diversität der Laufkäfer und ihrer funktionellen Gruppen zu analysieren und den Beitrag unterschiedlicher Grünlandflächen zur regionalen Artenvielfalt abzuschätzen (Kap. 1, 2)
- den Einfluss naturnaher Landschaftselementen auf die Ausbreitungsprozesse von Laufkäfern in der Agrarlandschaft (Kap. 3, 4) und ihre räumlichen und zeitlichen Abhängigkeit zu bestimmen (Kap. 4)
- neben der Einfluss der lokalen Bewirtschaftung auch den Einfluss der regionalen Bewirtschaftungsweise als landschaftliche Steuergrößen auf die ökosystemaren Dienstleistungen von Laufkäfern und anderen Taxa abzuschätzen (Kap. 5)

Kapitelübersicht

Kapitel 1: Ground beetles (Coleoptera: Carabidae) in anthropogenic grasslands in Germany: effects of management, habitat and landscape on diversity and community composition.

Im ersten Kapitel (publiziert in *Wiadomosci Entomologiczne*) wurde unter Berücksichtigung abiotischer Standorteigenschaften der Einfluss von Bewirtschaftungsintensität und landschaftlichem Kontext auf die Diversität und Artenzusammensetzung der Laufkäfer auf Wirtschafts-Grünlandflächen untersucht. Da die Qualität von Grünland häufig auf der Basis ihrer pflanzlichen Diversität gemessen wird, wurde zusätzlich überprüft, ob die Pflanzendiversität ebenfalls als Indikator für die Diversität von Laufkäfern gelten kann. Die Untersuchung fand auf 29 Flächen mit niedriger bis hoher Bewirtschaftungsintensität und einer hohen Varianz von abiotischen Faktoren in der Region Northeim statt.

Kapitel 2: Contrasting diversity patterns of epigeic arthropods between grasslands of high and low agronomic potential.

In diesem Kapitel (publiziert in *Basic and Applied Ecology*) wurde der Beitrag von Gebieten mit unterschiedlichem ackerbaulichem Ertragspotential zur regionalen Biodiversität untersucht. Die Untersuchung fand in der Region Northeim auf jeweils 13 Grünland-Flächen mit hohem oder niedrigem ackerbaulichem Ertragspotential statt, deren Beitrag zur regionalen

Biodiversität verglichen wurde. Die regionale Diversität (γ) wurde in die Komponenten Artenreichtum auf den Flächen (α), Verschiedenheit der Artengemeinschaften zwischen den Flächen einer Klasse (β_{within}) und Verschiedenheit der Artengemeinschaften zwischen den beiden Flächenklassen (β_{between}) eingeteilt. Die verschiedenen Komponenten der regionalen Biodiversität wurden anhand von vier Arthropodengruppen (Ameisen, Springschwänze, Spinnen und Laufkäfer) untersucht.

Kapitel 3: Trait-specific effects of habitat isolation on carabid species richness and community composition in managed grasslands.

Das dritte Kapitel (publiziert in *Insect Conservation and Diversity*) beschäftigt sich mit dem Einfluss der Habitat-Isolierung auf die Artengemeinschaften von Laufkäfern im Wirtschafts-Grünland. Die Untersuchung fand in der überwiegenden intensiv bewirtschafteten Region der Wetterau statt. Es wurden 21 Grünlandflächen in drei unterschiedlichen Isolations-Klassen hinsichtlich des Artenreichtums und der Artenzusammensetzung von Laufkäfern untersucht.

Kapitel 4: Delayed colonisation of arable fields by spring breeding ground beetles (Coleoptera: Carabidae) in landscapes with a high availability of hibernation sites

Im vierten Kapitel (publiziert in *Agriculture, Ecosystems & Environment*) wurde die räumlich-zeitliche Dynamik im Einfluss potentieller Überwinterungs-Habitate auf die Wiederbesiedlung von Äckern durch Laufkäfer untersucht. Die Untersuchung fand im Frühjahr auf zwölf Wintergerste-Äckern in der überwiegend extensiv bewirtschafteten Region des Lahn-Dill-Berglandes statt.

Kapitel 5: Landscape and management effects on structure and function of soil arthropod communities in winter wheat.

Im diesem Kapitel (publiziert in *Agriculture, Ecosystems & Environment*) wurde der Einfluss von ökologischer und konventioneller Anbauweise auf den Artenreichtum und die Abundanz von fünf Arthropodengruppen (Laufkäfer, Spinnen, Springschwänze, Tausendfüßer und Asseln) und deren ökosystemaren Leistungen (Samenprädation, bodenbiologische Aktivität, Streuzersetzung) untersucht. Die Untersuchung fand auf sechs ökologisch und sechs konventionell bewirtschafteten Winterweizenfeldern in der Region Wetterau statt, von denen

jeweils die Hälfte in einem überwiegend ökologisch bewirtschafteten und die andere Hälfte in einem überwiegend konventionell bewirtschafteten Umfeld lagen.

Ergebnisse und Schlussfolgerungen

Habitat- und Managementfaktoren beeinflussten erwartungsgemäß die Laufkäfergemeinschaften der Untersuchungsflächen. Bei mittlerer Bewirtschaftungsintensität wurde die höchste Laufkäferdiversität auf Grünland ermittelt (Kap. 1). Dies deckt sich mit dem Prinzip der mittleren Störungshäufigkeit (intermediate disturbance theory, Connell 1978), nach welchem regelmäßige Störungen die Koexistenz von spezialisierten Arten, Pionierarten und Generalisten fördern. Der Einfluss abiotischer Habitatfaktoren wie Bodenfeuchte und/oder Boden-pH auf die Artenzusammensetzung bzw. die Diversität und Aktivitätsdichte funktioneller Gruppen (Kap. 1, 2, 3) erklärt sich durch die unterschiedlichen Präferenzen von Arten für diese Faktoren (z.B. Thiele 1977; Paje & Mossakowski 1984; Holopainen et al. 1995; Holland et al. 2007). Die Vielzahl xerophiler Arten (vgl. Koch 1989) beispielsweise innerhalb der funktionellen Gruppe phytophager Laufkäfer erklärt den Einfluss der Bodenfeuchte auf ihre Arten- und Individuenzahl (Kap. 1) und ihre Verteilung auf den Flächen (Kap. 1, 3). Da die Varianz der Habitatansprüche innerhalb der Gruppe der Laufkäfer aber sehr groß ist, kommt es bei unterschiedlichen Habitatbedingungen zwar zu einer Verschiebung des Artenspektrums, nicht aber notwendigerweise zu einer Änderung der Artenzahl (vgl. Irmeler 2006). Die große Heterogenität der Laufkäfergemeinschaften auf den Wirtschafts-Grünlandflächen erklärt sich daher, unter anderem, durch die große Varianz der Habitat- und Managementfaktoren. Die Auswirkungen abiotischer Faktoren und des Flächenmanagements können aber im Vergleich zu Auswirkungen der Landschaftsstruktur vergleichsweise gering sein (z.B. Weibull et al. 2003; Purtauf et al. 2005b; Batary et al. 2007) und durch den Einfluss von Landschaftsvariablen überlagert werden (Maisonhaute et al. 2010, vgl. Kap. 4).

Insgesamt zeigen die Kapitel der vorliegenden Arbeit einen starken Einfluss der umgebenden Landschaft auf die Laufkäfergemeinschaften. Bei höherem Anteil von Ackerflächen in der Umgebung wurde eine höhere Diversität der Laufkäfer auf Grünland (Kap. 1) bzw. ihrer funktioneller Gruppen (Kap. 1, 2) nachgewiesen. Dies kann auf spill-over-

Effekte von generalistischen Ackerarten aus benachbarten Flächen zurückgeführt werden (Cole et al. 2005; Rand et al. 2006; Batary et al. 2007). Durch die hohe Heterogenität der Artengemeinschaften trugen aber in unseren Untersuchungen nicht die Diversität einzelner Flächen (α -Diversität), sondern die Unterschiede der Artenzusammensetzung zwischen den Flächen (β -Diversität) am stärksten zur Gesamtdiversität bei (Kap. 2). Zudem kamen viele Arten exklusiv auf bestimmten Flächenklassen vor (Kap. 1, 2, 3), beispielsweise auf Flächen in Grünlandverbänden (geringer Ackeranteil in der Umgebung; Kap. 3) oder in landwirtschaftlichen Ungunstregionen (im Mittel geringerer Ackeranteil, Kap. 2), aber auch auf in der Agrarlandschaft isolierten Grünlandflächen mit hohem Ackeranteil (Kap. 3). Die höchste Laufkäferdiversität insgesamt wäre hier also in einer Agrarlandschaft zu erwarten, in der sowohl großflächige Grünlandverbände, als auch isolierte Grünlandflächen in großflächigen Ackerverbänden vereint sind. Die Ergebnisse dieser Untersuchungen zeigen, dass für die Beurteilung von Schutzmaßnahmen zur Erhaltung einer möglichst hohen Diversität von Laufkäfern in der Landschaft eine Beurteilung der Diversität einzelner Flächen alleine nicht ausreicht.

Der Einfluss der umgebenden Landschaft zeigte bei den Untersuchungen der Ausbreitungsprozesse von Laufkäfern Unterschiede in den Systemen Ackerland und Grünland. Uferrandstreifen zwischen isoliert liegenden Grünflächen und einem größeren Grünlandverband wirkten positiv auf die Artenzahl zumindest von Laufkäfern mit niedrigem Ausbreitungspotential, aber negativ auf die Anzahl exklusiver Arten (Kap. 3). Streifenförmige Randstrukturen scheinen demnach vor allem die Ausbreitung von Arten in der Landschaft zu unterstützen, die auch in größeren Grünlandverbänden vorkommen. Gleichzeitig besteht die Gefahr, durch die Erhöhung der Konnektivität zwischen den Grünlandflächen konkurrenzschwächere Arten zu verlieren. Für Ackerflächen ist ein positiver Einfluss von Randstreifen und anderen potenziellen Überwinterungs- und Rückzugshabitaten auf die Diversität der Laufkäfer zwar nach wie vor zu vermuten (vgl. Holland & Luff 2000; Lee & Landis 2002; Purtauf et al. 2005b; Werling & Gratton 2008), unsere Untersuchungsergebnisse zeigten jedoch eine Verzögerung der Wiederbesiedlung im Frühjahr in Abhängigkeit dieser Habitate (Kap. 4). Da der negative Einfluss auf die Besiedlung im Verlauf der Untersuchung bei zunehmender Pflanzendeckung der Äcker verschwand, wurde dies auf die größere Attraktivität der Randstreifen durch höhere Pflanzendeckung und Ressourcenverfügbarkeit im Frühjahr zurückgeführt. Ackerrandstreifen weisen durch ihre grundsätzlich andere Struktur im Vergleich zum Acker selbst aber auch einen höheren Grenzwiderstand auf und können daher einen Wechsel zwischen den Habitaten erschweren (Frampton et al. 1995; Dauber & Wolters

2004), was ebenfalls die verzögerte Besiedlung erklären kann. Da die Präferenz von Laufkäfern für Ackerflächen unter anderem auch durch den geringeren Raumwiderstand von Äckern im Vergleich mit anderen Offenlandhabitaten bedingt ist (Frampton et al. 1995), liegt die Vermutung nahe, dass Randstreifen als Rückzugsgebiete und zur Überwinterung zwar wichtig, für die Ausbreitung der Ackerlaufkäfer in der Agrarlandschaft aber nur von geringerer Bedeutung sind als für Grünlandarten.

Während in Kapitel 3 und 4 der Einfluss von streifenförmigen Landschaftselementen auf die Besiedlung bzw. Ausbreitung von Laufkäfern grundsätzlich nachgewiesen werden konnte, beschränkte er sich jedoch in beiden Fällen auf Arten mit niedrigem Ausbreitungspotenzial. Die Untersuchungsergebnisse der Kapitel dieser Arbeit zu den verschiedenen funktionellen Gruppen (karnivor/mixophag/phytophag, hohes/niedriges Ausbreitungspotential) verdeutlichen, dass für unterschiedliche trophische Gruppen (Kap. 1, 2), ebenso wie für unterschiedliche Ausbreitungstypen (Kap. 3, 4) der Einfluss von Landschaftsparametern auf Abundanz und Diversität verschieden oder gegensätzlich sein kann. In welcher Weise die Landschaft auf eine Art wirkt, hängt von deren ökologischen Ansprüchen ab und begründet sich durch grundsätzliche Habitatpräferenz, Ernährungsweise, Ausbreitungsfähigkeit und Reproduktionsbiologie. Da daher auch die nach den ökologischen Eigenschaften gebildeten funktionellen Gruppen der Laufkäfer verschiedene ökologische Ansprüche haben, kann sich der Einfluss nicht nur von Flächencharakteristika sondern auch von Landschaftsfaktoren gravierend für sie unterscheiden.

Da sich aber verschieden funktionellen Gruppen hinsichtlich ihrer Artenzahl und Abundanz sehr stark voneinander unterscheiden können (vgl. Kap. 1-4), können die Eigenschaften einer einzelnen Gruppe bei starker Dominanz die Ergebnisse der anderen völlig überlagern (Kap. 3). Eine Interpretation der Ergebnisse der Gesamtdiversität kann daher zu einer Fehlinterpretation führen (Gobbi & Fontaneto 2008), während die Untersuchung funktioneller Gruppen eine detailliertere Auskunft über die Art und Wirkung von Landschaftseffekten auf die zugrunde liegenden ökologischen Prozesse geben kann. Die Untersuchung des landschaftsbedingten Einflusses auf ökologische Prozesse wie die Besiedlung von Flächen benötigt neben einer Differenzierung verschiedener funktioneller Gruppen auch eine hohe zeitliche und räumliche Auflösung, da die Sensitivität der Arten in Abhängigkeit ihrer ökologischen Bedürfnisse sowohl räumlich als auch zeitlich variiert (Kap. 4).

Während die ersten Kapitel dieser Arbeit den Einfluss von Komposition und Konfiguration verschiedener Landnutzungsformen auf die Laufkäfergemeinschaft untersuchen, beschäftigt sich das fünfte Kapitel neben dem lokalen auch mit dem regionalen Einfluss des Bewirtschaftungssystems. Viele Untersuchungen zum Einfluss der ökologischen Landwirtschaft auf die Diversität von Laufkäfern legen den Schluss nahe, dass die Effekte des Bewirtschaftungssystems durch Landschaftseinflüsse moduliert werden (z.B. Pfiffner & Luka 2000; Weibull et al. 2003; Bengtsson et al. 2005; Purtauf et al. 2005b; Winqvist et al. 2011; vgl. Kap. 5). Da durch den Einfluss des Bewirtschaftungssystems die Habitateigenschaften der Flächen variieren (Hole et al. 2005, Fließbach et al. 2007), trägt neben der Vielfalt von Landnutzungsformen auch die von Bewirtschaftungssystemen zur Heterogenität einer Landschaft bei. Die Präferenz verschiedener Arten für ökologisch oder konventionell bewirtschaftete Ackerflächen (z.B. Basedow 2002; Döring & Kromp 2003; Shah et al. 2003) und die Interaktion des Einflusses von lokalem und regionalem Bewirtschaftungssystem auf den Artenreichtum von Laufkäfern in unserer Untersuchung legen nahe, in zukünftigen Forschungen neben den unterschiedlichen Nutzungstypen auch die unterschiedlichen Bewirtschaftungssysteme in die Analyse von Landschaftseffekten einzubeziehen.

Neben dem interagierenden Einfluss von lokaler und regionaler Bewirtschaftung auf den Artenreichtum der Laufkäfer wurde ein Einfluss der lokalen Bewirtschaftung auf die ökologische Dienstleistung der Samenprädation nachgewiesen (Kap. 5). Frühere Untersuchungen legen nahe, dass die ökosystemaren Dienstleistungen von Laufkäfern von ihrer Diversität abhängen (z.B. Gaines & Gratton 2010). Die höhere Samenprädation ist sicherlich mit der Wahrscheinlichkeit einer höheren Artenzahl der die Dienstleistung vermittelnden Arten bei höherer Diversität zu erklären (hohe Diversität – höhere Zahl phytophager Carabiden – höhere Samenprädation), ist aber nicht zwangsläufig eine direkte Funktion der Diversität. Unsere Untersuchungen zeigten tatsächlich keinen direkten Zusammenhang zwischen der Diversität der Laufkäfer und der ökosystemaren Dienstleistung. Die Samenprädation ist auf ökologisch bewirtschafteten Flächen insgesamt am höchsten, während die Diversität nur auf den ökologisch bewirtschafteten Flächen im konventionellen Kontext hoch ist, auf ökologischen Flächen in gleichem Kontext im Gegenzug aber am niedrigsten. Ein Zusammenhang zwischen der Körpergröße samenfressender Laufkäfer und dem Anteil an ökologisch bewirtschafteten Flächen im Umfeld (Wamser et al. 2011) weisen auf einen direkten Landschaftseinfluss auf die ökosystemare Dienstleistung, ohne notwendigerweise die Abundanz der vermittelnden Arten zu beeinflussen.

Abschließend lässt sich sagen, dass die Diversität der Laufkäfer als alleinige Messgröße Rückschlüsse auf ihre Ausbreitung in der Agrarlandschaft oder die durch sie vermittelte ökosystemare Dienstleistungen nur sehr bedingt zulässt. Eine höhere Auflösung in funktionelle Gruppen sowie eine hohe zeitliche und räumliche Auflösung der Landschaftseinflüsse ist nötig, um den Zusammenhang zwischen landschaftlichen Steuergrößen und den ökologischer Prozessen und ökosystemaren Funktionen der Laufkäfer zu analysieren. Die Einflüsse von Landschaftsstruktur und Habitatisolation vor allem auf Laufkäfer mit geringem Ausbreitungspotential sowie der Einfluss der regionalen Bewirtschaftung auf lokale Artengemeinschaften und ihre ökosystemaren Dienstleistungen zeigen die Notwendigkeit auf, bei der Planung künftiger Schutzmaßnahmen das Landschaftsmanagement stärker einzubeziehen.

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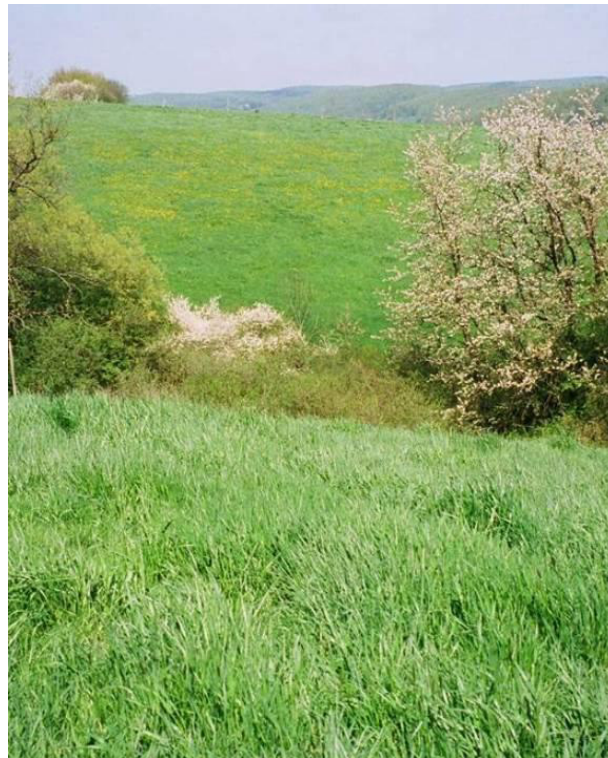
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KAPITEL 1

GROUND BEETLES (COLEOPTERA: CARABIDAE) IN ANTHROPOGENIC GRASSLANDS IN GERMANY: EFFECTS OF MANAGEMENT, HABITAT AND LANDSCAPE ON DIVERSITY AND COMMUNITY COMPOSITION

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Ground beetles (Coleoptera: Carabidae) in anthropogenic grasslands in Germany: effects of management, habitat and landscape on diversity and community composition

Biegaczowate (Coleoptera: Carabidae) łąk antropogenicznych w Niemczech: wpływ użytkowania, środowiska i krajobrazu na różnorodność i skład gatunkowy

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ABSTRACT: Grasslands are of great importance for the conservation and maintenance of biodiversity in agricultural landscapes. In order to sustain grasslands and their associated biodiversity, we need to widen our knowledge of the role of grassland management and the amount of grassland cover in a landscape. The aim of our study was to correlate the variability of community composition and diversity of carabid beetles in anthropogenic grasslands with management, habitat conditions, landscape composition and plant species richness. Since the condition of grassland biodiversity is often solely evaluated on the basis of species richness of vascular plants, we also wanted to assess whether plants could indicate the diversity of carabid beetles in grasslands. Therefore, we sampled carabid beetles on 29 grassland sites with low to high management intensity and a great variation of abiotic conditions in Central Germany. The diversity of carabid beetles was the highest in grasslands of medium management intensity and was positively affected by a high cover of crops in the surrounding landscape. Both the landscape and soil moisture had an impact on activity density of carabids but depended on the trophic group of the beetles. There was no connection between plant species richness and carabid diversity. The results of our study suggest that plant species richness as a sole indicator of grassland biodiversity might not be sufficient. Nevertheless, moderate management intensity which supports high plant species richness can also increase carabid diversity. We therefore conclude that moderate management intensity is crucial to provide highest biodiversity of carabid beetles in grasslands. Due to landscape effects on carabid communities, we suggest that besides management of single fields, the composition and structure of the whole landscape should be taken into consideration in order to sustain a rich species pool of carabid beetles in agricultural landscapes

KEYWORDS: Carabidae, grassland, management intensity, trophic groups, habitat, landscape.

Introduction

Grasslands are of great importance for the conservation and maintenance of biodiversity in agricultural landscapes of Central Europe (WALLISDEVRIES *et al.* 2002; DUELLI, OBRIST 2003). Changes in agricultural production systems affect both spatial cover and management intensity of grasslands. While areas favoured for crop production will undergo further intensification with decreasing the cover of grassland, the areas marginal in agricultural production will undergo further ‘extensification’, often associated with abandonment of land use and therefore also decreasing the cover of grassland (GIBON 2005). So both the intensification and abandonment of management can lead to habitat degradation of grasslands and in turn to a loss of biological diversity (VICKERY *et al.* 2001, SPIEGELBERGER *et al.* 2006). In order to sustain grasslands and their associated biodiversity, we need to increase our knowledge of the role of grassland management and amount of grassland cover in a landscape and find suitable indicators for the evaluation of grassland condition.

At present the condition of grassland biodiversity is often solely evaluated based on species richness of vascular plants (e.g. HARPOLE, TILMAN 2007; LORENZO *et al.* 2007; PÄRTEL *et al.* 2007); mostly due to the fact that plant species richness is an easily assessed indicator. Based on findings for vascular plants, moderate management intensity – particularly a reduction of nitrogen fertilisation on meadows and stocking rates on pastures – is suggested to support high plant species richness (e.g. KLIMEK *et al.* 2007; DIETSCHI *et al.* 2007; SPIEGELBERGER *et al.* 2006).

Yet the total biodiversity of grasslands includes a much higher number of taxa such as ground dwelling arthropods, many of which are not primarily associated with plants. It is still an open question whether inferences obtained from plant surveys can be assigned to other taxa as well and whether plants could function as biodiversity indicators in grasslands. The aim of our study was to correlate the variability of community composition and diversity of carabid beetles in anthropogenic grasslands with management, habitat conditions, composition of the surrounding landscape and finally, plant species richness. As carabid beetles of different trophic groups should respond to plant diversity and management intensity in different ways (PURTAUF *et al.* 2005), feeding preferences of the species were considered. We expect phytophagous species to be positively affected by higher plant diversity providing higher food resources. Other trophic groups might also prefer areas of high plant richness providing a diverse habitat structure but most carnivorous carabids should favour simpler habitat structure (caused by higher management intensity) which facilitates searching for food and hunting. Following

the medium disturbance theory (CONNELL 1978), the highest diversity should be archived by intermediate management intensity.

In this study, we asked the following questions: (1) Is plant species richness correlated with carabid diversity? (2) Does moderate management intensity increase the diversity of carabids? (3) How do the management, habitat conditions and landscape composition together affect the carabid diversity and community composition?

Material and Methods

Study area and study sites

The study was carried out within the rural district of Northeim, Lower Saxony (Germany). The district comprises lowland and upland areas with altitudes above sea level ranging from 72 to 527 m. Mean annual precipitation is 645 mm, mean annual temperature is 8.7° C. The land cover is characterized by a large proportion of arable land and forest, interspersed with patchily distributed fragments of grassland. Most of the grassland in the lowland areas is structurally uniform and poor in plant species richness, whereas in the steeper areas, fragments of plant species-rich semi-natural grassland can be found (KLIMEK et al. 2007). We studied 14 mown meadows and 15 mown pastures within the research area, including mesic to wet and neutral to moderately acidic loam, sandy loam and loamy sand soils. The 29 study sites were randomly distributed over the whole district. The management of the sites ranged from low-input to high intensity management. Not-mown pastures were not included. All sites were of approximately similar size (1.6 +/- 1.1 ha) but showed a great range of site specific conditions (Tab. I). The maximum distance between two sites was 38 km and minimum distance was larger than 1,500 m. The elevation of the study sites varied from 102 to 328 m a.s.l.

Sampling and species determination

Carabids were sampled using pitfall traps (diameter: 85 mm, volume: 500 ml) from 20th to 27th July 2005 and from 03rd to 16th May 2006. The traps were filled with approximately 100 ml of Ethylenglycol-solution (1:2) with a detergent added to reduce surface tension. Each trap was shielded with a 25 × 25 cm acrylic glass pane about 10 cm high to avoid flooding by rain. All the individuals were determined down to species level (TRAUTNER, GEIGENMÜLLER 1987; FREUDE 1976) and characterized according to their feeding type following LUFF (1998), LINDROTH (1985, 1986) and RIBERA et al. (2001). Carabid species were assorted into three trophic groups: carnivorous, mixophagous, and phytophagous (Tab. II).

Tab. I. Range of variation (maximum, minimum, mean) of vegetation, habitat, landscape and management variables of the study sites. LU: livestock units

Zakres zróżnicowania (maksimum, minimum, średnie) roślinności, środowiska, krajobrazu i zróżnicowanie użytkowania stanowisk badawczych. LU: jednostki przeliczeniowe inwentarza

	min.	max.	mean średnio
Vegetation – Roślinność			
plant species richness – bogactwo gatunkowe roślin	5.7	24.3	14.9
Landscape – Krajobraz			
crop cover – pokrycie uprawami (750 m radius – promień)	0	82.0	35.9
grassland cover – pokrycie łąkami (750 m radius – promień)	3.7	32.6	17.3
Habitat – Środowisko			
soil moisture – wilgotność gleby (Ellenberg ind. F-Z – liczba Ellenberga F-Z)	5.1	6.9	5.7
soil pH value – wartość pH gleby (Ellenberg ind. R-Z – liczba Ellenberga R-Z)	4.3	6.8	6.1
insolation – usłonecznienie (SI)	2.7	4.3	3.6
Management – Użytkowanie			
grazing pressure – intensywność wypasu [LU*days/ha]	0	363	76.6
number of mowings / year – ilość koszeń / rok	1	4	2.1
management intensity – intensywność użytkowania	25	125	74.6

Habitat and landscape characteristics

Plant species richness and management data (grazing pressure in the form of livestock units [LU], times of mowing per year) of the study sites were provided by the Research Centre for Agriculture and the Environment in Göttingen (ZLU; see KLIMEK et al. 2007 for a description of the methods used). Habitat conditions were characterized by Ellenberg indicator values for soil moisture (F-Z) and pH-value (R-Z; ELLENBERG et al. 2001) and by microclimate in terms of insolation of the sites. Insolation was calculated as the mean annual intensity of solar radiation (kW m^{-2}) that reaches a position on the earth's surface derived from a Digital Elevation Model using the formula provided by SHARY et al. (2002).

Because landscape composition could affect carabid diversity (DAUBER et al. 2005), we calculated a percentage cover of grassland and arable land in 750 m around each study site from a digital land use map with the help of ArcView 3.2 GIS software (ESRI, Redlands, Cal.). We expected a high

Tab. II. Species recorded during this study, the total number of individuals (**A**), percentage of study sites where species could be detected (**B**) and a trophic group (**C**): c – carnivorous, m – mixophagous, p – phytophagous, ? – no classification possible

Gatunki zarejestrowane podczas badań, całkowita liczba osobników (**A**), udział procentowy stanowisk badawczych, gdzie gatunek był obecny (**B**) i grupa troficzna (**C**): c – drapieżne, m – wszystkożerne, p – roślinożerne, ? – sklasyfikowanie nie-
możliwe

Carabid species Gatunek	A	B	C
1	2	3	4
<i>Abax parallelepipedus</i> (PILLER et MITTERPACHER, 1783)	2	6.9	c
<i>Acupalpus meridianus</i> (LINNAEUS, 1761)	1	3.4	c
<i>Agonum mülleri</i> (HERBST, 1784)	37	48.3	c
<i>Agonum piceum</i> (LINNAEUS, 1758)	1	3.4	c
<i>Agonum sexpunctatum</i> (LINNAEUS, 1758)	6	10.3	c
<i>Agonum viduum</i> (PANZER, 1796)	65	13.8	c
<i>Agonum viridicupreum</i> (GOEZE, 1777)	2	3.4	c
<i>Amara aenea</i> (DE GEER, 1774)	26	24.1	p
<i>Amara communis</i> (PANZER, 1797)	8	17.2	p
<i>Amara eurynota</i> (PANZER, 1797)	2	3.4	p
<i>Amara familiaris</i> (DUFTSCHMID, 1812)	23	41.4	p
<i>Amara lunicollis</i> SCHIÖDTE, 1837	3	10.3	p
<i>Amara montivaga</i> STURM, 1825	7	13.8	p
<i>Amara ovata</i> (FABRICIUS, 1792)	4	3.4	p
<i>Amara plebeja</i> (GYLLENHAL, 1810)	15	27.6	p
<i>Amara similata</i> (GYLLENHAL, 1810)	6	13.8	p
<i>Anchomenus dorsalis</i> (PONTOPPIDAN, 1763)	8	6.9	c
<i>Anisodactylus binotatus</i> (FABRICIUS, 1787)	7	20.7	c
<i>Asaphidion flavipes</i> (LINNAEUS, 1761)	3	10.3	c
<i>Badister sodalis</i> (DUFTSCHMID, 1812)	2	3.4	?
<i>Bembidion biguttatum</i> (FABRICIUS, 1779)	32	20.7	c
<i>Bembidion gilvipes</i> STURM, 1825	6	6.9	c
<i>Bembidion guttula</i> (FABRICIUS, 1792)	4	10.3	c
<i>Bembidion lampros</i> (HERBST, 1784)	67	62.1	c
<i>Bembidion lunulatum</i> (FOURCROY, 1785)	3	6.9	c

1	2	3	4
<i>Bembidion obtusum</i> (SERVILLE, 1821)	3	6.9	c
<i>Bembidion properans</i> (STEPHENS, 1829)	45	31.0	c
<i>Bembidion quadrimaculatum</i> (LINNAEUS, 1761)	5	10.3	c
<i>Bembidion tetracolum</i> SAY, 1823	3	10.3	c
<i>Calathus fuscipes</i> (GOEZE, 1777)	16	17.2	c
<i>Carabus auratus</i> LINNAEUS, 1761	972	41.4	c
<i>Carabus auronitens</i> FABRICIUS, 1792	1	3.4	c
<i>Carabus granulatus</i> LINNAEUS, 1758	250	62.1	m
<i>Carabus irregularis</i> FABRICIUS, 1792	1	3.4	c
<i>Carabus nemoralis</i> O. F. MÜLLER, 1764	117	72.4	m
<i>Carabus violaceus</i> LINNAEUS, 1758	1	3.4	m
<i>Claenius nigricornis</i> (FABRICIUS, 1787)	17	10.3	c
<i>Clivina fossor</i> (LINNAEUS, 1758)	42	51.7	m
<i>Dyschirius globosus</i> (HERBST, 1784)	24	13.8	c
<i>Harpalus affinis</i> (SCHRANK, 1781)	6	10.3	m
<i>Harpalus anxius</i> (DUFTSCHMID, 1812)	1	3.4	p
<i>Harpalus latus</i> (LINNAEUS, 1758)	9	13.8	p
<i>Harpalus rufipes</i> (DE GEER, 1774)	4	13.8	p
<i>Harpalus tardus</i> (PANZER, 1796)	2	3.4	p
<i>Loricera pilicornis</i> (FABRICIUS, 1775)	17	34.5	c
<i>Microlestes maurus</i> (STURM, 1827)	8	3.4	c
<i>Nebria brevicollis</i> (FABRICIUS, 1792)	3	3.4	c
<i>Notiophilus aquaticus</i> (LINNAEUS, 1758)	1	3.4	c
<i>Notiophilus biguttatus</i> (FABRICIUS, 1779)	2	6.9	c
<i>Notiophilus palustris</i> (DUFTSCHMID, 1812)	7	17.2	c
<i>Oodes helopioides</i> (FABRICIUS, 1792)	8	6.9	c
<i>Platynus assimile</i> (PAYKULL, 1790)	6	10.3	c
<i>Poecilus cupreus</i> (LINNAEUS, 1758)	609	89.7	m
<i>Poecilus versicolor</i> (STURM, 1824)	2284	89.7	c
<i>Pterostichus anthracinus</i> (PANZER, 1795)	15	10.3	c
<i>Pterostichus burmeisteri</i> HEER, 1841	12	27.6	c
<i>Pterostichus madidus</i> (FABRICIUS, 1775)	1	3.4	c
<i>Pterostichus melanarius</i> (ILLIGER, 1798)	316	75.9	c

1	2	3	4
<i>Pterostichus niger</i> (SCHALLER, 1783)	9	13.8	c
<i>Pterostichus nigrita</i> (PAYKULL, 1790)	31	13.8	c
<i>Pterostichus oblongopunctatus</i> (FABRICIUS, 1787)	2	6.9	c
<i>Pterostichus strenuus</i> (PANZER, 1796)	6	20.7	c
<i>Pterostichus vernalis</i> (PANZER, 1795)	68	65.5	c
<i>Trechoblemus micros</i> (HERBST, 1784)	1	3.4	?
<i>Trechus secalis</i> (PAYKULL, 1790)	3	10.3	?
<i>Zabrus tenebrioides</i> (GOEZE, 1777)	1	3.4	p

cover of crops to provide more generalist open land species, whereas a high grassland cover should support more specialised grassland species. In contrast, a low cover of crops and grassland indicates a high amount of surrounding forest which should increase the number of forest carabid species.

Grazing pressure and times of mowing per year are indices for management intensity. To compare management intensity of mown pastures and meadows we determined the maximum land use impact for each management form. The maximum grazing pressure, specified as livestock-units multiplied with grazing days per hectare was 363 and maximum number of mowing was 4 times (Tab. I). We calculated the percentage of maximum grazing pressure and the times of mowing for each study site and added both parts. To detect a supposed non-linear impact of management intensity, we defined three intensity classes: “low intensity” ranged from management intensity up to 60%, “medium intensity” from >60 to 90% and “high intensity” comprised grasslands of management intensity >90%. All classes comprise a comparable number of study sites.

Statistical analyses

Carabid species number and activity density were cumulated for each site over both sampling periods. Carabid diversity is described with the Shannon-index and evenness. The impact of plant species richness, habitat characteristics, management intensity and landscape on carabid diversity and evenness as well as on species richness and activity density of each trophic group was analyzed separately using General Regression Models (GRM; forward stepwise procedure). GRM implements stepwise and best-subset regression for Analysis of Covariance (ANCOVA) design with categorical and continuous predictor variables (StatSoft Inc., 2001).

Mean plant species richness (plant), Ellenberg indicators for moisture (F-Z) and pH value (R-Z), insolation (SI) and grassland and crop cover in 750m surrounding were included in the models as continuous variables. The management intensity was included as a categorical variable (low, medium, high). As the study was conducted in a small geographical area with moderate differences in altitude, no impact of geographic position and altitude of the study sites on the observed species richness or community composition of carabid beetles was expected. Therefore, we did not include altitude or geographical location as explanatory variables in our statistical models.

To determine an impact of the explanatory variables on community composition we conduct Principal Components Analyses (PCA) with dominance data of species found on more than 25% of the investigated grasslands and the environmental variables. To permit the interpretation of the PCA results, environmental parameters were added to the analysis as supplementary variables so they did not influence the ordination of species data.

The data were tested for normal distribution and were log-transformed prior to statistical analysis whenever necessary. Parameters calculated as percentage were ArcSin transformed (angular transformation) prior to statistical analyses. All the analyses were performed using the STATISTICA 7.0 software package (STATISTICA software V 7.0, StatSoft Inc., Tulsa, USA).

Results

In total, we found 66 carabid species with 5,269 individuals (Tab. II). Species richness ranged from 7 to 21 on the investigated grasslands. Out of the total, 42 species were carnivorous, ranging from 4 to 13; 7 were mixophagous species, ranging from 1 to 6 and 14 were phytophagous, ranging from 0 to 6. Species number was highest under medium management intensity. Of the 55 species occurring in medium-intensity managed grasslands, 10 species were solely found here (Fig. 1).

Shannon-diversity of carabids ranged from 0.3 to 2.8 and evenness ranged from 0.15 to 0.92. Shannon-diversity and evenness of carabid beetles increased with increasing crop cover in 750m surrounding (Tab. III). The diversity was also affected by management intensity. The grasslands of intermediate management intensity harboured the highest diversity (Fig.2).

Species richness of carnivorous and phytophagous carabids was only affected by soil moisture. While the richness of carnivorous species was positively affected by soil moisture, phytophagous species were negatively affected (Tab. III). No impact on the richness of mixophagous species could be detected.

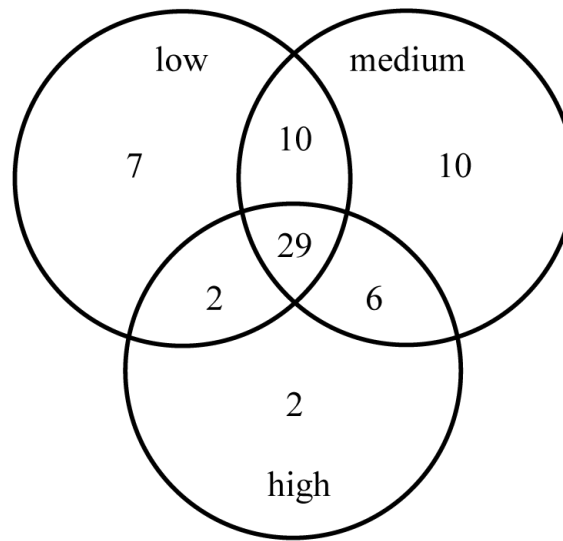


Fig. 1. Number of carabid species on grasslands of different management intensity class and numbers of species shared among the classes

Ryc. 1. Liczba gatunków biegaczowatych na łąkach o zróżnicowanych klasach użytkowania, intensywności użytkowania i ilość gatunków wspólnych dla różnych klas użytkowania

Activity density of the trophic groups was also differentially affected by the tested variables. While no impact on activity density of carnivorous beetles was detectable, mixophagous activity density increased with increasing moisture, whereas phytophagous activity density decreased. Mixophagous activity density also increased with the increasing cover of grassland in the landscape, while phytophagous activity density increased with the increasing crop cover (Tab. III).

The carabid community was dominated by only a few species. *Poecilus versicolor* provided more than 40% of total individuals, *Carabus auratus* nearly 20% and *Poecilus cupreus* more than 10%. Only eight species could be found on more than 50% of the investigated fields. More than a third of the species could not be found on more than 10% of the investigated fields, 17 species could be found only at one grassland site (Tab. II).

The first axis in the PCA accounted for 25.25 % (eigenvalue: 3.79) of the variance in carabid species composition (Fig. 3), the second axis accounted for 13.77 % (eigenvalue 2.07). Correlations of the environmental variables with the PC axis are given as vectors in the biplot (Fig. 3). The first axis was strongest correlated to medium management intensity and soil moisture described by Ellenberg indicator of moisture (F-Z), the second axis strongest to Ellenberg indicator for pH value (R-Z) and plant species richness.

Tab. III. The results of GRM for Carabid diversity and evenness and for species richness and activity density of the trophic groups, F and p-level, percentage of explained variance (VE) and sign of influence (I) for significant variables and R^2 and p for the whole model. Only significant variables are shown. MI – management intensity, F-Z – Ellenberg indicator for moisture, crop – crop cover in 750 m landscape radius, grassland – grassland cover in 750 m landscape radius

Wyniki GRM dla różnorodności gatunkowej biegaczowatych, jednolitości, bogactwa gatunkowego, łowności poszczególnych grup troficznych, F i poziom p-miary rozproszenia, udział procentowy objaśnionych wariancji i wpływ (I) zmiennych istotnych modelu oraz modele R^2 i p dla całego modelu. Przedstawiono tylko zmienne istotne. MI – intensywność użytkowania, F-Z – liczby Ellenberga dla wilgotności, crop – pokrycie uprawami w promieniu terenu wynoszącym 750 m, grassland – pokrycie łąkami w promieniu terenu wynoszącym 750 m

diversity – różnorodność					evenness – jednolitość			
	F	p	VE	I	F	P	VE	I
MI	4.22	0.026	20.6					
crop	7.51	0.011	18.3	+	8.74	0.006	24.5	+
model R^2	0.43				0.24			
model p	0.002				0.006			
carnivorous species richness bogactwo gatunkowe drapieżników ($\ln x + 1$)					phytophagous species richness bogactwo gatunkowe roślinożerców			
	F	p	VE	I	F	P	VE	I
F-Z	6.32	0.018	19.0	+	6.33	0.018	19.0	–
model R^2	0.19				0.19			
model p	0.018				0.018			
mixophagous activity density łowność gatunków wszystkożernych ($\ln x + 1$)					phytophagous activity density łowność gatunków roślinożernych ($\ln x + 1$)			
	F	p	VE	I	F	P	VE	I
F-Z	4.79	0.038	13.3	+	9.98	0.004	23.2	–
crop					6.99	0.014	16.3	+
grassland	5.18	0.031	14.4	+				
model R^2	0.33				0.40			
model p	0.005				0.001			

There was a clear differentiation between varying preferences of carabid species to soil moisture. Hygrophilous species like *Carabus granulatus*, *Pterostichus vernalis*, *Clivina fossor*, *Agonum mülleri*, *Loricera pilicornis* and *Poecilus cupreus* were orientated towards higher F-Z. *C. auratus*, a thermophilous species, was orientated opposite. The silvicolous species *Pt. burmeisteri* and *C. nemoralis* were orientated towards a lower cover of open landscapes but increasing forest cover. *Pterostichus melanarius* and *Amara familiaris* were orientated to the second PCA axis, which reflected a high pH value and low plant species richness. Additional to moisture requirements preference to different intensity of management and landscape structure might explain orientation of other species.

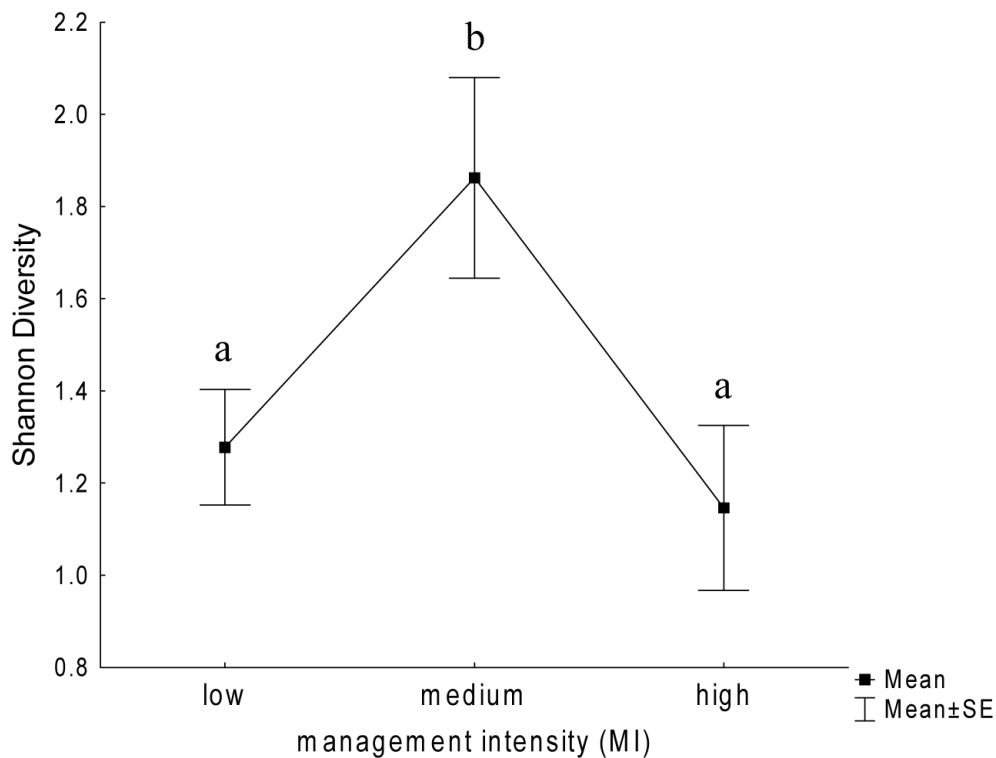


Fig. 2. Mean carabid beetle diversity on grasslands with low, medium and high management intensity. Bars represent standard error. Values with identical letters are not significantly different at the $p < 0.05$ level (Tukey HSD-test)

Ryc. 2. Średnia różnorodność gatunkowa biegaczowatych na łąkach o niskiej, średniej i wysokiej intensywności użytkowania. Grafy obrazują standardowe odchylenie. Wartości oznaczone identycznymi literami nie różnią się znacząco (na poziomie $p < 0.05$, wg. testu HSD Tukey'a)

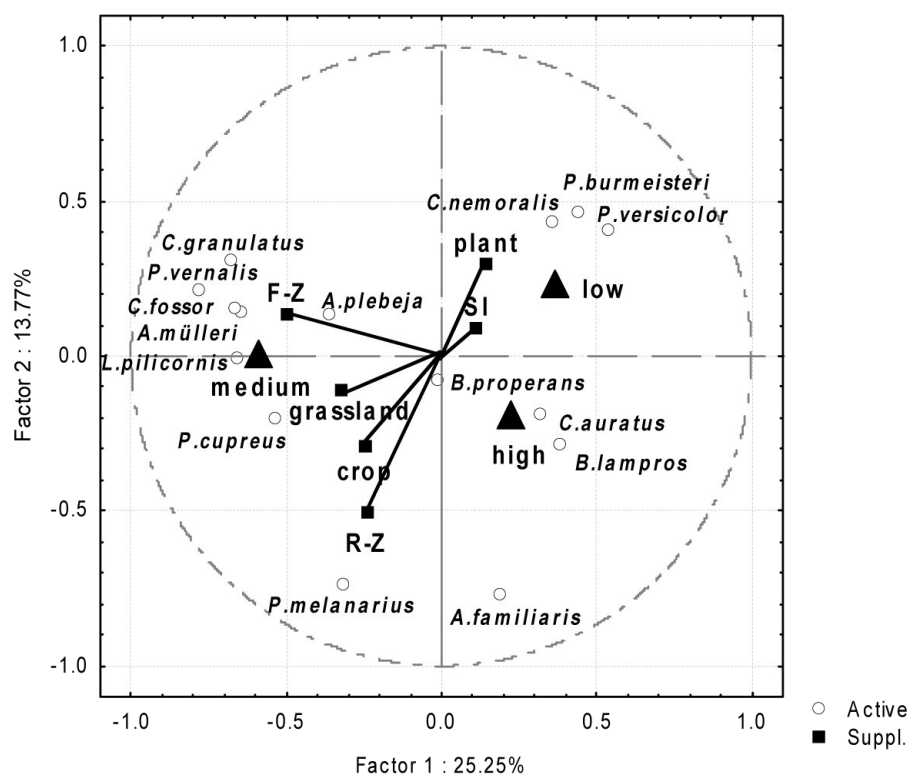


Fig. 3. Ordination diagram showing species scores from the principal component analysis (PCA) of carabid species composition at the 29 study sites. Environmental variables are presented by lines indicating the direction of increasing value. Management intensity classes are indicated by triangles, species are marked with open circles

Ryc. 3. Diagram porządkowy obrazujący wyniki analizy komponentów głównych (PCA) składu gatunkowego biegaczowatych (Carabidae) dla 29 badanych stanowisk. Zmienne środowiskowe są obrazowane przez linie wskazujące kierunek wzrastających wartości. Klasy intensywności użytkowania są oznaczone trójkątami, gatunki pustymi kółkami

Discussion

We found a comparatively high number of carabid species in the grasslands of our study region and a variability of community composition on a single grassland was equally high (Figs. 1 and 3). Carabid diversity was highest on the grassland with medium management intensity. This is in accordance with the medium disturbance theory (CONNELL 1978), which predicts that the presence of specialised grassland species together with generalist and pioneer species will lead to a higher diversity in sites of medium disturbance. Indeed, the total number of carabids and the number of species unique in one of the management classes were higher in medium than in low or high intensity management. Although plant species richness is supposed to

be the highest under medium management intensity as well (PÄRTEL et al. 2007), no impact of plant species richness on carabid diversity or any trophic carabid group was found. This indicates that carabid communities respond to a different spectrum of grassland characteristics than plants (compare KLIMEK et al. 2007). Indeed, the surrounding landscape and soil moisture had an additional strong impact on carabid diversity and on species richness and activity density of different trophic groups.

Cutting and mowing grasslands affects habitat conditions like temperature and soil moisture by changing sward height. Intensive management is related to higher disturbance and degradation of hiding places, low management intensity in contrast leads to strong changes in habitat conditions after mowing. Grasslands with medium management intensity should exhibit smaller annual variation in habitat conditions. This should primarily benefit the species sensitive to disturbance. However, many carabid beetles which are typical of agricultural landscapes are adapted to disturbance and even frequently appear in crop fields (PURTAUF et al. 2004a). This explains a high number of species found even in intensively managed grasslands (Fig. 1) and it also explains the positive influence of high land cover of crop fields in the surroundings on the diversity and evenness of carabid beetles. Even though semi-natural habitats like grasslands are important habitats for breeding and hibernation (e.g. WALLIN 1985; PFIFFNER; LUKA 2000; DUELLI, OBRIST 2003), crop fields are a source of high species richness of generalist carabid beetles enhancing carabid diversity and evenness of grasslands (compare PURTAUF et al. 2004b).

In contrast to carnivorous carabids in crop fields, which are strongly affected by the amount of non-crop habitat in the surrounding landscape (PURTAUF et al. 2005), carnivorous beetles in grasslands of our study region were not affected by landscape composition. Instead, we found a landscape impact on activity density of mixophagous and phytophagous carabid beetles. Mixophagous carabid beetles were more numerous in the areas with high cover of grassland. This seems to be remarkable, because many mixophagous species like *Carabus granulatus* and *Poecilus cupreus* prefer crop fields over grasslands (see DAUBER et al. 2005), although they can reach high densities in both habitats. In areas with a high crop cover, some beetles of these species might change habitat from grassland to crops, whereas in areas with a low crop cover, these species remain in the grasslands reaching higher densities there. Most phytophagous species are xerophilous open land species common in both grasslands and crops (KOCH 1989). Because most of these species are able to fly, they can alter between these habitats very fast. A higher cover of arable land is often associated with higher cover of open landscape in total and this might explain the positive impact of crop cover on density of phytophagous carabids.

Besides landscape composition, habitat characteristics and especially soil moisture affected species richness and activity density of different trophic groups of carabid beetles. A strong influence of soil moisture on habitat selection of ground beetles is well known and has been described by several authors (e.g. THIELE 1977; HOLOPAINEN et al. 1995). The differences between the trophic groups are related to the preference of either moist or dry soils by various common species as indicated by the PCA results (Fig. 3). Dominant mixophagous species *Carabus granulatus* and *Poecilus cupreus* for example were positively affected by high soil moisture and even many carnivorous species preferred high soil moisture, but most of these species are not dominant, which explains an impact of soil moisture on the species number but not on activity density. Most species of the phytophagous *Harpalus* spp. and *Amara* spp. in contrast are xerophile, whereas the group of carnivorous carabids contains more hygrophilous species (KOCH 1989).

The results of our study suggest that plant species richness as a sole indicator of grassland biodiversity might not be sufficient. Nevertheless, moderate management intensity which supports high plant species richness can also increase carabid beetle diversity. We therefore conclude that moderate management intensity is crucial to provide the highest biodiversity of carabid beetles on grasslands in agricultural landscapes. The effects of landscape composition on carabid diversity and composition of trophic groups found indicate a strong interaction between grasslands and other landscape elements such as crop fields and forests. Therefore we suggest that besides management of single fields, the composition and structure of the whole landscape should be taken into consideration in order to sustain a rich species pool of carabid beetles in agricultural landscapes.

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STRZESZCZENIE

Łąki mają duże znaczenie dla zachowania i utrzymania bioróżnorodności w krajobrazie rolniczym. Po to, by zachować zasady zrównoważonej gospodarki krajobrazem i związaną z nim bioróżnorodność, nieodzowny jest ciągły rozwój wiedzy o roli sposobu użytkowania łąk oraz udziale łąk w ogólnym pokryciu terenu. Celem prowadzonych badań było

wykazanie czy istnieje korelacja zróżnicowania składu gatunkowego chrząszczy z rodziny biegaczowatych z typem gospodarowania, warunkami siedliskowymi, strukturą krajobrazu i bogactwem gatunkowym roślin w środowisku łąk antropogenicznych.

Jako że bioróżnorodność łąk jest często oceniana jedynie na podstawie bogactwa gatunkowego roślin naczyniowych, postanowiono ocenić czy rośliny mogą być jednocześnie wskaźnikiem zróżnicowania gatunkowego biegaczowatych w tym środowisku. Dlatego w rejonie środkowych Niemiec dokonano odłowu biegaczowatych na 29 stanowiskach wytyczonych na łąkach różniących się intensywnością użytkowania i warunkami abiotycznymi.

Zróżnicowanie zgrupowań biegaczowatych było największe na łąkach o średnio intensywnym użytkowaniu i zależało od wielkości udziału upraw rolnych w pokryciu otaczającego terenu. Oba czynniki: krajobraz i wilgotność gleby miały wpływ na łowność biegaczowatych uzależnioną również od grup troficznych do których należały chrząszcze. Nie stwierdzono zależności pomiędzy bogactwem gatunkowym roślin a zróżnicowaniem gatunkowym biegaczowatych. Wynik przeprowadzonych studiów zatem sugeruje, że bogactwo gatunkowe roślin nie jest miarodajnym wskaźnikiem bioróżnorodności łąk. Jednakże, umiarkowana intensywność użytkowania z połączeniem z wysokim bogactwem gatunkowym roślin może wpływać na wzrost różnorodności gatunkowej również biegaczowatych.

Dlatego stwierdzono, że umiarkowana intensywność użytkowania jest kluczowa dla zachowania najwyższej bioróżnorodności chrząszczy z rodziny biegaczowatych bytujących w środowiskach łąkowych. Mając na uwadze wpływ krajobrazu na zgrupowania biegaczowatych, by zachować cały potencjalny skład gatunkowy biegaczowatych w zrównoważonym gospodarowaniu łąkami pod uwagę należy brać kompozycję i strukturę otaczającego krajobrazu rolniczego.

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KAPITEL 2

CONTRASTING DIVERSITY PATTERNS OF EPIGEIC ARTHROPODS BETWEEN GRASSLANDS OF HIGH AND LOW AGRONOMIC POTENTIAL

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Contrasting diversity patterns of epigeic arthropods between grasslands of high and low agronomic potential

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Abstract

Increasing demand for food, fuel and fibre promotes the intensification of land-use, particularly in areas favourable for agricultural production. In less-favourable areas, more wildlife-friendly farming systems are often either abandoned or under pressure of conversion, e.g. for bioenergy production. This raises the question, to which extent areas of different agronomic potential contribute to regional biodiversity. To approach this question on a regional scale, we established our study within a region where sites of high and low agronomic potential (AP) alternate on a small spatial scale. We selected 13 high-AP and 13 low-AP grasslands to quantify the contribution of these classes to the regional diversity of four epigeic arthropod taxa (ants, springtails, functional groups of ground beetles, and spiders). The regional diversity (γ) was partitioned into species richness per site (α -diversity), diversity among sites within one class (β_{within} -diversity), and diversity between the two classes ($\beta_{between}$ -diversity). The β -diversity generally accounted for the largest share of the γ -diversity, with patterns of diversity components being highly taxon- and class-specific. Carnivorous carabids had a higher α -diversity at high-AP sites. Ants, springtails, and cursorial spiders had a higher β_{within} -diversity in low-AP grasslands. Low-AP sites also harboured many more species that occurred exclusively in one grassland class. We conclude that grasslands that may be unfavourable for agricultural production contributed more to regional diversity of epigeic arthropods than favourable grasslands. We therefore suggest that future agricultural schemes should promote arthropod biodiversity by specifically targeting agri-environment schemes or other wildlife-friendly farming approaches to areas of low agronomic potential, since this bears the greatest potential to preserve a comparatively high species turnover (β -diversity) and in consequence high regional diversity.

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Zusammenfassung

Der steigende Bedarf an Lebensmitteln, Energie und Rohstoffen fördert die Intensivierung der Landnutzung, insbesondere in Gebieten, die günstig für landwirtschaftliche Produktion sind. In weniger geeigneten Gebieten werden umweltfreundlichere Bewirtschaftungssysteme häufig entweder aufgegeben, oder laufen Gefahr, z.B. für die Produktion von Bioenergie, umgewandelt zu werden. Dies wirft die Frage auf, welchen Beitrag Gebiete mit

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unterschiedlichem ackerbaulichen Ertragspotential zur regionalen Biodiversität leisten. Um dieser Frage auf regionaler Ebene nachzugehen, haben wir unsere Studie in einen Landkreis durchgeführt, in dem Flächen mit hohem und niedrigem Ertragspotential (AP) auf kleiner räumlicher Skala wechseln. Wir haben jeweils 13 Grünlandflächen mit hohem und niedrigem AP ausgewählt, um den Beitrag dieser Klassen zur regionalen Diversität von vier Arthropodengruppen (Ameisen, Springschwänze, funktionelle Gruppen von Laufkäfern und Spinnen) zu quantifizieren. Die regionale Diversität (γ) wurde unterteilt in den Artenreichtum pro Fläche (α), die Diversität zwischen den Flächen innerhalb einer Klasse (β_{within}) und zwischen den Klassen ($\beta_{between}$). Die β -Diversität hatte insgesamt den größten Anteil an der γ -Diversität, wobei die Anteile der Diversitätskomponenten sowohl tiergruppen- als auch klassenspezifisch waren. Die karnivoren Laufkäfer hatten eine höhere α -Diversität in hoch-AP Flächen. Die β_{within} -Diversität von Ameisen, Springschwänzen und laufaktiven Spinnen war größer in niedrig-AP Grünländern. Die niedrig-AP Flächen erbrachten außerdem einen deutlich höheren Anteil von Arten, die in nur einer Grünlandklasse gefunden wurden. Wir schlussfolgern, dass Grünländer, die ungünstiger für die landwirtschaftliche Produktion sind, mehr zur regionalen Diversität epigäischer Arthropoden beitragen als Grünländer in Gunstlagen. Daher schlagen wir vor, in zukünftigen Agrar-Umweltprogrammen die Biodiversität von Arthropoden insbesondere durch den Schutz von Flächen mit einem niedrigen Ertragspotential zu erhalten, da dies den höchsten Arten-‘turnover’ (β -Diversität) gewährleistet.

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Keywords: Agri-environmental schemes; Diversity partitioning; Species turnover; Alpha and beta diversity

Introduction

Due to the increasing demand for food, fuel, and fibre (Millennium Ecosystem Assessment 2005), agricultural management is intensified in areas favourable for agriculture, in order to optimize productivity. In contrast, more wildlife-friendly traditional farming systems in areas less suitable for agriculture are often abandoned (Strijker 2005) or under pressure of conversion for bioenergy production (Campbell, Lobell, Genova, & Field 2008). Counteracting the negative impacts of those trends is essential to protect biodiversity in European agricultural landscapes. Policy instruments such as providing subsidies to farmers for environmentally friendly agricultural practices in the form of agri-environmental schemes (AES) have recently been questioned with regard to their effectiveness in producing ecological benefits to farmland (Kleijn et al. 2006). Several studies have shown that the response of biodiversity to AES or Common Agricultural Policy in general is landscape and/or region specific (Kleijn & Sutherland 2003; Gottschalk et al. 2007) and AES are not targeted enough to effectively halt biodiversity losses in the respective regions (Wrbka, Schindler, Pollheimer, Schmitzberger, & Peterseil 2008). Large-scale schemes are therefore often not very efficient in protecting arthropod diversity (Kleijn et al. 2006). A better understanding of biophysical properties and their relation to patterns of regional diversity is therefore prerequisite to developing regionally aligned policy guidelines that successfully protect biodiversity (Fischer et al. 2008).

We compared the contribution of grasslands with a high agronomic potential (AP) and grasslands with a

low AP to the regional species pool of abundant epigeic arthropod taxa (ants, springtails, carabid beetles, spiders). Diversity partitioning (Lande 1996) was applied to understand regional diversity patterns of these taxa. This analysis partitions the regional diversity into (i) α -diversity, being the mean species richness per site; (ii) β -diversity, being the variance of species richness between the sites and a measure of variance in species composition; and (iii) γ -diversity, being the total species richness across all sites (Veech, Summerville, Crist, & Gering 2002). We further separated β -diversity into two components: diversity among sites within one class (β_{within}) and diversity between high-AP and low-AP sites ($\beta_{between}$). We focused on grasslands, because these habitats are specifically threatened by land-use change and subsequent loss of biodiversity (<http://faostat.fao.org/>). In particular, we addressed three questions: (i) Do high- and low-AP grasslands differ in their α - and β -diversity components, depending on the taxon? (ii) Do low-AP sites contribute more to the regional γ -diversity than high-AP sites? (iii) Would it be possible to derive recommendations for the targeting of conservation efforts for arthropod diversity based on the agronomic potential of the sites?

Methods

Study region and site selection

The study was carried out in the rural district of Northeim, Lower Saxony, Germany (approximate north-south boundaries 51°55'–51°61'N), which covers

a total area of approximately 1260 km². The mean annual temperature of this region is 8.7°C and the average precipitation amounts to 645 mm per year. The region is dominated by arable land and forest, interspersed with patchily distributed managed grassland. The natural agronomic potential quantifies the potential yield (dt/ha) of a site without melioration. It is derived from an integration of several abiotic factors, e.g. soil type, bulk density, humus content, clay content, moisture, groundwater level, temperature, and precipitation. In Lower Saxony the agronomic potential is classified into seven categories ranging between extremely high and extremely low (Müller 2004; http://www.lbeg.niedersachsen.de/master/C42411148_N42376049_L20_D0_I31802357.html) and varies in the region on a small spatial scale. Thirteen grassland sites of very high AP and 13 of low to medium AP were included in our study. Sites were spread over the study region with a minimum distance of 700 m between two sites. The mean distance to the nearest neighbour in high-AP sites was 4830.3 m (SD: ± 4118.5) and 3034.7 m (± 2098.7) in low-AP sites. Sites were not paired and located within several non-connected clusters of high- and low-AP.

Environmental factors

Elevation (m a.s.l.) and slope angle (deg) of study sites were derived from a digital elevation model with a grid size of 12.5 m. We also measured soil pH (extracted in H₂O) following established protocols. According to the answers of the farmers to a standardized questionnaire, the study sites cover a gradient of management intensity, ranging from intensively used, frequently mown meadows with high fertilizer input to semi-natural pastures with no additional fertilization and low stocking rates. Meadows ($n = 11$) were cut one to four times a year and included fertilized as well as unfertilized sites. All mown pastures ($n = 15$) were fertilized with mineral nitrogen, farmyard manure or liquid manure. Management included rotational grazing at low to medium intensity between May and September to November with additional cuttings one to three times a year. Grazing intensity was estimated as standard livestock unit days per hectare and year. Three variables characterizing the landscape in a 2 km radius around the center of each study site were calculated using Arc View GIS (Version 3.2, ESRI Inc., Redlands, California): percentage of (i) permanent grassland, (ii) arable land, and (iii) forest. Data on topography, management, and the surrounding landscape were obtained from the Research Center for Agriculture and the Environment, Göttingen (see Klimek, Marini, Hoffmann, & Isselstein 2008 for details).

Sampling

We used a standardized sampling scheme with the same number of traps per site for each arthropod group. Ants, carabids, and spiders were sampled using four large pitfall traps (diameter 85 mm); epigeic springtails were sampled by means of eight small pitfall traps (diameter 30 mm) at each site. The latter have proven to provide reliable estimates of species richness for springtails (Winklehner, Winkler, & Kampichler 1997). Traps were established with a minimum distance of 10 m to field edges. The distance between traps was 20 m for large and 10 m for small traps. All traps were exposed for five days at the end of July 2005. Large traps were additionally exposed for 12 days at the beginning of May 2006, but determination of invertebrates was restricted to carabids and ants. Traps were filled with 100 ml (large traps) or 15 ml (small traps) of a 50% ethylene glycol/water solution. All taxa were determined to species level (ants: Seifert (2007); spiders: Heimer and Nentwig (1991); carabids: Freude (1976); springtails: Gisin (1960); Fjellberg (1980); and Potapow (2001)). Spider species were categorized as 'cursorial' or 'web-building' (Uetz, Halaj, & Cady 1999). Carabid species were further classified as phytophagous or carnivorous according to Luff (1998), Lindroth (1985/86), and Ribera, Doledec, Downie, and Foster (2001). Ant and carabid data of the two sampling periods were pooled. Species richness of springtails is given as the total number of species found in all eight traps per site.

Data analysis

For each taxon, the total number of species observed at all sites was γ_{regio} . This component can be partitioned as follows (Clough et al. 2007):

$$\gamma_{\text{regio}} = \alpha + \beta_{\text{within}} + \beta_{\text{between}}$$

$$\alpha = \frac{1}{n} \sum_{ij} \alpha_{ij}$$

$$\beta_{\text{within}} = \frac{1}{n} \sum_{ij} (y_i - \alpha_{ij})$$

$$\beta_{\text{between}} = \frac{1}{N} \sum_{ij} (y_{\text{regio}} - y_i)$$

with α is the mean species richness per site, β_{within} the mean diversity among sites within one class, and β_{between} the mean diversity between the two classes (high-AP, low-AP). N is the number of classes ($= 2$) and n the total number of sites ($= 26$), i is the identifier for the class (high-AP, low-AP), and j the identifier for sites within the classes (from 1 to 13).

Since not all data met the assumptions of parametric statistical tests, we used permutational analyses of variance (PERMANOVA, Anderson 2001, McArdle & Anderson 2001) based on Euclidean distances to test for differences in environmental factors, α - and β_{within} -diversity between high-AP and low-AP sites. Since topographic, management, soil, and landscape factors were strongly dependent on each other, we abstained

from relating individual factors to α - and β_{within} -diversity. PERMANOVA's were calculated using the software PAST 1.77 (Hammer, Harper, & Ryan 2001). Furthermore, we calculated the percentage of species that occurred exclusively in one of the two classes. A chi square statistic was used to test for differences in exclusive versus non-exclusive species between the two classes.

Table 1. Environmental factors of grasslands with high ($n = 13$) and low ($n = 13$) agronomic potential (AP).

	High-AP				Low-AP				$F_{[1, 24]}$	P
	Mean (SE)	CV	Median	Min–Max	Mean (SE)	CV	Median	Min–Max		
Elevation (m)	149 (12.8)	0.3	146.7	102.0–265.0	260.6 (15.2)	0.2	268.0	161.0–328.0	31.6	***
Slope (deg)	3.9 (1.4)	1.2	1.7	0.2–13.4	7.4 (0.8)	0.4	7.2	3.1–13.9	4.7	*
Stocking rate	60.1 (23.6)	1.4	0.0	0.0–266.7	112.5 (33.4)	1.1	74.2	0.0–326.5	–	ns
Cuts per year	2.2 (0.3)	0.4	3.0	1.0–3.0	1.8 (0.3)	0.6	1.0	1.0–4.0	–	ns
N fertilization	128.9 (22.4)	0.6	137.0	0.0–286.4	91.6 (23.1)	0.9	91.1	0.0–252.1	–	ns
pH	6.3 (0.3)	0.2	6.9	4.7–7.4	5.6 (0.2)	0.1	5.3	4.8–7.2	–	ns
% Arable land	42.9 (3.5)	0.3	44.6	23.7–66.2	26.9 (0.4)	0.8	21.4	0.0–81.2	5.2	*
% Grassland	13 (1.4)	0.4	13.4	5.8–22.2	10.7 (1.6)	0.5	9.9	3.8–22.8	–	ns
% Forest	25.5 (3.2)	0.5	23.9	2.7–45.2	49.5 (7.2)	0.5	50.5	0.4–94.6	9.3	**

PERMANOVA results (F - and P -values) for differences between the two classes are given. Stocking rate = standard livestock unit days per hectare and year, Nitrogen fertilization = kg N ha⁻¹ year⁻¹; NS = non significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; SE = standard error; CV = coefficient of variation.

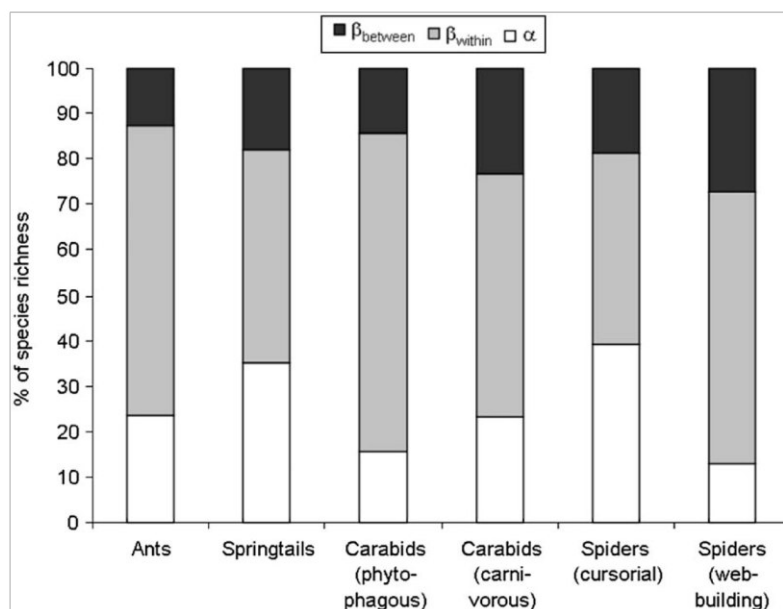


Fig. 1. Diversity components for ants, springtails, phytophagous carabids, carnivorous carabids, cursorial spiders, and web-building spiders in grasslands with high ($n = 13$) and low ($n = 13$) agronomic potential. α : mean species richness per site; β_{within} : mean diversity within sites of one class; $\beta_{between}$: mean diversity between the two classes.

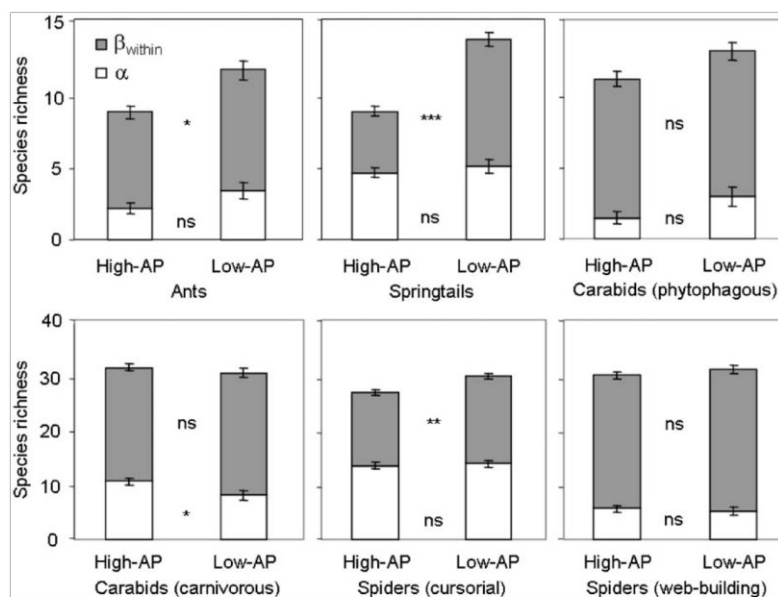


Fig. 2. Diversity components for ants, springtails, phytophagous carabids, carnivorous carabids, cursorial spiders, and web-building spiders in grasslands with high ($n = 13$) and low ($n = 13$) agronomic potential (AP). α : mean species richness per site; β_{within} : mean diversity within sites of one class. ns = non significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; Error bars are $\pm$ SE of the means.

Results

Altogether, high- and low-AP grasslands had a high variation in environmental factors. However, grasslands of the two AP categories differed significantly in their topography and the surrounding landscape. Elevation ranged from 102 to 328 m above sea level and the slope varied between 0.2° and 13.9° , with low-AP sites being located at significantly higher altitudes and on slopes with a significantly steeper incline. Low-AP sites had a higher share of forests and a lower share of arable land in their immediate surroundings. All three management-related factors showed a high variation in both classes, but we did not find any significant differences between the classes (Table 1).

A total of 12 ant species (1043 individuals), 14 epigeic springtail (2933 individuals), 55 carabid (3774 individuals), and 77 spider species (13,796 individuals) were identified (see Appendix A). Among the carabids, 14 species were phytophagous (101 individuals) and 41 were carnivorous (3673 individuals). Spiders could be separated into 35 cursorial (13,471 individuals) and 42 primarily web-building species (325 individuals). The median of species richness per site was 2 (min–max: 0–8) for ants, 5 (2–10) for epigeic springtails, 2 (0–8) for phytophagous carabids, 8.5 (4–16) for carnivorous carabids, 14 (9–18) for cursorial spiders, and 5 (2–10)

for web-building spiders. Calculation of the different diversity components revealed that the contribution of species richness per site to total diversity was very low for web-building spiders and phytophagous carabids, and particularly high for cursorial spiders (Fig. 1).

In general, the β -components accounted for the largest proportion of total diversity of all groups. Despite the pronounced differences in environmental conditions, diversity within the classes (β_{within} -diversity) contributed more to total diversity than heterogeneity between the two classes ($\beta_{between}$ -diversity; Fig. 1). The share of $\beta_{between}$ -diversity was highest for web-building spiders (25.6%) and lowest for ants (12.5%). Carnivorous carabids were the only group for which species richness per site was significantly different between the classes (Fig. 2). Average species richness of this group was significantly higher at high-AP sites (high-AP: 10.4 ± 2.7 ; low-AP: 8.2 ± 3.3). Diversity of sites within one class (β_{within} -diversity) differed significantly between high- and low-AP grasslands, with values being higher for low-AP sites for ants, springtails, and cursorial spiders. Altogether, low-AP sites contributed more to regional diversity than high-AP sites (Fig. 2).

By averaging across sites or site classes, the diversity components do not consider the number of species that were exclusively found in a certain class. These species

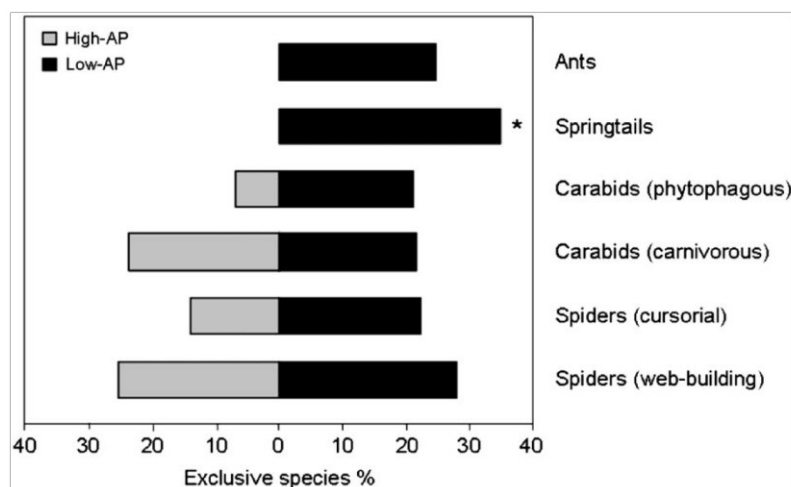


Fig. 3. Share of ant, springtail, phytophagous carabid, carnivorous carabid, cursorial spider, and web-building spider species, found exclusively in agricultural grasslands with high ($n = 13$) and low ($n = 13$) agronomic potential (AP). Significant differences between the two classes are marked. * $P < 0.05$.

may be of particular interest when considering the conservation of overall diversity. In fact, one-fourth of all ant species and about one-third of all springtail species only occurred at low-AP sites (Fig. 3). The number of exclusive phytophagous carabid (low-AP: 3; high-AP: 1) and cursorial spider species (low-AP: 8, high-AP: 5) was higher in low-AP sites. In contrast, the number of exclusive carnivorous carabid and web-building spider species was almost identical in both classes (Fig. 3). However, only the number of exclusive springtail species differed significantly between the two classes ($P < 0.05$).

Discussion

Our results highlight the fact that studies focusing on α - or β -diversity may differ substantially in terms of their conclusions and recommendations for policy makers. The study sites covered a range of environmental conditions, but we still found surprisingly little difference in α -diversity (species richness per site) between high- and low-AP areas. In contrast, β_{within} -diversity (diversity within classes) was higher for three arthropod groups in low-AP sites and those sites also harboured a higher share of exclusive species. Grasslands of low agricultural productivity therefore contributed more to the regional diversity of epigeic arthropods than highly productive sites. In addition to species richness per site (α -diversity), species turnover (β -diversity) is thus a valuable complement for managing biodiversity on regional scales in agricultural landscapes (Gering, Crist, & Veech 2003).

Patterns of species richness per site (α -diversity) were strongly group-specific. Springtail species are rather ubiquitous with limited effects of agricultural management on diversity (Brennan, Fortune, & Bolger 2006; Chauvat, Wolters, & Dauber 2007). This is reflected by a large contribution of species richness per site in springtails. Diversity of cursorial spiders was also characterized by high species richness per site. Species from this functional group may have less specific and narrow habitat needs than e.g. carabids (Eyre & Woodward 1996). However, differences in environmental conditions did not result in differences in species richness of high- and low-AP sites in most arthropod groups. Only carnivorous carabids had significantly higher species richness at sites that were favourable for agriculture. This group generally reaches a high species richness in arable land (Dauber, Purtauf, Allsach, Frisch, Voigtlander, et al. 2005) and depending on the landscape context species numbers in grasslands may even increase with the share of arable land due to spill-over effects (Rand, Tylianakis, & Tscharntke 2006).

The main objective of preserving an overall high regional diversity (γ) can be achieved by conserving either α , or β , or both depending on the contribution of the two diversity components to the regional diversity. Species richness per site accounted for a small fraction of total species richness in all groups as compared to β -diversity. This also holds true for diversity patterns of vascular plants in grasslands in the same study region (Klimek et al. 2008) and is in accordance with other studies on other plant and animal taxa (Gabriel, Roschewitz, Tscharntke, & Thies 2006; Clough et al. 2007). Crist (2008), for example, reports a constant

turnover of 75% in species composition of ant communities across a wide range of habitats. Variance in species composition (β -diversity) could reflect, e.g., habitat conditions, dispersal ability, and management-related differences, which may increase regional heterogeneity (Crist & Veech 2006).

The grasslands studied here were quite heterogeneous (see CV in Table 1), covering a wide range of habitat conditions and management regimes, resulting in a high species turnover between sites within classes (β_{within} -diversity). The high contribution of diversity within the classes in web-building spiders may reflect the limited short-range mobility of this group. Although long-range dispersal (ballooning) is common among web-building species, web-site search tends to be characterized by short-range walking bouts. Many common spider species are able to recolonize disturbed grasslands quickly (e.g. after cutting; Birkhofer, Scheu, & Wise 2007), whereas less-abundant species may only persist if a site provides specific conditions or remains undisturbed. Therefore, species composition may reflect variation in site conditions and diversity may be added by different management regimes between sites (e.g. Schmidt, Roschewitz, Thies, & Tschardtke 2005; Birkhofer, Fließbach, Wise, & Scheu 2008). However, data on web-building spiders are limited due to the use of pitfall traps and a bias towards web-building linyphiids. Diversity within classes was higher in low-AP grasslands for ants, springtails, and cursorial spiders. This is consistent with studies that found a high diversity of plants and arthropods in traditional, low-input systems in marginal areas (Bignal & McCracken 1996; Kleijn et al. 2009). The higher diversity of ants within low-AP grasslands may be attributed to the steeper locations on slopes, which result in more heterogeneous microclimates and soil conditions. Insolation (Kaspari, Alonso, & O'Donnell 2000; Dauber et al. 2005) and soil attributes (Boulton, Davies, & Ward 2005; Dahms, Wellstein, Wolters, & Dauber 2005) are important factors for ant communities, and many Central European species prefer warm and dry habitats (Seifert 2007). Springtail diversity may be affected positively by low-AP sites, as the percentage of forest in the vicinity is generally higher. Springtails are known to be most diverse in forest-rich and heterogeneous landscapes (Sousa et al. 2006).

Differences in diversity patterns between the two grassland classes ($\beta_{between}$ -diversity) are most likely attributable to differences in the surrounding landscape structure and topography. Sites with a low agronomic potential were located at higher altitudes and on steeper slopes, the latter resulting in higher contrasts in microclimatic conditions. Due to the lower profitability of agriculture in these areas, low-AP sites were primarily surrounded by forest. In contrast, sites with high AP were mainly embedded in arable land. However, low-AP

sites covered a larger variability with respect to composition of their surrounding landscape than high-AP sites (Table 1). Thus, the higher β_{within} -diversity might also be attributed to the overall higher heterogeneity of landscape and microclimates within the low-AP class.

Recent studies suggested that increased landscape heterogeneity and habitat connectivity or reduced management intensity may promote the conservation of arthropod diversity (Clough, Kruess, & Tschardtke 2007; Hendrickx et al. 2007). These concepts primarily aiming at promoting α -diversity should be coupled with targeted concepts for promoting high β -diversity taking landscape dissimilarity within a region into account.

Conclusions

Fischer et al. (2008) pointed out that the feasibility and appropriateness of wildlife-friendly farming depend on the landscape's biophysical properties and socio-economic conditions. Regionally aligned policy guidelines are therefore needed to reduce the negative impact of intensified agriculture and land-use change on biodiversity. Our results suggest that regional diversity patterns of epigeic arthropods in grasslands can be related to the agronomic potential of the sites. We conclude that in regions of high landscape dissimilarity, targeting AES or outcome-based schemes for environmental services (Bertke, Gerowitt, Hespelt, Isselstein, Marggraf, et al. 2005) to areas with a low agronomic potential would conserve more species than an undirected scheme covering a whole region. AES specifically tailored for such unfavourable areas are needed to maintain farming in the areas threatened by abandonment and at the same time secure food production in the areas favourable for farming.

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Appendix A. Supporting Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2009.06.004.

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ZUSÄTZLICHES INFORMATIONSMATERIAL:ZU

Contrasting diversity patterns of epigeic arthropods between grasslands of high and low agronomic potential (2010) Basic and Applied Ecology 11, 6-14
(Verfügbar online auf der Homepage des Journals)

Appendix A Number of sites occupied by the respective species of ants, springtails, phytophagous carabids, carnivorous carabids, cursorial spiders and web-building spiders sampled in high-AP (n= 13) and low-AP (n= 13) grasslands. The agronomic potential (AP) quantifies the natural capacity of a site, i.e. its potential yield without any melioration techniques, integrating water availability, potential nutrient supply, soil characteristics, and climate.

	High-AP	Low-AP
Ants		
<i>Formica cunicularia</i>	0	1
<i>Formica fusca</i>	1	1
<i>Formica rufa</i>	0	1
<i>Lasius</i> sp.	1	1
<i>Lasius flavus</i>	1	2
<i>Lasius niger</i>	10	10
<i>Myrmica rubra</i>	10	11
<i>Myrmica ruginodis</i>	2	1
<i>Myrmica rugulosa</i>	0	2
<i>Myrmica sabuleti</i>	1	5
<i>Myrmica scabrinodis</i>	2	6
<i>Myrmica specioidea</i>	1	4
Springtails		
<i>Desoria olivacea</i>	8	7
<i>Dicyrtoma fusca</i>	0	1
<i>Dicyrtomina minuta</i>	1	3
<i>Entomobrya multifasciata</i>	0	2
<i>Isotoma antennalis</i>	0	1
<i>Isotoma palustris</i>	1	1
<i>Isotoma viridis</i>	12	13
<i>Lepidocyrtus curvicolis</i>	5	1
<i>Lepidocyrtus cyaneus</i>	10	12
<i>Lepidocyrtus lanuginosus</i>	10	10
<i>Orchesella villosa</i>	1	1
<i>Pogonognathellus flavescens</i>	0	1
<i>Sminthurus viridis</i>	13	13
<i>Tomocerus</i> sp.	0	1
Carabids (phytophagous)		
<i>Amara aenea</i>	1	5
<i>Amara communis</i>	1	4
<i>Amara familiaris</i>	4	5
<i>Amara lunicollis</i>	1	3
<i>Amara montivaga</i>	0	3
<i>Amara ovata</i>	0	1
<i>Amara plebeja</i>	5	3
<i>Amara similata</i>	1	2
<i>Anisodactylus binotatus</i>	1	5
<i>Harpalus affinis</i>	1	1

<i>Harpalus latus</i>	2	2
<i>Harpalus rufipes</i>	1	3
<i>Harpalus tardus</i>	0	1
<i>Zabrus tenebrioides</i>	1	0
Carabids (carnivorous)		
<i>Agonum mülleri</i>	10	3
<i>Agonum piceum</i>	1	0
<i>Agonum sexpunctatum</i>	1	2
<i>Agonum viduum</i>	4	0
<i>Agonum viridicupreum</i>	1	0
<i>Asaphidion flavipes</i>	1	1
<i>Bembidion biguttatum</i>	6	0
<i>Bembidion gilvipes</i>	0	1
<i>Bembidion guttula</i>	1	2
<i>Bembidion lampros</i>	4	12
<i>Bembidion lunulatum</i>	1	1
<i>Bembidion obtusum</i>	0	1
<i>Bembidion properans</i>	6	2
<i>Bembidion quadrimaculatum</i>	3	0
<i>Bembidion tetracolum</i>	2	1
<i>Calathus fuscipes</i>	0	4
<i>Carabus auratus</i>	5	6
<i>Carabus convexus</i>	1	0
<i>Carabus granulatus</i>	11	6
<i>Carabus nemoralis</i>	9	9
<i>Claenius nigricornis</i>	3	0
<i>Clivina fossor</i>	9	4
<i>Dyschirius globosus</i>	2	1
<i>Loricera pilicornis</i>	7	3
<i>Microlestes maurus</i>	0	1
<i>Notiophilus aquaticus</i>	0	1
<i>Notiophilus biguttatus</i>	0	1
<i>Notiophilus palustris</i>	3	2
<i>Oodes helopioides</i>	2	0
<i>Platynus assimile</i>	0	4
<i>Platynus dorsalis</i>	0	1
<i>Poecilus versicolor</i>	10	13
<i>Pterostichus anthracinus</i>	3	0
<i>Pterostichus burmeisteri</i>	1	6
<i>Pterostichus melanarius</i>	10	9
<i>Pterostichus niger</i>	2	1
<i>Pterostichus nigrita</i>	3	1
<i>Pterostichus oblongopunctatus</i>	0	2
<i>Pterostichus strenuus</i>	5	2
<i>Pterostichus vernalis</i>	12	4
<i>Trechoblemus micros</i>	1	0
Spiders (cursorial)		
<i>Alopecosa cuneata</i>	6	11
<i>Alopecosa pulverulenta</i>	11	13
<i>Antistea elegans</i>	1	0
<i>Apostenus fuscus</i>	1	0
<i>Aulonia albimana</i>	0	1
<i>Clubiona reclusa</i>	0	1

<i>Coelotes inermis</i>	1	1
<i>Coelotes terrestris</i>	0	1
<i>Dysdera erythrina</i>	1	0
<i>Erigone atra</i>	12	10
<i>Erigone dentipalpis</i>	12	7
<i>Hahnia nava</i>	5	3
<i>Hahnia pusillus</i>	1	0
<i>Micaria pulicaria</i>	0	1
<i>Oedothorax apicatus</i>	4	2
<i>Oedothorax fuscus</i>	11	9
<i>Oedothorax retusus</i>	13	10
<i>Pachygnatha clercki</i>	11	9
<i>Pachygnatha degeeri</i>	13	13
<i>Pardosa alacris</i>	0	1
<i>Pardosa amentata</i>	13	12
<i>Pardosa palustris</i>	13	12
<i>Pardosa pullata</i>	13	13
<i>Pirata piraticus</i>	1	0
<i>Trochosa ruricola</i>	10	6
<i>Trochosa spinipalpis</i>	3	1
<i>Trochosa terricola</i>	8	13
<i>Xysticus audax</i>	0	1
<i>Xysticus bifasciatus</i>	0	2
<i>Xysticus cristatus</i>	5	13
<i>Xysticus kochi</i>	2	6
<i>Xysticus ulmi</i>	1	2
<i>Zelotes latreillei</i>	1	4
<i>Zelotes lutetianus</i>	0	1
<i>Zelotes pusillus</i>	3	2

Spiders (web-building)

<i>Areaoncus humilis</i>	2	2
<i>Baryphyma pratenese</i>	2	0
<i>Bathypantes gracilis</i>	9	5
<i>Centromerita bicolor</i>	4	4
<i>Centromerus prudens</i>	0	1
<i>Ceratinella brevis</i>	4	4
<i>Dicymbium nigrum</i>	10	9
<i>Diplocephalus latifrons</i>	1	0
<i>Diplostyla concolor</i>	3	1
<i>Enoplognatha thoracica</i>	2	1
<i>Eperigone trilobata</i>	0	1
<i>Erigone longipalpis</i>	1	0
<i>Erigonella hiemalis</i>	2	3
<i>Gongylidiellum vivum</i>	3	3
<i>Halorates distinctus</i>	2	0
<i>Harpactea lepida</i>	0	2
<i>Lepthyphantes pallidus</i>	1	0
<i>Leptorhoptrum robustum</i>	3	0
<i>Meioneta rurestris</i>	0	1
<i>Meioneta beata (affinis)</i>	0	2
<i>Micrargus herbigradus</i>	2	1
<i>Microlinyphia pusilla</i>	0	1
<i>Milleriana inerrans</i>	1	1
<i>Panamomops sulcifrons</i>	0	2

<i>Pelecopsis parallela</i>	1	2
<i>Porrhomma campbelli</i>	1	1
<i>Porrhomma errans</i>	1	0
<i>Porrhomma lativelum</i>	0	1
<i>Porrhomma oblitum</i>	0	1
<i>Porrhomma pygmaeum</i>	1	1
<i>Savignya frontata</i>	1	0
<i>Stemonyphantes lineatus</i>	0	1
<i>Tallusia experta</i>	1	0
<i>Tapinocyba pallens</i>	0	1
<i>Tenuiphantes tenuis</i>	3	4
<i>Tiso vagans</i>	7	7
<i>Troxochrus scabriculus</i>	1	0
<i>Walckenaeria acuminata</i>	1	1
<i>Walckenaeria antica</i>	1	1
<i>Walckenaeria cuspidata</i>	0	1
<i>Walckenaeria obtusa</i>	1	1
<i>Walckenaeria vigilax</i>	1	0

KAPITEL 3

TRAIT-SPECIFIC EFFECTS OF HABITAT ISOLATION ON CARABID SPECIES RICHNESS AND COMMUNITY COMPOSITION IN MANAGED GRASSLANDS

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Trait-specific effects of habitat isolation on carabid species richness and community composition in managed grasslands

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Abstract. 1. Isolation of natural and semi-natural habitats, a consequence of increasing management intensification, has been identified as a major threat to the diversity of many taxa in agricultural landscapes. Yet, it is increasingly apparent that the effects of habitat isolation vary not only among distantly but also closely related taxa, depending on their respective ecological traits.

2. We studied the effects of habitat isolation on carabid beetles with different dispersal potential in common perennial grasslands. The grasslands belonged to three isolation classes: (i) situated in a continuous belt of grasslands, (ii) in an arable matrix but connected to the continuous belt via corridors or (iii) completely isolated in the arable matrix.

3. Neither total carabid species richness nor richness of carabids with high dispersal potential was affected by habitat isolation. In contrast, richness of carabid species with low dispersal potential was more than two times lower in isolated than in continuous grasslands. Communities of isolated sites were characterised by species with high dispersal potential whereas species with low dispersal potential were associated with continuous or well connected grasslands.

4. Our results revealed trait-specific responses of carabids to habitat isolation and highlight the need for considering these differences when predicting effects of landscape structure on carabid diversity. Grassy corridors seemed to assist the dispersal of carabids with low dispersal potential, thereby allowing these species to persist also in non-continuous but connected habitats. Thus, corridors represent a suitable measure to maintain the diversity of carabids in spatially structured grasslands in agricultural landscapes.

Key words. Agricultural landscapes, connectivity, corridors, dispersal potential.

Introduction

The intensification of agriculture during the past decades reduced the structural heterogeneity of landscapes and induced a decrement and isolation of natural and semi-natural habitats in agricultural regions of Europe (e.g. Stoate *et al.*, 2001). Because many species in agricultural landscapes depend on less intensively managed land-use types, changes in diversity, cover-

age, size and isolation of these habitats often result in a decline of biodiversity in agroecosystems (e.g. Stoate *et al.*, 2001). Yet, the extent to which species are affected by these factors is often trait-specific (e.g. Batary *et al.*, 2007; Jauker *et al.*, 2009).

Habitat isolation disrupts species distribution patterns and forces dispersing individuals to traverse a matrix that separates suitable habitat fragments from each other. Thereby, the success of inter-patch dispersal will not only depend on the distance but also on the kind of matrix that separates these habitat elements (Ricketts, 2001). Yet, effects of distance and matrix on patch isolation are also trait-specific (Kindlmann & Burel, 2008). The same landscape may be perceived differently by species with similar movement abilities but differing in resource requirements

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(Jauker *et al.*, 2009) or species with similar resource requirements but different dispersal potential (Collinge, 2000). In any case, trait-specific differences among species may result in different dispersal patterns and different conservation measures that will enhance species persistence.

Dispersal between spatially separated patches serves many ecological purposes including access to resources (Diekötter *et al.*, 2006), genetic exchange between subpopulations (Leisnham & Jamieson, 2002), colonisation of empty habitat patches (Berggren *et al.*, 2001) and escape from adverse environmental conditions (Hill *et al.*, 2001). Reduced inter-patch dispersal increases the probability of local extinctions due to e.g. decreasing population sizes (Connor *et al.*, 2000), loss of genetic variability (Keller & Largiadèr, 2003) and higher vulnerability to environmental and demographic stochasticity (Hanski, 1999). Consequently, dispersal is regarded one of the key factors influencing population dynamics and the persistence of species, especially in highly variable landscapes such as agricultural ones (Hanski, 1999).

In highly intensified and structurally simple agricultural landscapes, managed grasslands are often the only perennial habitats of some semi-natural character left. Their occurrence is often restricted to riparian corridors or they represent scattered and isolated elements in an arable matrix. Still, their existence in those high input landscapes is important for maintaining biodiversity and ecosystem services (Tscharntke *et al.*, 2005). For a long term persistence of populations, connectivity and dispersal among such isolated habitat patches is essential to ensure recolonisation following local extinctions (c.f. Hanski & Simberloff, 1997). To enhance connectivity among patches, corridors have been proposed as a management strategy for various taxa (Gonzalez *et al.*, 1998; Holzschuh *et al.*, 2009). Efficient corridors for connecting non-ploughed habitats might consist of linear perennial elements such as grassy strips along farm roads or drainage ditches (Berggren *et al.*, 2002; Mazerolle, 2004). However, whether corridors are necessary and effective to counteract habitat isolation effects depends on the permeability of the agricultural matrix and on the vagility of the respective organisms in focus (Baum *et al.*, 2004; Kindlmann & Burel, 2008).

In the present study, we investigated effects of habitat isolation on species richness and community composition of carabid beetles with different dispersal potential and the effectiveness of narrow corridors for mitigating those isolation effects. Carabid beetles are characteristic inhabitants of agricultural landscapes and occur in arable land as well as grasslands (Thiele, 1977). As the impact of landscape structure on given taxa is known to depend on their dispersal potential (e.g. Diekötter *et al.*, 2008) species-specific differences in vagility make carabid beetles an ideal taxon to study the impact of habitat isolation and connectivity in agricultural landscapes. Carabid beetles disperse either by walking or flying, depending on the morphology of wings and wing muscles (Den Boer, 1977, 1990; Desender, 1989; Matalin, 2003). Concordantly, the beetles' response to landscape configuration depends on their respective mode of dispersal (Dauber & Purtauf, 2007; Hendrickx *et al.*, 2009). Carabid beetles are important for several ecological processes in agricultural systems (Holland, 2002). They are predators of a great variety of pests (e.g. Lang, 2003), but are also an important food resource

for farmland birds and mammals (Holland, 2002). Most carabid species living in agroecosystems have multiple habitat requirements and temporarily depend on perennial habitats in close vicinity to the arable crops to find shelter or successfully complete their life cycles (Aviron *et al.*, 2005; Werling & Gratton, 2008).

We surveyed managed grasslands in an intensively managed agricultural region in Germany which were either situated in a continuous belt of grasslands, in an arable matrix but connected to the continuous belt via grassy corridors alongside ditches or completely isolated in an arable crop matrix with regard to species richness and composition of carabid beetle communities. We hypothesised that (i) habitat isolation negatively affects carabid species richness in grasslands, (ii) habitat isolation affects species with low dispersal potential more than species with high dispersal potential, (iii) these trait-specific responses lead to changes in community composition, and (iv) grassy strips bordering ditches enhance the connectivity of grassland sites and therefore reduce negative isolation effects on carabid diversity.

Material and methods

Study region and study sites

The Wetterau Region in Central Germany is characterised by highly fertile loess soils and is one of the most profitable regions for agriculture in Hesse. About half of the area is agriculturally managed land (54%) dominated by crop fields (76%) (Hess-

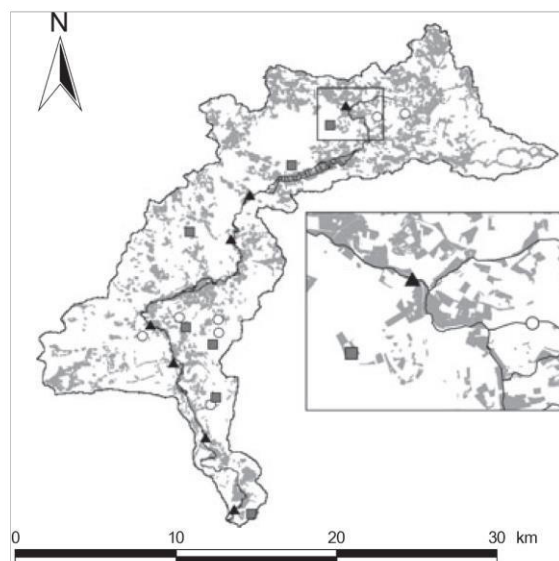


Fig. 1. Distribution of the 21 study sites within the watershed of the river Wetter [filled triangle: 'green vein' sites (GV); open circles: 'connected' (Con) grassland; filled squares: 'isolated' (Iso) grassland]. The Wetter is marked with a black line, grasslands are shown in light grey. Exemplarily, feeder ditches that link 'connected' grassland to the 'green vein' are shown in the close-up.

ches Statistisches Landesamt, 2008). In the structurally poor and tillage dominated landscape grassland mainly forms continuous belts in the riparian zones of the rivers Wetter and Nidda. Apart from that, managed grasslands are isolated and sparsely scattered among the dominating crop fields. Mean annual precipitation of the region ranges from 500 to 700 mm, mean annual temperature from 9.1 to 10.0 °C.

We conducted our study in the north-western part of the region, which is the watershed of the river Wetter (50°19'24–50°34'04N, 8°42'00–8°57'05E). Three classes of grasslands with different degrees of isolation were investigated (Fig. 1). In the first class, grasslands were part of the continuous grassland belt along the Wetter. This belt consists of grassland plots partly separated by farm tracks and only sparsely interrupted by villages and forest. The belt ranged from 100 to more than 1000 m in width. This class is further referred to as 'green vein' ($n = 7$). The second class encompassed grasslands scattered among crop fields but connected with the grassland belt by narrow grassy corridors bordering feeder ditches of the Wetter. The width of the grassy corridors varied considerably along their respective length but they were at a minimum two meters wide. This class is further referred to as 'connected'. The distance between the 'connected' sites and the grassland belt along the Wetter ranged from 315 to 3230 m (Median 835 m, $n = 7$). A third class contained grassland sites separated from the grassland belt by crop fields and without any connection via grassy corridors or any other perennial linear

elements that could have served as dispersal corridors. Their distance to the grassland belt ranged from 530 to 2725 m (Median 1200 m, $n = 7$). This class is further referred to as 'isolated'.

Elevation (m a.s.l.) of the study sites was derived from a digital elevation model with a grid size of 12.5 m. Altitude varied between 125 and 224 m a.s.l. Main soil separates were silt and clay in all grassland classes (digital map of soil types, HLUG, 2003). We measured soil pH (CaCl₂) and soil water content from soil samples following established protocols. All sampled sites were managed grasslands for at least 5 years. Irrespective of the isolation class of the grasslands, grass was cut one to three times a year. Minimum distance between two study sites was 0.65 km, maximum distance 28.7 km. Grassland size ranged from 0.3 to 6.3 hectares. To describe differences of land-use composition in the immediate surrounding of the study sites, we calculate the amount of arable crops and grassland in non-overlapping 300 m radii as well as the mean distance to the next ten grassland patches larger than 0.01 hectare. The size of the grasslands and the land-use parameters were calculated from a land-cover map with spatially explicit information on agricultural land-use (EFTAS Fernerkundung Technologietransfer GmbH, 2007). Average width of grassy corridors were estimated from digitised and spatially referenced aerial photographs of 2005 with 0.5 m resolution by multiplying length and width of all segments of a grassy corridor and dividing by total length of the corridor. A summary of the grassland characteristics is given in Table 1.

Table 1. Site characteristics and environmental variables of the study sites.

Category	ID	Altitude [m a.s.l.]	pH	Soil water content [%]	Size [ha]	Number of cuts	Distance to green belt [m]	Average width of grassy strips [m]	NN-dist 10 [m]	Grassland cover [%]	Crop cover [%]
GV	1	194	6.0	19.7	3.1	2	0	—	98	27.7	16.4
GV	7	166	5.8	18.4	6.3	1	0	—	171	43.2	2.0
GV	8	159	7.7	22.2	2.3	1	0	—	90	26.3	12.3
GV	14	143	6.2	15.4	0.4	2	0	—	48	42.2	10.4
GV	16	141	7.5	27.8	1.5	2	0	—	33	32.1	4.5
GV	21	134	6	24.8	1.9	3	0	—	207	7.8	12.7
GV	22	125	7.5	28.6	2.1	2	0	—	231	21.5	10.1
Con	3	198	5.6	18.8	1.3	2	730	4	224	13.5	20.5
Con	4	216	5.8	16.6	3.4	2	315	20	137	23.9	18.9
Con	10	193	6.4	23.2	1.9	2	3230	11	211	14.5	22.4
Con	11	198	6.2	24.1	1.5	2	2850	9	576	6.4	6.9
Con	13	172	5.5	19.8	0.3	1	835	5	117	24.1	17.1
Con	15	156	7.6	20.5	0.7	2	740	6	201	23.8	20.1
Con	20	157	5.8	17.3	0.6	3	1010	3	349	2.7	24.2
Iso	2	208	6.4	25.0	4.5	2	775	—	480	21.3	12.2
Iso	6	179	5.6	22.5	0.8	2	530	—	383	9.9	12.7
Iso	9	224	6.6	16.3	0.8	1	2725	—	219	10.2	22.3
Iso	12	185	7.9	9.4	0.5	1	1200	—	215	17.0	21.6
Iso	18	206	6.2	17.2	0.9	2	2340	—	546	4.3	6.9
Iso	19	180	6.3	19.4	2.1	1	1400	—	326	11.3	20.3
Iso	23	155	6.5	13.1	3.9	3	660	—	270	12.4	11.2

GV, 'green vein' sites; Con, 'connected' sites; Iso, 'isolated' sites.

NN-dist 10 denotes the mean distance to the next ten grassland patches greater than 0.01 hectare. Grassland cover and crop cover denotes the amount of grassland and arable crops in a 300 m landscape radius.

Sampling and species identification

Carabids were sampled using pitfall traps (diameter: 85 mm, volume: 500 ml), filled with 150 ml of an ethylenglycol-water-solution (1:2) with a detergent added to reduce surface tension. Each trap was shielded by a 25 × 25 cm acrylic glass pane at a height of about 10 cm to avoid flooding by rain. Four pitfall traps were placed in a row in the interior of each study site with a minimum distance of 20 m to the boundary and a distance of about 20 m to each other. Sampling took place in two-week periods between 13 May and 27 May and between 27 July and 10 August in 2006. All individuals were identified to species level (Freude *et al.*, 2004) and characterised according to their dispersal potential following Den Boer (1977, 1990), Desender (1989), and Hürka (1996) and habitat requirement following Koch (1989).

Flight ability within species depends not only on the development of hind wings but also on e.g. the morphology of flight muscles. Latter can differ among individuals within a macropterous or dimorphous species. In general the highest dispersal power is reported for macropterous species with always functional wing muscles, followed by macropterous species with dimorphic or polymorphic state of wing muscles and a lower dispersal power is reported for dimorphous species (Matalin, 2003). In our study, carabid species were assigned to five different functional groups according to their assumed vagility ranging from low to high dispersal potential (Table S1, see Supporting Information): 1: unquestioned brachypterous (rudimentary or reduced hind wings, low dispersal potential), 2: mostly brachypterous (usually rudimentary or reduced hind wings but macropterous individuals very rarely occurring (less than 2%, low dispersal potential assumed), 3: dimorphous with 2 to 50% macropterous individuals (unknown dispersal potential), 4: mostly macropterous (dimorphous but macropterous individuals frequently observed (more than 50%), high dispersal potential assumed), 5: macropterous (well developed hind wings, high dispersal potential). The proportion of individuals capable of flying is often region specific (Den Boer, 1977; Thiele, 1977; Desender, 1989). Therefore, classifications of flight ability based on literature reporting catches with window traps or dissection of flight muscles from different regions have to be handled with care. Only the low dispersal potential of brachypterous species

can be classified unambiguously. In our study, we distinguish two groups with different dispersal potential and presumed a higher potential of dispersal for species with macropterous hind wings and for species with more than 50% of macropterous individuals (class 4 and 5) than for brachypterous carabids and dimorphous species with very rare macropterous individuals (class 1 and 2). Typical forest species generally depending on woods and hedgerows in the vicinity and only occurring as 'transients' on adjacent grassland (Thiele, 1977) were omitted from further analyses ($n = 10$ species, see Supporting Information Table S1).

Statistical analyses

To check whether our predefined isolation classes were not biased by systematic differences in abiotic conditions we ran PERMANOVA (=NPMANOVA, permutational/non-parametric analyses of variance) tests with 10 000 permutations (Anderson, 2001). PERMANOVA is a non-parametric permutational test for significant differences between two or more groups, based on any distance measure (Anderson, 2001). We used the same method to detect differences in species composition and richness among isolation classes. We chose the Euclidean distance measure to identify differences in abiotic site conditions and landscape composition. No significant differences in abiotic conditions between isolation classes (cutting frequency; mean grassland size; soil water content; soil pH) were detected ($F_{2, 18} = 1.877$, $P = 0.171$). In accordance with our site selection, however, the surrounding of the isolation classes significantly differed in landscape composition. The amount of arable crops was highest around 'connected' sites ($F_{2, 18} = 4.5$, $P < 0.05$), the amount of grasslands was highest around 'green vein' sites ($F_{2, 18} = 6.133$, $P < 0.01$), and the distance to the next ten grassland patches was largest for 'isolated' sites ($F_{2, 18} = 5.544$, $P < 0.05$; Table 2).

Carabid species richness and activity density at each site were analysed by pooling all traps from each study site over the two sampling dates. To exclude any effect of geographic distance (longitude, latitude) on carabid species composition, we performed a Mantel test using both matrices (Legendre & Legendre, 1998; based on Spearman correlations, 10,000 permu-

Table 2. Characteristics of abiotic conditions and surrounding landscape for the three isolation classes.

	GV			Con			Iso			
	Median	Min	Max	Median	Min	Max	Median	Min	Max	
pH	6.2	5.8	7.7	5.8	5.5	7.6	6.4	5.6	7.9	n.s.
soil water content [%]	22.2	15.4	28.6	19.8	16.6	24.1	17.2	9.4	25.0	n.s.
size [ha]	2.1	0.4	6.3	1.3	0.3	3.4	0.9	0.5	4.5	n.s.
number of cuts	2	1	3	2	1	3	2	1	3	n.s.
NN-dist 10 [m]	97.9	32.6	231.4	211.2	116.8	576.2	325.8	215.2	546.3	*
grassland cover [%]	27.7	7.8	43.2	14.5	2.7	24.1	11.3	4.3	21.3	**
crop cover [%]	36.6	7.0	58.0	71.2	24.2	85.6	44.9	24.6	79.0	*

GV, 'green vein'; Con, 'connected'; Iso, 'isolated'.

Given are median and minimum to maximum range. PERMANOVA results are given as not significant (n.s.), * for $P < 0.05$ and ** for $P < 0.01$.

tations). No spatial autocorrelation in species composition was found ($R = -0.001$, $P = 0.894$). PERMANOVA and Mantel test were calculated using the software package PAST (version 1.80; Hammer *et al.*, 2001).

Prior to analyses of carabid community composition, observed abundance data were log transformed and then relativised by species maximum abundance to downweigh the impact of abundant species. This transformation is well-suited for pitfall trap data as trap catches are often influenced by species size or behaviour, rather than population density (Rykken *et al.*, 2007). To reduce noise in the data set, we excluded species occurring on less than 10% of the study sites from community analyses (McCune & Grace, 2002). Differences in carabid species composition were analysed using the Bray-Curtis distance measure.

Species richness of (i) total carabids (65 species observed), (ii) species with low dispersal potential (class 1 and 2, 14 species observed) and (iii) species with high dispersal potential (class 4 and 5, 36 species observed) were estimated per site based on Chao's abundance-based estimator Chao 1. The Chao 1 estimator is the sum of the observed number of species and the quotient $a^2/2b$ (a , the number of singletons and b , the number of doubletons) using the information on the presence of rare species in the assemblage, assuming that the greater the number of rare species was recorded, the more likely it is that other rare species are present although not recorded (Gotelli & Colwell, 2001). Chao 1 is a low bias and high precision species richness estimator (Walther & Moore, 2005). We estimated species richness using the program EstimateS (version 8.0.0, Colwell, 2006). Differences in carabid species richness per site between isolation classes were analysed using the Euclidean distance measure. Species with unknown dispersal power (class 3, dimorphous species with 2 to 50% or unknown amount of macropterous individuals, 13 species, Table S1, see Supporting Information) were excluded from PERMANOVA analyses to separate the species with low and the species with high dispersal potential more distinctly. However, they were included in a nonmetric multidimensional scaling (NMS) ordination analysing carabid community composition.

We used the software program PC ORD (McCune & Meford, 2006) to display the relationships among sites of different isolation classes using NMS (Kruskal, 1964). Since the NMS ordination does not rely on other than species variables to construct the axes, the interrelationships between species composition and site characteristics (in this case frequency of grass cutting, mean grassland size, soil water content, soil pH) can be displayed by joint-plotting of environmental variables. We followed the general procedure for NMS as suggested in McCune and Grace (2002). To seek the best NMS solution by sequentially stepping down in dimensionality, we used a Bray-Curtis distance matrix (random starting configuration, 40 runs with real data, stability criterion = 0.00001, 400 maximum iterations, and 50 runs of the Monte Carlo test to determine the lowest number of appropriate dimensions). The final 3-dimensional rerun was started with the best working configuration from this forerun, no step-down in dimensionality, one real run and no Monte Carlo test. The proportion of variance represented by each axis in the ordination was calculated by distance-based evaluation of the coefficient of determination (r^2) between dis-

tances in the 3-dimensional ordination space and distances in the original n -dimensional space (McCune & Grace, 2002). Correlations between the ordination and the environmental variables were calculated with both Pearson's r^2 and Kendall's τ . Only environmental variables with both τ and $r^2 \geq 0.200$ were displayed.

Results

A total of 65 observed open-land species with 2825 individuals were analysed (Supporting Information, Table S1). We sampled a total of 48 carabid species on 'green vein' sites, 43 on 'connected' sites and 43 on 'isolated' sites. Sampled number of species with low dispersal potential was 11 on 'green vein' sites, 10 on 'connected' sites and 7 on 'isolated' sites, of species with high dispersal potential it was 24 on 'green vein' sites, 24 on 'connected' sites and

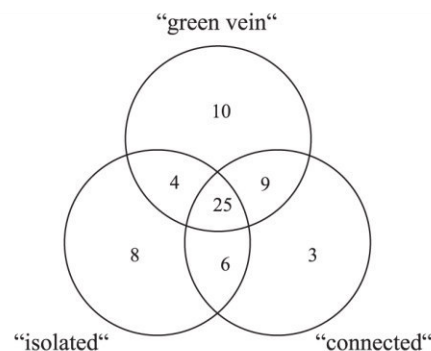


Fig. 2. Number of exclusive and shared carabid species trapped on grasslands of the three classes with different degrees of isolation.

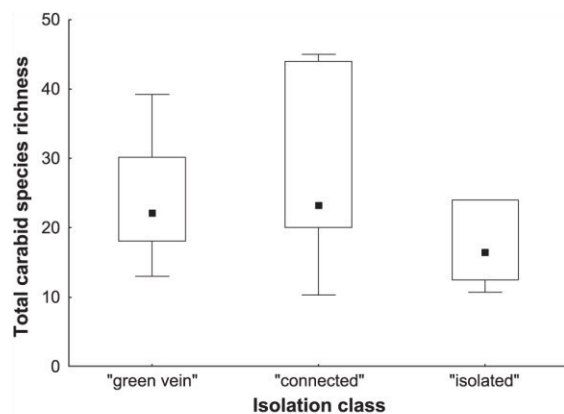


Fig. 3. Species richness (Chao 1) of total carabid beetles on grasslands of different isolation classes. Given are Median, 25% Percentiles (Boxes) and Range (Whiskers).

26 on 'isolated' sites. 'Green vein' sites harboured the highest and 'connected' sites the lowest number of exclusive species (Fig. 2). In addition, the share of common species was highest for 'green vein' and 'connected' sites and lowest for 'green vein' and 'isolated' sites (Fig. 2).

Estimated total species richness per site did not differ significantly among isolation classes ($S_{\text{est Chao1}}$: $F_{2, 18} = 0.636$, $P = 0.533$, Fig. 3). Similarly, the estimated species richness of carabids with high dispersal potential per site was not significantly affected by habitat isolation ($S_{\text{est Chao1}}$: $F_{2, 18} = 0.177$, $P = 0.843$, Fig. 4b). In contrast, the estimated richness of species with low dispersal potential per site differed significantly among grasslands of varying isolation ($S_{\text{est Chao1}}$: $F_{2, 18} = 4.181$, $P < 0.05$, Fig. 4a). The class of 'isolated' sites had over two times less species with low dispersal potential than 'green vein' sites and the 'connected' sites were situated in-between.

The PERMANOVA results revealed significant differences in the species composition of the isolation classes ($F_{2, 18} = 1.523$, $P < 0.05$). Those differences are visible in the NMS ordination of the carabid species composition (Fig. 5). The final three-dimensional solution of the NMS ordination represented a total of 66% of the total variation of the original space (axis 1:22.3%; axis 2:23.9%; axis 3:19.0%) at a final stress of 15.57 (Monte Carlo test, $P = 0.040$). The final instability was 0.00001 with 409 iterations. Along axis 2 the 'green vein' sites were clearly separated from the 'isolated' sites with exception of one 'isolated' site (Fig. 5a). The 'connected' sites were either located close to the 'isolated' (four sites) or close to the 'green vein' sites (three sites). Most species with low dispersal potential were considerably more frequent in 'green vein' sites. Sites from all classes were separated along axis 1 indicating a generally high variability in the community composition within all classes. Unfortunately, this axis could not be interpreted neither based on the environmental variables taken into account nor by comparing characteristics of species located at opposing ends of the axis. Soil humidity of the study sites was only slightly correlated with axis 2 ($\tau = 0.28$; $r^2 = 0.19$). Axis 3, however, was more strongly correlated with soil humidity (Fig. 5b; $\tau = 0.55$; $r^2 = 0.51$) and had a strong influence on the community composition. This influence was independent from the isolation classes as sites from all classes were separated along this axis.

Discussion

Our study revealed trait-specific effects of habitat isolation of perennial grasslands on the diversity of carabid beetles in an intensively managed agricultural landscape. Whereas total species richness was unaffected by habitat isolation, isolated grasslands were dominated by species with high dispersal potential and showed significantly lower species richness of carabid beetles with low dispersal potential than connected grasslands. This negative effect of habitat isolation on species with low dispersal potential was mitigated by grassy corridors that connected grasslands in a predominantly arable matrix with larger source habitats.

Because in central Europe many carabid species are well adapted to arable land in which they occur in high numbers (e.g. Cole *et al.*, 2005), carabid diversity in grasslands that are surrounded by a high percentage of arable land may be affected by species spill-over from arable land (Rand *et al.*, 2006). Here, carabid beetles that were commonly found in arable crops in the region (S. Wamser, unpubl. data) made up 35% of the local carabid diversity in isolated grasslands embedded in an arable matrix whereas they had a share of only 23% in grasslands that were part of the belt of grassland along the river Wetter. With a share of 30% of carabid species commonly found in arable land, grasslands connected to the this belt took an intermediate position pointing at the potential function of grassy corridors in allowing grassland species to persist also in small habitat patches by fostering dispersal from sources to potential sinks (Pulliam, 1988).

Corridors have long been suggested to enhance connectivity among patches (c.f. Simberloff *et al.*, 1992). Yet, despite early demands (Simberloff *et al.*, 1992), scientific support for the efficacy of corridors in enhancing habitat connectivity and thereby population persistence remains limited to selected groups of species or systems (Baum *et al.*, 2004; Öckinger & Smith, 2007). That connected grasslands in the present study shared more species with grasslands situated in the green belt than with their isolated counterparts indicates that corridors enable individual dispersal between sources and surrounding habitat patches of the same kind. Lower species richness of carabids with low dispersal potential in similar sized but isolated grasslands also indicates that local populations in these grasslands are too small for

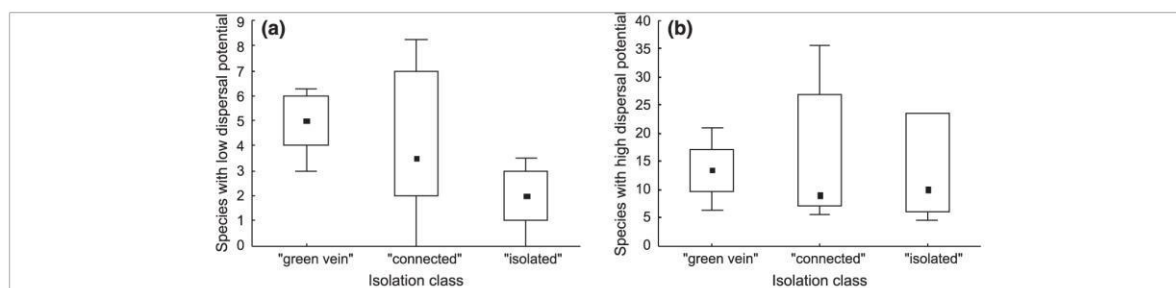


Fig. 4. Species richness (Chao 1) of carabid species with low dispersal potential (a) and species with high dispersal potential (b) on grasslands of different isolation classes. Given are Median, 25% Percentiles (Boxes) and Range (Whiskers). Note the difference in scale.

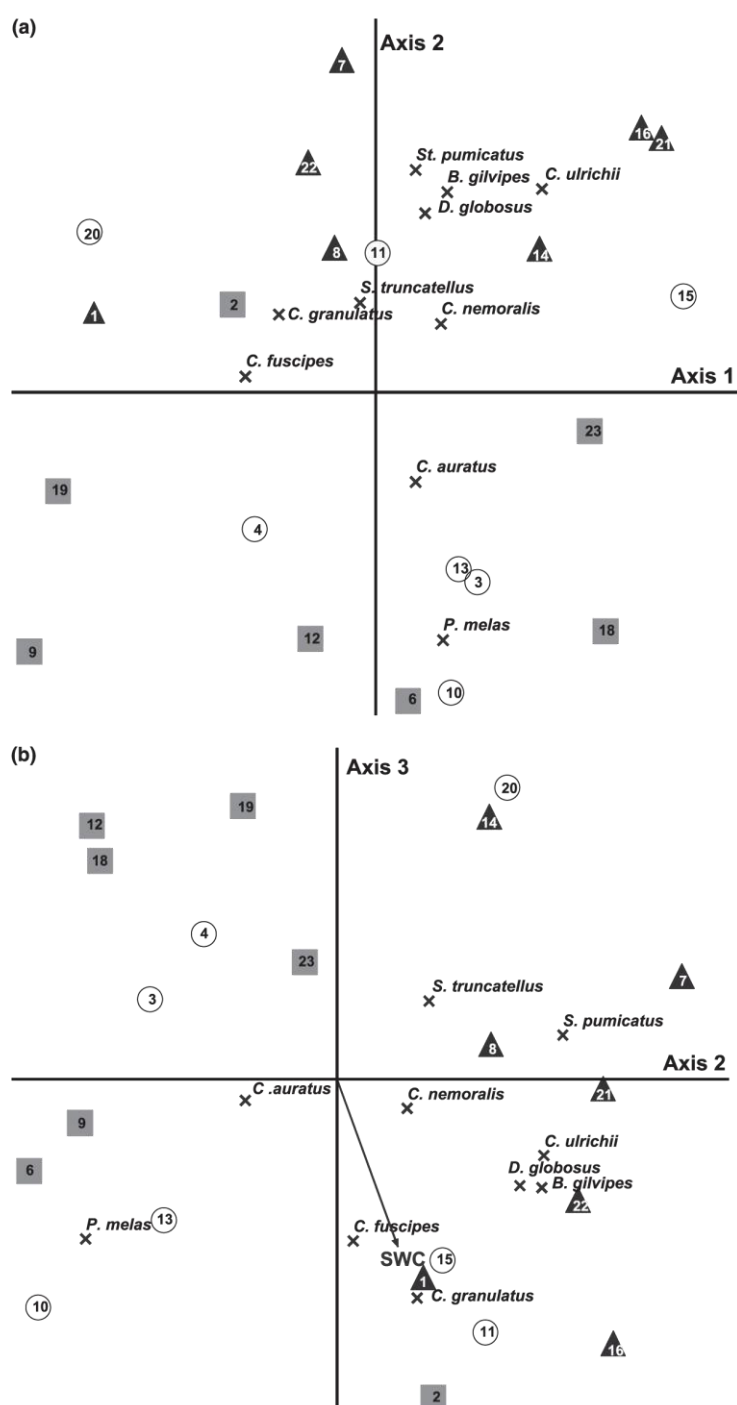


Fig. 5. Nonmetric multidimensional scaling (NMS) ordination of carabid beetle assemblages among the three grassland classes: (▲) 'green vein' (GV) sites; (○) 'connected' (Con) sites; (■) 'isolated' (Iso) sites based on the 40 species that occurred in more than 10% of the plots, axis 1 and 2 (a) and axis 2 and 3 (b) of the 3-dimensional solution, species are plotted as crosses, only names of species with low dispersal potential are given. Length of correlation vectors represents the strength of the correlation. The environmental variable SWC (soil water content) is plotted as vector (τ and $r^2 \geq 0.200$). Numbers in the symbols display ID of the study sites.

long-term persistence without immigration (Den Boer, 1990). The significant effect of habitat isolation on species with low dispersal potential but not on carabid species with high dispersal potential, however, suggests that the effectiveness of corridors in maintaining carabid diversity is trait-specific benefiting especially less mobile species (Collinge, 2000).

Trait specific-responses to landscape structure and management practices in agricultural landscapes become increasingly apparent for a variety of traits and taxa. Responses of carabids to management and landscape structure have been shown to differ among trophic groups (Purtauf *et al.*, 2005a; Schweiger *et al.*, 2005), between breeding types (Purtauf *et al.*, 2005b) and among groups of different dispersal ability (Schweiger *et al.*, 2005). Hendrickx *et al.* (2009) showed that for species assemblages of carabids with low dispersal abilities, local diversity decreased as the proximity of semi-natural habitat decreased, while mobile species showed an opposite trend. This local loss, however, was compensated at least in part by an increase with high dispersal abilities, which – similar to our results – obscured the effect of fragmentation when investigated across dispersal groups.

The efficacy of corridors in mitigating habitat fragmentation was shown in modelling approaches with typical representatives of forest carabids (Tischendorf *et al.*, 1998; Jordan *et al.*, 2007). Empirical studies on the effects of corridors on carabid richness or community composition are surprisingly scarce (Eggers *et al.*, 2010). However, regarding the results of these single-species modelling approaches and the case study on the effects of corridor length, quality and structure on landscape connectivity together with the trait-specific responses observed here and previously suggests that these structural as well as other abiotic characteristics, such as microclimate, need to be carefully considered in future to maximise the efficacy of corridors in maximising carabid (and other) species diversity in the landscape. In addition, care needs to be taken that corridors end up in the same type and quality of habitat thereby minimising population sinks and ensuring successful reproduction (Noordijk *et al.*, 2006). Also, it should be considered that connecting isolated habitats may not always be beneficial for instance when they harbour species weak in competition which could be disadvantaged when connected to highly competitive habitat specialists (Tilman, 1994).

We conclude that in order to protect the diversity of carabid beetles in agricultural regions it is crucial to maintain and properly manage grasslands and semi-natural habitats, as they harbour many species that are restricted to these less frequently disturbed habitats (Batory *et al.*, 2007) or influence the species richness and composition in adjacent arable crops (Werling & Gratton, 2008). Thus, mitigating the impact of habitat isolation – especially on species with restricted dispersal potential – through corridors may benefit the diversity of carabid beetles not only locally but also regionally. In general, grasslands alongside ditches or other linear landscape features should be maintained and managed to promote the dispersal not only of carabid beetles but also other species with restricted dispersal potential. Whether a specific management of linear grassy elements or their widening could further improve their function as corridors requires further investigations. Our results also under-

line that generalisations regarding the effects of corridors on carabid species richness in grasslands across different ecological traits within a taxon are not justified and must lead to erroneous recommendations to landscape planning and nature conservation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2010.00110.x:

Table S1. Species list. Table includes total abundance (Ab), Frequency (number of sites occupied by the respective species) within grassland classes 'green vein' (GV), 'connected' (Con) and 'isolated' (Iso). Wing development (W): (b, brachypterous; d, dimorphous, m, macropterous; ?, no classification possible). Classification: F (forest species) which were excluded from analyses, 1 (brachypterous), 2 (dimorphous, low dispersal power, less than 2% macropterous individuals), 3 (dimorphous, unknown dispersal power), 4 (dimorphous, high dispersal potential, more than 50% macropterous individuals), 5 (macropterous).

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Supporting Information

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Species	Ab	Frequency			W	Classification	Dispersal potential
		GV	Con	Iso			
<i>Abax ovalis</i>	1	0	1	0	b	F	
<i>Abax parallelepipedus</i>	28	1	3	2	b	F	
<i>Acupalpus luteatus</i>	1	1	0	0	m	5	high
<i>Amara aenea</i>	103	5	4	3	m	5	high
<i>A. aulica</i>	1	1	0	0	m	5	high
<i>A. communis</i>	37	2	2	3	m	5	high
<i>A. convexior</i>	6	1	2	3	m	5	high
<i>A. equestris</i>	7	3	0	1	m	5	high
<i>A. eurynota</i>	3	1	1	1	m	5	high
<i>A. familiaris</i>	35	4	2	0	m	5	high
<i>A. kulti</i>	1	0	0	1	?		
<i>A. littorea</i>	1	0	1	0	m	5	high
<i>A. lunicollis</i>	93	4	5	3	m	5	high
<i>A. montivaga</i>	2	2	0	0	m	5	high
<i>A. plebeja</i>	26	4	2	4	m	5	high
<i>A. similata</i>	2	0	0	1	m	5	high
<i>A. strenua</i>	20	3	3	0	m	5	high
<i>Anchomenus dorsalis</i>	6	3	0	1	m	5	high
<i>Anisodactylus binotatus</i>	44	4	2	0	m	5	high
<i>Asaphidion flavipes</i>	2	0	1	1	m	5	high
<i>Badister bullatus</i>	20	3	2	5	m	5	high
<i>B. lacertosus</i>	1	0	1	0	m	F	
<i>Bembidion gilvipes</i>	17	4	1	0	d	2	low
<i>B. guttula</i>	2	0	1	0	d	3	?
<i>B. lampros</i>	11	2	3	2	d	3	?
<i>B. obtusum</i>	41	5	3	2	d	3	?
<i>B. properans</i>	28	3	1	1	d	3	?
<i>Brachinus crepitans</i>	3	0	0	1	m	5	high
<i>B. explodens</i>	2	1	0	0	m	5	high
<i>Calathus fuscipes</i>	37	2	3	3	d	2	low
<i>C. melanocephalus</i>	2	1	0	0	d	2	low
<i>Carabus auratus</i>	452	2	4	3	b	1	low
<i>C. auronitens</i>	1	0	0	1	b	F	
<i>C. convexus</i>	2	0	1	1	b	1	low
<i>C. coriaceus</i>	1	0	0	1	b	F	
<i>C. granulatus</i>	12	2	1	2	d	2	low

Species	Ab	Frequency			W	Classification	Dispersal potential
		GV	Con	Iso			
<i>C. monilis</i>	3	1	0	0	b	1	low
<i>C. nemoralis</i>	44	6	6	2	b	1	low
<i>C. ulrichii</i>	34	4	1	0	b	1	low
<i>C. violaceus</i>	23	1	1	1	b	F	
<i>Clivina fossor</i>	2	2	0	0	d	3	?
<i>Cychrus caraboides</i>	1	0	1	0	b	F	
<i>Dyschirius globosus</i>	17	2	1	0	d	2	low
<i>Harpalus affinis</i>	38	4	3	2	m	5	high
<i>H. latus</i>	9	0	3	1	m	5	high
<i>H. luteicornis</i>	88	4	3	3	m	5	high
<i>H. rubripes</i>	24	2	1	1	m	5	high
<i>H. rufipes</i>	173	4	6	7	m	5	high
<i>H. subcylindricus</i>	21	0	0	1	m	5	high
<i>H. tardus</i>	1	0	0	1	m	5	high
<i>Leistus ferrugineus</i>	5	1	0	1	d	3	?
<i>Loricera pilicornis</i>	2	0	1	1	m	5	high
<i>Microlestes maurus</i>	42	4	1	3	d	3	?
<i>M. minutulus</i>	5	1	2	0	d	3	?
<i>Nebria brevicollis</i>	6	1	3	1	m	F	
<i>Notiophilus biguttatus</i>	3	0	0	1	d	4	high
<i>N. palustris</i>	24	2	3	3	d	3	?
<i>Ophonus ardosiacus</i>	2	0	0	1	m	5	high
<i>Panagaeus cruxmajor</i>	2	1	1	0	m	5	high
<i>Paratachys spec.</i>	1	1	0	0	?		
<i>Poecilus cupreus</i>	214	6	3	2	m	5	high
<i>P. versicolor</i>	480	7	6	3	m	5	high
<i>Pterostichus anthracinus</i>	1	1	0	0	d	3	?
<i>P. burmeisteri</i>	1	1	0	0	b	F	
<i>P. macer</i>	52	0	2	2	m	5	high
<i>P. madidus</i>	1	0	0	1	b	1	low
<i>P. melanarius</i>	469	6	6	6	d	3	?
<i>P. melas</i>	16	0	2	1	b	1	low
<i>P. niger</i>	6	1	2	1	m	F	
<i>P. vernalis</i>	10	2	1	1	m	5	high
<i>Stomis pumicatus</i>	5	3	0	0	d	2	low
<i>Syntomus truncatellus</i>	5	2	2	0	d	2	low
<i>Synuchus vivalis</i>	3	2	0	1	d	3	?
<i>Trechus quadristriatus</i>	1	0	1	0	d	3	?
<i>Zabrus tenebrioides</i>	9	1	1	2	m	5	high

Wing development according to Den Boer (1977; 1990), Desender (1989), and Hůrka (1996), classification depending on amount of macropterous individuals reported by Den Boer (1977; 1990) and Desender (1989).

KAPITEL 4

DELAYED COLONISATION OF ARABLE FIELDS BY SPRING BREEDING GROUND BEETLES (COLEOPTERA: CARABIDAE) IN LANDSCAPES WITH A HIGH AVAILABILITY OF HIBERNATION SITES

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Delayed colonisation of arable fields by spring breeding ground beetles (Coleoptera: Carabidae) in landscapes with a high availability of hibernation sites

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ABSTRACT

The colonisation of winter barley fields by spring breeding carabids and its temporal modulation by the amount of potential hibernation sites was studied. Species richness of carabids was lower in landscapes with high length of boundaries and a high amount of non-cropped open habitats during early stages of the beetles' colonisation of arable fields. Species number of beetles with high dispersal potential responded to this landscape features at coarse spatial scales whereas beetles with low dispersal potential responded to intermediate scales. However, the negative impact of potential hibernation sites on colonisation diminished in later sampling phases. The patterns observed may be explained by both overwintering in arable soils in less complex landscapes and delayed colonisation in more complex landscapes. The seasonal patterns of landscape control suggest a need to account for temporal dynamics in interactions between species or functional groups and landscape properties. A high temporal resolution is needed in studies that focus on ecosystem function and services in agricultural landscapes, as direction of effect (positive/negative) of management on animal communities may change across spatial scales and within short time periods.

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1. Introduction

Several studies on invertebrate taxa have shown that a diverse landscape composition may positively affect local species richness and that landscape simplification in contrast may have adverse effects (e.g.: Hendrickx et al., 2007; Diekötter et al., 2010). Taxa that use multiple habitat types are particularly sensitive to the spatial and temporal availability of appropriate microsites, as they have to switch between different localities in their daily activity or during the annual life cycle (Thomas et al., 2002).

Most species of ground beetles at times depend on non-crop habitats like grasslands, forests, hedgerows, tree lines and field margins, and landscape impact on carabid beetles is shown for scales up to several kilometres (e.g. Dauber and Purtauf, 2007). Many species use non-crop habitats for shelter, breeding or dispersal (Holland and Luff, 2000), and it is shown that non-crop habitats are important hibernation sites for generalist predators such as carabid beetles (Geiger et al., 2009). Spring breeding, adult carabids often hibernate in boundary structures (Holland et al., 2009) such as grassy banks and stripes, edges of groves, shrubbery, forests

(Sotherton, 1984; Pfiffner and Luka, 2000), or grassland habitats (Desender et al., 1981). These species need to colonise crop fields in spring, whereas autumn-breeding carabids predominantly hibernate as larvae in arable soils and therefore do not have to colonise fields (Holland et al., 2009).

The amount of potential hibernation sites adjacent to crop fields affects the choice of hibernation sites and therefore the initial colonisation patterns of carabid beetles in spring which may be a key factor determining subsequent community structure. This consideration is based on observations that habitats providing refugia for polyphagous predators in winter continue to influence the distribution of those species during spring and summer by providing favourable zones of microclimate, shelter and food (Dennis et al., 2000). Consequently, species richness and composition of ground beetles in agricultural landscapes may at least partially depend on the availability of hibernation sites and refuges (Duelli and Obrist, 2003).

The aim of the present study was to assess the temporal variability of colonisation rates by carabid beetles at consecutive time intervals early in the season. It was distinguished between carabid species of low dispersal potential (in the following called brachypterous species; i.e. with short or absent hind wings) and species of high dispersal potential (in the following called macropterous species; i.e. with well developed hind wings). The spatial extent was identified to which colonisation was influenced by the amount of potential hibernation habitats in the surrounding

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landscapes. It was hypothesized that (i) the timing of spring-colonisation of carabids into winter barley fields depends on the composition of the surrounding landscape and that (ii) less mobile, brachypterous species are affected by the amount of potential hibernation sites at shorter distances than more mobile macropterous species.

2. Methods

The samples were collected in the Lahn-Dill-Bergland, a region situated in the low mountain ranges of Central Hesse, Germany, as part of a comprehensive sampling campaign (see Öberg et al., 2008). The total area of the study region covered about 700 km². Agriculture is characterized by low-input systems with small field sizes (mean size around 0.4 ha; Simmering et al., 2006). Land cover is dominated by forest (48.0%), arable fields (16.6%), and managed grassland (17.7%). Mean annual temperature ranges from 7 to 9 °C; mean annual precipitation varies from 650 to 1100 mm. Scattered over the whole study region, 12 areas with non-overlapping circles of 1050 m radius were selected. The landscapes within these areas strongly differed in their availability of potential hibernation sites for carabids (i.e. field boundaries, perennial grasslands, fallow land and forest edges) and ranged from highly heterogeneous land use with a high amount of non-cropped open habitats and high edge density to more homogeneous land use with a high cover of arable land and low edge density (see Appendix A for a summary of landscape characteristics). Mantel tests (based on Spearman correlations, 1000 permutations) were performed to relate geographic distance of the landscapes to the amount of potential hibernation sites (see Section 2.1). No spatial autocorrelation was detected ($R = 0.28$, $p = 0.12$). The actual study sites located within the centre of each circle were conventionally managed winter-sown barley fields ranging in size between 0.9 and 3.3 ha (mean 1.6 ha) which reflects the mean field size in Hesse (Engelhardt, 2004). The elevation of the sites ranged between 170 and 505 m a.s.l. All 12 fields were ploughed before sowing to a depth between about 15 and 30 cm and the preceding crops were cereals. According to questionnaires completed by the farmers, the numbers of external input events during the growing season (fertilisation, herbicides, fungicides, or growth regulator applications) varied between two and six until the end of observations and provide a proxy for anthropogenic disturbance. No insecticides were applied and the total application of nitrogen ranged from 90 to 140 kg ha⁻¹ yr⁻¹.

Soil moisture is a key factor affecting oviposition, larval survival, and within-field distribution of carabids, respectively (Holland et al., 2007). The compound topographic index (CTI) (Beven and Kirkby, 1979) was calculated as an index of soil moisture to check whether soil moisture may have an effect on the timing of colonisation. The CTI was calculated by means of a digital elevation model (DEM) with a 20 m grid size (HLBG, 2005).

2.1. Landscape analyses

Landscape parameters were calculated within non-overlapping circles of 1050 m radius around each study site using ArcView 3.2 GIS software (ESRI, Redlands, California), based on a digital land-use map derived from aerial photographs of 2002 (updated by a field survey in 2004). Each 1050 m circle was again subdivided in seven circles in 150 m steps (150, 300, 450, 600, 750, 900, and 1050 m) to identify specific distance ranges at which carabid beetles with different dispersal potential (macropterous and brachypterous) were affected by landscape structure. Radius sizes of up to 1050 m with 150 m steps were chosen based on the fact that most carabid beetles move distances between just a few to a few hundred meters in several weeks (Thiele, 1977). Macropterous carabids with high

dispersal potential may move over distances of several hundred meters up to kilometres even in short times (Thiele, 1977; Chapman et al., 2005). In order to evaluate the amount of potential hibernation sites for carabid beetles, the cover of non-crop open habitats such as permanent grassland and fallow land was calculated for each 150 m circle as well as length of boundaries between patches of different land use. Within the study region, boundary structures between different land-use types (arable crops, grassland, forest, fallow land, roads/tracks, urban structures and waters) provide semi-natural habitats (usually grassland-strips, banks, edges of groves, shrubbery, or forest).

2.2. Sampling and species determination

Carabids were sampled in 2004 using pitfall traps (diameter: 85 mm, volume: 500 ml) filled with approximately 100 ml of saturated NaCl-solution. A detergent was added to reduce surface tension. Each trap was shielded by a 25 cm × 25 cm acrylic glass pane at a height of about 10 cm to avoid flooding by rain. As the spatial distribution of carabid beetles is discontinuous (see Thomas et al., 2002 for a review), pitfall traps were located in a way that each field was fully covered by our sampling. Traps were placed along three parallel diagonal running transect lines within each field, in a way that six traps were covering the centre (>15 m edge distance) and four traps were covering the edge areas (5–15 m edge distance). As fields differed in size, distances between traps could not always be identical, but the minimum distance between neighbouring traps was 10 m to assure independency of the individual traps (Digweed et al., 1995). The traps were emptied every three days between 22nd March when barley was still in its seedling stage and 9th May before milk-ripe stage. All carabids were identified to species level (Freude, 1976; Trautner and Geigenmüller, 1987) and assorted to ecological groups according to both breeding type and dispersal potential (Appendix B; Lindroth, 1985, 1986; Hürka, 1996; Luff, 1998; Ribera et al., 2001). Autumn breeding carabids, which have their main activity period in a later season (Fadl and Purvis, 1998), and species which could not unambiguously be classified according to their vagility were excluded from further analyses.

Carabids were assigned to three functional groups, i.e. brachypterous (rudimentary or reduced hind wings, low dispersal potential), macropterous (well developed hind wings, potential for higher dispersal potential), and dimorphous (species with either brachypterous or macropterous individuals). To unequivocally characterize the wing-dimorphic species *Carabus granularis* (Linné) within the group of brachypterous spring-breeders, the development of the wings for each individual was examined. Out of 254 individuals of this species 249 were found to have rudimentary wings. Only these brachypterous individuals were included in our statistical analyses. Pooled data of all 10 traps per site were used to calculate species richness and activity density for every sampling interval. Activity density was defined as number of individuals captured per sampling interval per field, following Thiele (1977).

2.3. Data treatment and analysis

Since site-specific differences in microclimate caused by regional variations in altitude and aspect may significantly affect ground beetle activity (e.g. temperature, Honek, 1997), sampling intervals were adjusted to the blossoming of *Taraxacum officinale* G.H. Weber. Ex. Wiggers recorded at plots next to each site as suggested by Schweiger et al. (2005); for additional details see Öberg et al., 2008). After the 30th of April activity density of beetles rapidly decreased due to bad weather conditions. Therefore, later sample intervals were not taken into the analyses to avoid compromising

the comparability of sites with late blossoming of *Taraxacum*. As a consequence, only data from the sampling period spanning from 15 days before to 12 days after the inset of *T. officinale* blooming was used for the comparison between study sites. To further minimize the effect of climatic short-term differences between sites on capture numbers, trap data from three subsequent samplings were pooled to form three major phases of colonisation, each covering an interval of nine days.

The impact of management on carabid activity density or species richness could persist for several days/weeks or only for a short time and may not be strictly related to a single sampling phase. Thus, an analysis testing for the cumulative impact of management and abiotic site characteristics on brachypterous and macropterous beetles was conducted by means of a linear model approach covering the whole sampling period. The number of external inputs (2–6), ploughing depth (cm), fertilisation (N [kg ha⁻¹ yr⁻¹]), and field size (ha) as well as soil humidity (CTI) were included as continuous variables. The test revealed that neither activity density nor species richness were affected by the factors included in this analysis which reconfirmed previous studies that found management variables for ground beetles in low input farming systems not having a strong influence compared to landscape descriptors (Maisonhaute et al., 2010). Therefore, the analysis continued without further consideration of management differences.

Data on carabid activity density and species richness was analysed analogously to the approach outlined in Öberg et al. (2008). A repeated measures ANOVA was used to test for differences in between phases ($n = 3$), using Greenhouse and Geisser (1959) correction.

To test whether landscape effects on colonisation patterns differed between phases, effects of the amount of potential hibernation sites on the activity density and species richness was analysed with separate linear regression models for each phase. To display the results Pearson product moment coefficients were shown as they further provide information about the direction of a relationship (by the sign) and as they are directly related to r^2 (Gotelli and Ellison, 2004). To test whether brachypterous species were more sensitive to the amount of potential hibernation sites and if these species responded at shorter distances than macropterous species separate models between these dependent variables and the amount of potential hibernation sites in each landscape radius were analysed.

The two landscape parameters amount of non-cropped open habitats (permanent grassland and fallow land) and length of boundaries were correlated in five out of seven cases (Appendix C, see also Öberg et al., 2008). Therefore they were not included into a multivariate analysis. The relationship between these parameters

and species richness and activity density was tested separately in identical regression models. This approach avoids confounding the importance of different landscape parameters in statistical analyses due to multicollinearity (Graham, 2003). The explanatory power of the parameter length of boundaries was considerably higher than that of the parameter amount of non-cropped open habitats in 39 out of 42 cases (Appendix D). On average the mean r^2 derived from using length of boundaries as predictor explained 20% more of the variance compared to the predictor amount of non-cropped open habitats (length of boundaries, r^2 : 0.5262; amount of non-cropped open habitats, r^2 : 0.333). As the direction of the relationship was similar for all significant results and the trend in progression was similar in scale and time dependency for both landscape predictors, length of boundaries was chosen as predictor for the amount of potential hibernation sites in further analyses.

Statistical analyses were conducted using STATISTICA for Windows Package 6.0 (StatSoft Inc., Tulsa, USA) and PAST (version 1.80; Hammer et al., 2001).

3. Results

A total of 1669 carabids belonging to 42 species were trapped at the 12 study sites during the sampling period (Appendix B). The carabid assemblage was dominated by spring-breeding species (1588 individuals, 37 species). Of these, 1266 individuals (22 species) were macropterous, while 202 individuals (4 species) were brachypterous. Eleven dimorphous species represented by 120 individuals were excluded from further analyses.

Species richness and activity density of brachypterous (activity density: $F_{1,1,12,3} = 10.66$, $p < 0.01$; species richness: $F_{1,5,16,2} = 9.22$, $p < 0.01$) and macropterous species (activity density: $F_{1,1,12,5} = 23.18$, $p < 0.001$; species richness: $F_{1,5,16,7} = 15.9$, $p < 0.001$) significantly increased over time (Fig. 1).

Boundary length had a negative relationship with activity density and species richness of brachypterous carabids that was particularly strong during the early period of investigation (Fig. 2, Appendix D). During phase 1 (first 9 days of investigation), the correlations became significant at a distance of 450 m and reached maximum strength at 900 m (activity density; Fig. 2a) or 750 m (species richness; Fig. 2c). Concerning activity density, this pattern strengthened during phase 2 and diminished during phase 3. The maximum strength during phase 2 already occurred at 600 m. Regarding species richness the correlation became significant during phase 2 at a distance of 300 m and reached maximum strength at 750 m. During phase 3 species richness was only negatively related to length of boundaries at 600 m.

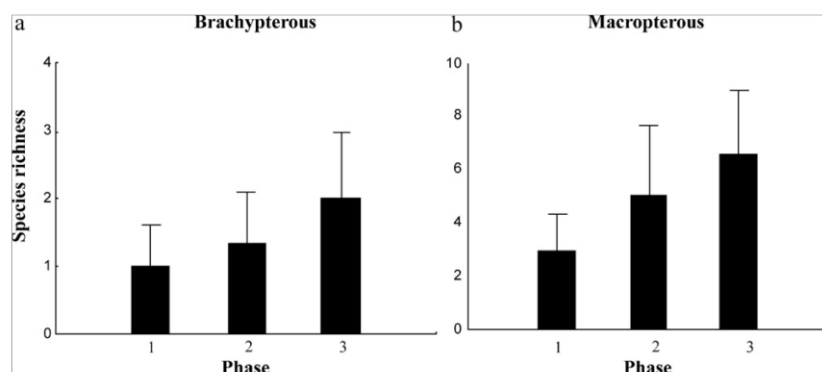


Fig. 1. Changes in mean brachypterous (a) and macropterous (b) species richness of spring breeding carabid beetles at three consecutive sampling phases. Given are mean (boxes) and standard error (error bars).

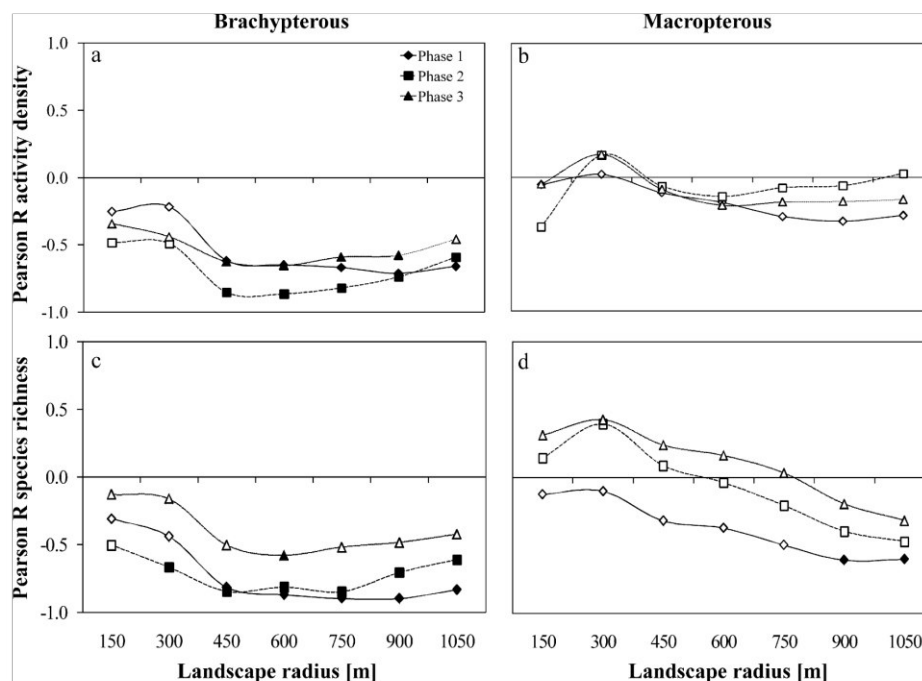


Fig. 2. Pearson correlation coefficient for the relationship between boundary length at different scales and activity density of brachypterous (a) and macropterous (b), spring breeding carabid beetles and species richness of brachypterous (c) and macropterous (d), spring breeding carabid beetles at consecutive sampling phases in spring: phase 1 ($\diamond$), phase 2 ($\square$) and phase 3 ($\triangle$). Filled symbols represent significant effect of boundary length.

Activity density of macropterous spring-breeders remained unaffected by boundary length during the whole period of investigation (Fig. 2b, Appendix D). In contrast, species richness was negatively related to boundary length during phase 1 (Fig. 2d). The correlations became significant at a distance of 900 m and reached maximum strength at 1050 m radius.

4. Discussion

The increase of species number and activity density during the course of our investigation reflects the progressive colonisation of winter barley fields from hibernation refuges by spring breeding carabids. However, the major result of this study is that a high amount of boundary structures and non-cropped open habitats in a landscape has a negative impact on the colonisation speed of spring breeding carabids, with brachypterous species being particularly sensitive to this parameter. These findings seem to contradict studies reporting a positive effect of land-use heterogeneity and availability of overwintering habitats on carabid beetle diversity (e.g. Werling and Gratton, 2008). Contrary to the present investigation these studies were mostly carried out later in the season when carabid beetles achieve highest densities. The negative relationship between the amount of potential hibernation sites and the activity density and diversity of carabid beetles observed in this study was largely confined to the early phase of the investigation and diminished in later sampling phases.

While field boundaries are usually preferred (Holland et al., 2009), hibernation can as well take place in the soil of arable fields or in less adequate field edges (Sotherton, 1984; Pfiffner and Luka, 2000). For the early phase of the present investigation, this may partly explain the high share of brachypterous species captured in fields located in simplified landscapes (low amounts of boundary structures and non-cropped open habitats) due to large patch sizes

and a low heterogeneity of land use. Given a lack of high quality hibernation habitats in simplified landscapes, carabids that were hibernating in the fields themselves, were most likely the first individuals to be captured in our pitfall traps in early spring. In contrast, in regions with a high availability of boundary strips and/or semi-natural habitats, carabid beetles might have spent more time in perennial hibernation habitats before colonising the arable fields.

The impact of potential hibernation sites on carabid colonisation may suggest that species are more attracted to boundary and non-cropped habitats in general. Dennis et al. (2000) found habitats providing refugia for generalist predators after disturbance may also affect those species during spring and summer by still providing favourable zones of microclimate, shelter, and food. Weed strips may therefore prevent further colonisation of arable fields by some species (Saska et al., 2007). Also Bommarco and Fagan (2002) showed that the carabid beetle *Poecilus cupreus* (Linné) was more strongly attracted to leys than to barley fields early in the growing season. This pattern reverses afterwards indicating a higher attraction of crop habitats for this species in the later season.

Perennial habitats can reduce the dispersal of ground beetles by providing higher resource supply and more favourable microclimatic conditions for beetles in spring (e.g. Bommarco, 1999). Honek and Jarosik (2000), for example, report about a higher aggregation tendency of carabids due to microclimatic conditions and food availability. This factor should particularly affect less mobile species, which are not able to rapidly move between habitats.

Landscape structures, functioning as barriers, can additionally modulate the time course of carabid colonisation by constraining dispersal (Frampton et al., 1995). Landscapes that are rich in boundaries as potential hibernation sites may thus at the same time be quite "impermeable". This factor probably is negligible for the very mobile macropterous species dispersing by flight (Thiele, 1977), but it could have dramatic effects on the colonisation of

arable fields by brachypterous species, which can only disperse by walking.

Significant effects of boundary length and non-cropped open habitats on the colonisation of arable fields by spring breeding carabids could only be established, when landscape radii ≥ 300 m were included into the analysis. This may partly be due to a statistical bias, since the amount of potential hibernating sites occurring in smaller radii may be too low for making their effect detectable in a highly variable data set. A complementing explanation is that the various effects of landscape features on the sequence of colonisation discussed in the previous paragraphs reciprocally compensate each other within the immediate surroundings of arable fields. However, this does not explain scale-specific differences in the response of brachypterous and macropterous species. These differences are most likely due to the fact that the scale at which landscape factors alter carabid abundance and diversity depends on their dispersal potential (Dauber and Purtauf, 2007). Thus, landscape composition probably affected less mobile brachypterous species already at comparatively small distances (≥ 300 m), while the effect on flying macropterous species during the first sampling phase was confined to distances ≥ 900 m (cf. Dauber and Purtauf, 2007). This may also explain why the species richness but not the activity density of macropterous beetles was negatively affected by landscape composition.

A positive influence of surrounding boundaries and grasslands was demonstrated on spiders colonising barley fields after winter (Öberg et al., 2008). In contrast to spiders, carabid assemblages in agroecosystems include many species that consume plant material (Thiele, 1977) that is largely provided in spring by plants in adjacent perennial habitats. Spiders and carabid beetles further differ in their ability to tolerate starvation (cf. Anderson, 1974; Young, 2008) and differ in their dispersal capabilities. Ballooning by spiders as a passive flight mode often only leads to dispersal distances of up to 500 m (Schmidt and Tschardt, 2005), whereas flying carabid beetles actively disperse over larger distances (Chapman et al., 2005).

To conclude, the present results support the hypothesis that the early phase of winter barley field colonisation by spring breeding carabids depends on the availability of boundary structures and non-cropped open habitats providing potential hibernation habitats. They also confirm that brachypterous species are much more sensitive to these landscape features than more mobile, macropterous species. It was shown that the return of ground beetles from overwintering refuges can be delayed in arable fields located in landscapes rich in boundary structures and non-cropped open habitats. This does not necessarily imply, however, that land-use heterogeneity and availability of grasslands and semi-natural habitats have no positive effect on carabids (cf. Werling and Gratton, 2008). In fact, investigations carried out in the same region as the present study suggest that the negative effects of boundary structures and grasslands on the early sequence of carabid colonisation can be compensated later during the year (e.g. Dauber and Purtauf, 2007). Nevertheless, the findings of the present study clearly demonstrate that environmental factors modulating the dispersal of taxa with multiple habitat requirements deserve much more attention in future studies on the relationship between landscape composition and species diversity. The long-term compensation of boundary structures on colonisation processes mentioned above could be largely due to the fact that these studies were conducted in a region, where agriculture is characterized by low-input systems with small field sizes (Simmering et al., 2006). In landscapes more impoverished in boundary structures and grasslands, where such compensation is not possible, the sequence of assemblage establishment may have lasting effects on assemblage structure, an aspect that should be considered in developing biological control strategies (Barbosa, 1998).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2011.08.019.

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Appendix A: Landscape characteristics of the investigated fields: cover of perennial grassland, fallow land, arable land and length of forest edges in a 1050 m landscape circle and length of boundaries in the seven landscape circles with different radii

Study site	Grassland cover [%]	Fallow land [%]	Arable land cover [%]	Forest edges [km]
	Radius 1050 m	Radius 1050 m	Radius 1050 m	Radius 1050 m
1	18.3	1.7	42.8	12.0
2	34.9	1.8	22.1	40.3
3	25.6	0.5	41.1	11.8
4	24.2	0.8	35.7	17.0
5	17.0	0.1	32.2	25.1
6	7.2	0.1	81.6	0.2
7	7.5	0.6	67.3	11.5
8	20.5	1.5	26.0	23.8
9	14.8	0.4	56.4	14.8
10	31.4	0.2	27.5	21.8
11	31.7	0.7	22.4	11.7
12	13.4	1.0	51.2	15.0

Study site	Length of boundaries [km]						
	Radius						
	150 m	300 m	450 m	600 m	750 m	900 m	1050 m
1	1.6	8.2	17.5	30.4	45.4	60.0	79.6
2	2.1	8.6	21.6	35.9	57.8	82.7	113.1
3	1.5	5.7	12.6	23.3	40.1	62.6	87.5
4	1.7	5.2	15.5	28.3	43.2	64.3	86.5
5	1.9	7.3	13.4	23.8	37.4	54.6	74.8
6	1.6	4.5	10.7	20.5	36.0	53.8	77.6
7	2.3	7.6	17.6	31.8	48.3	69.4	91.3
8	2.3	8.0	19.3	31.0	48.8	67.4	89.1
9	2.1	8.5	17.8	28.0	41.8	57.9	80.4
10	2.3	8.0	22.0	38.6	58.0	78.6	100.3
11	2.8	10.2	20.9	32.6	47.2	61.4	76.0
12	1.5	6.3	15.9	27.6	40.5	60.4	84.7

Appendix B: Activity density of carabids captured on 12 winter-sown barley fields and activity density after temporal standardisation of sampling periods (Phases 1-3) by bloom of *Taraxacum officinale*. Classification of breeding type (BT) and dispersal ability (DA)

	BT ^a	DA ^b	Total activity density	After standardisation		
				Phase 1	Phase 2	Phase 3
<i>Poecilus cupreus</i> (Linné 1758)	I	m	2184	20	125	671
<i>Carabus granulatus</i> Linné 1758	I	(b)*	249	14	38	87
<i>Poecilus versicolor</i> (Sturm 1824)	I	m	186	2	40	103
<i>Asaphidion flavipes</i> (Linné 1761)	I	m	146	36	20	36
<i>Loricera pilicornis</i> (Fabricius 1775)	I	m	103	11	26	37
<i>Pterostichus melanarius</i> (Illiger 1798)	L	d	94	4	23	36
<i>Bembidion lampros</i> (Herbst 1784)	I	d	88	14	26	24
<i>Carabus nemoralis</i> Müller 1764	I	b	58	8	10	21
<i>Harpalus affinis</i> (Schränk 1781)	I	m	49	4	5	22
<i>Agonum mülleri</i> (Herbst 1784)	I	m	44	8	8	14
<i>Bembidion obtusum</i> (Serville 1821)	I	d	30	7	9	3
<i>Anchomenus dorsalis</i> (Pontoppidan 1763)	I	m	30	0	0	6
<i>Carabus auratus</i> Linné 1761	I	b	24	0	1	11
<i>Carabus cancellatus</i> Illiger 1798	I	b	23	0	0	12
<i>Trechus quadristriatus</i> (Schränk 1781)	L	d	20	1	4	1
<i>Bembidion tetracolum</i> Say 1823	I	d	19	4	6	3
<i>Clivina fossor</i> (Linné 1758)	I	d	16	1	2	6
<i>Amara plebeja</i> (Gyllenhal 1810)	I	m	15	0	0	9
<i>Bembidion lunulatum</i> (Fourcroy 1785)	I	m	13	4	3	0
<i>Nebria salina</i> Fairmaire 1854	L	m	13	2	1	3
<i>Amara similata</i> (Gyllenhal 1810)	I	m	11	0	5	6
<i>Amara aenea</i> (Degeer 1774)	I	m	10	3	5	2
<i>Amara familiaris</i> (Duftschmid 1812)	I	m	10	0	6	4
<i>Notiophilus biguttatus</i> (Fabricius 1779)	I	d	9	0	4	1
<i>Amara communis</i> (Panzer 1797)	I	m	7	1	3	1
<i>Amara eurynota</i> (Panzer 1797)	L	m	7	0	1	4
<i>Bembidion quadrimaculatum</i> (Linné 1761)	I	m	7	1	2	2
<i>Amara lunicollis</i> Schiödt 1837	I	m	5	0	1	3
<i>Anisodactylus binotatus</i> (Fabricius 1787)	I	m	4	0	0	1
<i>Bembidion properans</i> (Stephens 1829)	I	d	4	2	0	1
<i>Acupalpus meridianus</i> (Linné 1761)	I	m	3	0	1	1
<i>Harpalus rubripes</i> (Duftschmid 1812)	I	m	3	1	0	2
<i>Harpalus rufipes</i> (Degeer 1774)	L	m	3	0	0	0
<i>Notiophilus aquaticus</i> (Linné 1758)	I	d	3	1	1	0
<i>Amara convexior</i> Stephens 1828	I	m	2	0	1	1
<i>Amara ovata</i> (Fabricius 1792)	I	m	2	0	1	0
<i>Bembidion guttula</i> (Fabricius 1792)	I	d	2	0	0	2
<i>Molops elatus</i> (Fabricius 1801)	?	b	2	1	0	0
<i>Platynus assimile</i> (Paykull 1790)	I	m	2	0	0	1
<i>Pterostichus nigrata</i> (Paykull 1790)	I	d	2	0	0	0
<i>Stomis pumicatus</i> (Panzer 1796)	I	d	2	0	0	1
<i>Trechoblemus micros</i> (Herbst 1784)	I	m	2	0	0	0
<i>Badister sodalis</i> (Duftschmid 1812)	I	m	1	0	1	0
<i>Bembidion biguttatum</i> (Fabricius 1779)	I	m	1	0	0	0
<i>Bembidion gilvipes</i> Sturm 1825	I	d	1	0	0	1
<i>Brachinus explodens</i> Duftschmid 1812	?	m	1	0	0	0
<i>Carabus convexus</i> Fabricius 1775	I	b	1	0	0	0
<i>Harpalus signaticornis</i> (Duftschmid 1812)	?	m	1	0	0	0
<i>Notiophilus palustris</i> (Duftschmid 1812)	I	d	1	0	0	1

^a I = imago hibernation (spring-breeders), L = larval hibernation (autumn-breeders), ? = no classification possible

^b b = brachypterous, d = dimorph, m = macropterous;

* = brachypterous individuals of the wing-dimorphic species *Carabus granulatus*

Characterizations according to Lindroth (1985,1986), Luff (1998) and Ribera et al. (2001).

Appendix C: Pearson correlation coefficient for the relationship between length of boundaries and the amount of grassland and fallows

		Amount of non-cropped open habitats [ha]						
		150 m	300 m	450 m	600 m	750 m	900 m	1050 m
Length of boundaries [km]	Landscape radius							
	150 m	0.4730	0.4991	0.5346	0.4706	0.5105	0.4474	0.3678
	300 m	0.4548	0.6123	0.5540	0.5342	0.5626	0.5081	0.4550
	450 m	0.4447	0.6312	0.7149	0.6920	0.6863	0.6622	0.6374
	600 m	0.3265	0.5381	0.6900	0.6842	0.6642	0.6465	0.6168
	750 m	0.3828	0.5766	0.7161	0.7024	0.6895	0.6887	0.6659
	900 m	0.3710	0.5176	0.6461	0.6141	0.5979	0.6306	0.6359
	1050 m	0.3242	0.4440	0.5084	0.4598	0.4400	0.5038	0.5387

Appendix D: Relation between the landscape predictors length of boundaries [km] (BOUND) and amount of non-cropped open habitats (NON-CROP) and species richness (Sobs) and activity density (AD) for macropterous and brachypterous carabid beetles during different phases at different scales (Table 1). Pearson product moment correlation coefficients (Table 2) are shown to display the direction of a relationship.

Table 1: Regression coefficient (r^2)

		Macropterous carabid beetles					
Landscape radius		Phase 1		Phase 2		Phase 3	
		AD	Sobs	AD	Sobs	AD	Sobs
150 m	BOUND	0.0033	0.0152	0.1384	0.0206	0.0029	0.0968
	NON-CROP	0.0704	0.1258	0.0252	0.0214	0.1904	0.0271
300 m	BOUND	0.0004	0.0101	0.0267	0.1553	0.0278	0.1807
	NON-CROP	0.0973	0.1491	0.0699	0.0080	0.1910	0.0005
450 m	BOUND	0.0138	0.1016	0.0048	0.0075	0.0086	0.0564
	NON-CROP	0.1222	0.1755	0.0206	0.0145	0.1100	0.0077
600 m	BOUND	0.0356	0.1372	0.0213	0.0014	0.0446	0.0261
	NON-CROP	0.1445	0.1665	0.0458	0.0146	0.1286	0.0104
750 m	BOUND	0.0866	0.2472	0.0065	0.0426	0.0347	0.0011
	NON-CROP	0.1553	0.1876	0.0554	0.0115	0.1645	0.0145
900 m	BOUND	0.1083	0.3695	0.0041	0.1573	0.0334	0.0379
	NON-CROP	0.1328	0.1883	0.0668	0.0253	0.1953	0.0079
1050 m	BOUND	0.0820	0.3606	0.0007	0.2234	0.0282	0.1003
	NON-CROP	0.1370	0.2213	0.0880	0.0299	0.2114	0.0018
		Brachypterous carabid beetles					
Landscape radius		Phase 1		Phase 2		Phase 3	
		AD	Sobs	AD	Sobs	AD	Sobs
150 m	BOUND	0.0649	0.0965	0.2352	0.2552	0.1178	0.0171
	NON-CROP	0.0526	0.0888	0.2200	0.1575	0.0079	0.0641
300 m	BOUND	0.0478	0.1937	0.2413	0.4472	0.1954	0.0268
	NON-CROP	0.0899	0.2569	0.3505	0.4040	0.0349	0.0081
450 m	BOUND	0.3820	0.6639	0.7315	0.7166	0.3940	0.2544
	NON-CROP	0.1921	0.4351	0.5328	0.4921	0.1576	0.0168
600 m	BOUND	0.4226	0.7566	0.7500	0.6632	0.4311	0.3370
	NON-CROP	0.2007	0.4432	0.5252	0.4790	0.1713	0.0180
750 m	BOUND	0.4472	0.8044	0.6757	0.7210	0.3512	0.2704
	NON-CROP	0.1916	0.4169	0.4768	0.4821	0.1704	0.0119
900 m	BOUND	0.5084	0.8051	0.5475	0.4998	0.3365	0.2355
	NON-CROP	0.2164	0.4691	0.4477	0.4941	0.1578	0.0117
1050 m	BOUND	0.4341	0.6927	0.3521	0.3750	0.2112	0.1803
	NON-CROP	0.2445	0.4939	0.4591	0.4738	0.1574	0.0173

Table 2: Pearson product moment coefficient (R)

			Macropterous carabid beetles					
Landscape radius			Phase 1		Phase 2		Phase 3	
			AD	Sobs	AD	Sobs	AD	Sobs
150 m	BOUND		-0.0577	-0.1234	-0.3720	0.1434	-0.0543	0.3111
	NON-CROP		-0.2653	-0.3547	0.1589	-0.1462	0.4363	-0.1646
300 m	BOUND		0.0195	-0.1006	0.1633	0.3941	0.1668	0.4251
	NON-CROP		-0.3119	-0.3861	0.2643	-0.0895	0.4370	-0.0232
450 m	BOUND		-0.1175	-0.3188	-0.0695	0.0866	-0.0929	0.2375
	NON-CROP		-0.3496	-0.4189	0.1436	-0.1203	0.3317	0.0880
600 m	BOUND		-0.1887	-0.3704	-0.1458	-0.0378	-0.2113	0.1617
	NON-CROP		-0.3801	-0.4080	0.2139	-0.1210	0.3586	0.1018
750 m	BOUND		-0.2942	-0.4972	-0.0805	-0.2064	-0.1863	0.0329
	NON-CROP		-0.3941	-0.4331	0.2353	-0.1074	0.4056	0.1206
900 m	BOUND		-0.3291	-0.6079	-0.0644	-0.3966	-0.1827	-0.1948
	NON-CROP		-0.3644	-0.4339	0.2585	-0.1590	0.4419	0.0888
1050 m	BOUND		-0.2863	-0.6005	0.0255	-0.4726	-0.1679	-0.3167
	NON-CROP		-0.3702	-0.4704	0.2967	-0.1730	0.4598	0.0429
			Brachypterous carabid beetles					
Landscape radius			Phase 1		Phase 2		Phase 3	
			AD	Sobs	AD	Sobs	AD	Sobs
150 m	BOUND		-0.2547	-0.3106	-0.4850	-0.5052	-0.3432	-0.1308
	NON-CROP		-0.2293	-0.2980	-0.4690	-0.3969	-0.0891	0.2531
300 m	BOUND		-0.2187	-0.4401	-0.4912	-0.6687	-0.4420	-0.1636
	NON-CROP		-0.2999	-0.5069	-0.5920	-0.6356	-0.1867	0.0899
450 m	BOUND		-0.6181	-0.8148	-0.8553	-0.8465	-0.6277	-0.5044
	NON-CROP		-0.4383	-0.6596	-0.7299	-0.7015	-0.3970	-0.1296
600 m	BOUND		-0.6501	-0.8698	-0.8660	-0.8144	-0.6566	-0.5805
	NON-CROP		-0.4480	-0.6657	-0.7247	-0.6921	-0.4139	-0.1342
750 m	BOUND		-0.6687	-0.8969	-0.8220	-0.8491	-0.5926	-0.5200
	NON-CROP		-0.4377	-0.6457	-0.6905	-0.6943	-0.4128	-0.1089
900 m	BOUND		-0.7130	-0.8973	-0.7399	-0.7070	-0.5801	-0.4853
	NON-CROP		-0.4652	-0.6849	-0.6691	-0.7029	-0.3973	-0.1081
1050 m	BOUND		-0.6589	-0.8323	-0.5934	-0.6124	-0.4596	-0.4246
	NON-CROP		-0.4945	-0.7028	-0.6776	-0.6883	-0.3967	-0.1314

KAPITEL 5

LANDSCAPE AND MANAGEMENT EFFECTS ON STRUCTURE AND FUNCTION OF SOIL ARTHROPOD COMMUNITIES IN WINTER WHEAT

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Landscape and management effects on structure and function of soil arthropod communities in winter wheat

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ABSTRACT

This study evaluates the impact of agricultural management (organic vs. conventional) and landscape context on species richness and abundance of five soil arthropod taxa (ground beetles, spiders, springtails, millipedes, woodlice) and associated ecosystem functions (soil biological activity, weed seed predation, litter decomposition). A significant interaction between management type and landscape context was revealed in several cases. Activity density of millipedes and wood lice and species richness of ground beetles were higher in fields where local and regional management types were complementary, indicating a beneficial effect of environmental heterogeneity. In addition, seed predation on arable weeds was higher in organically than conventionally managed fields. It is concluded that the effect of agricultural management on soil arthropod biodiversity and functioning is often context dependent. The diversity of functionally important taxa such as ground beetles and decomposers may be enhanced by increasing environmental heterogeneity, a measure that is also beneficial for other components of agrobiodiversity. Thus, in a conventional agricultural context even managing only a fraction of fields organically may help to increase environmental heterogeneity and thereby promote soil arthropod diversity and the associated ecosystem functions.

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1. Introduction

Organic farming goes without synthetic pesticides and mineral fertilizers and relies on frequent crop rotations that result in increased spatial and temporal heterogeneity (Benton et al., 2003). Therefore, a positive effect of organic farming on local species richness and abundance may be more pronounced in homogenous landscapes with large proportions of arable land than in heterogeneous ones that already offer a diverse range of habitats (Rundlöf et al., 2008). This relationship has frequently been documented for mobile, flower dependent pollinators (Bengtsson et al., 2005; Rundlöf and Smith, 2006; Rundlöf et al., 2008). In contrast, our knowledge on the interacting effects of agricultural management and landscape context on surface-dwelling soil macroinvertebrates and the associated ecosystem services, such as seed predation, litter decomposition or biological control remains scarce (e.g. Dauber et al., 2005; Purtauf et al., 2005b; Farwig et al., 2009).

In these few studies on local vs. landscape controls of surface-dwelling soil macroinvertebrates, diversity was affected by local land use when comparing arable fields with grasslands and fallow land (Dauber et al., 2005). In contrast, when comparing carabid species richness in organic and conventional fields, management had no significant effect (Purtauf et al., 2005b). Landscape context, however, was always important in explaining the soil macroinvertebrate diversity, though sometimes significantly interacting (Dauber et al., 2005) and sometimes independent (Purtauf et al., 2005b) of land-use type or management. Additionally, a diverse range of habitat and trophic needs in different species (Dauber et al., 2005; Purtauf et al., 2005a; Schweiger et al., 2005) seems to complicate a general understanding of how agricultural management and landscape context affect the diversity of surface-dwelling soil macroinvertebrates and associated ecosystem.

Here, the effects of agricultural management and landscape context on species richness and abundance of ground beetles, spiders, springtails, millipedes and wood lice and associated ecosystem functions, namely soil biological activity (Beare et al., 1992), weed seed predation (Westerman et al., 2003) and plant litter decomposition (Bradford et al., 2002) were studied. As weed seed predation and litter decomposition rates have both been shown to be affected by the diversity of soil organisms (Hattenschwiler et al., 2005; Baraibar et al., 2009) and the diversity of soil organisms, in turn, is known to be affected by microclimate

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(Harte et al., 1996), resource availability (Ilieva-Makulec et al., 2004), habitat complexity and landscape diversity (Vanbergen et al., 2007) it was hypothesised that (i) surface-dwelling soil macroinvertebrates would show higher diversity in organically than in conventionally managed fields, (ii) this positive effect of organic farming would be more pronounced in a simple compared to a complex landscape context, and (iii) a higher diversity of surface-dwelling soil macroinvertebrates would lead to higher seed predation and a higher litter decomposition rate in organically managed fields.

2. Methods

2.1. Study sites

The study was conducted in the Wetterau, an intensively managed agricultural region of about 1000 km² in central Hesse, Germany. More than 50% of the area is farmland (ca. 3/4 crops and 1/4 grassland), about 30% is woodland. These dominant land-use types are interspersed with settlements and semi-natural habitat elements. Mean annual precipitation of the region ranges from 500 to 700 mm, mean annual temperature from 9.1 to 10.0 °C. In this area, altogether 12 winter-wheat fields were selected for arthropod sampling (six organically and six conventionally managed fields). The proportion of organically and conventionally managed arable land as well as other main land-use types was determined in a landscape sector with a radius of 1000 m radius around each field using spatially explicit information on agricultural land-use in Arc View GIS 3.2. Based on this proportion of organically and conventionally managed arable land, within each management type, three fields were situated in an organic or a conventional landscape context, respectively. Fields in an organic landscape context had a significantly higher proportion of organically managed crops in a 1000 m radius than those in a conventional context (Mann-Whitney *U*-test; $N = 12$, $Z = -2.88$, $P = 0.004$; org.: 6–21%, con.: 0–4%). Otherwise, landscape sectors with an organic or conventional context did not significantly differ in landscape composition (Mann-Whitney *U*-test; $N = 12$, $P \geq 0.128$; Table 1). Whereas conventional fields received 160–220 kg inorganic N per hectare, organic fields received no such synthetic fertilizer but 0–125 kg organic N per hectare in form of animal or green manure. In organic fields, nitrogen was also provided by including legumes in the crop rotation. Preceding crops included winter wheat, oilseed rape and sugar beet in conventional fields and winter wheat, sugar beet, or legumes in organic ones. Organic fields have been under this management for 5–13 y. Organically managed fields did not differ significantly in wheat stand density (Mann-Whitney *U*-test; $N = 12$, $Z = 0.38$, $P = 0.378$), pH ($N = 12$, $Z = 0.15$, $P = 0.159$) or soil water content ($N = 12$, $Z = 0.64$, $P = 0.522$) from conventionally managed fields but wheat stands were significantly higher ($N = 12$, $Z = 2.32$, $P = 0.020$) and weed species richness tended to be higher in organically compared to conventionally managed fields ($N = 5$, $Z = 1.73$, $P = 0.083$).

Table 1

Range of the area percentage of different land-use types in landscape sectors with a radius of 1000 m around focal winter-wheat fields with an organic ($N = 6$) or conventional ($N = 6$) landscape context.

Land-use type	Organic [%]	Conventional [%]
Arable crop	52.4–76.3	51.3–80.7
Grassland	1.3–14.0	4.9–19.4
Groves and shrubbery	0.3–2.5	0.4–4.2
Forest	0.0–22.5	0.0–12.9
Settlement	1.7–16.4	4.0–23.0

2.2. Arthropod diversity

Arthropods were sampled with 36 pitfall traps in each of the 12 winter-wheat fields. Traps within a field were placed in a regular grid of six rows and six columns using a spacing of six meters between neighbouring traps. Pitfall traps were 90 mm in diameter and had a volume of 500 ml. They were filled with 150 ml of an ethyleneglycol–water solution (1:3) with a detergent added to reduce surface tension. Traps were left open for 14 d in May/June 2007. All samples were returned to the laboratory and ground beetles (Carabidae), spiders (Araneae), millipedes (Diplopoda), woodlice (Isopoda) and epedaphic springtails (entomobryid Collembola) were sorted and counted from all 432 pitfall traps. All millipedes and woodlice were identified to genus or species level. Ground beetles and spiders from a random subsample of eight traps per field were identified to species level. Pitfall catches reflect the activity and density of species and results should be presented as activity density (Topping and Sunderland, 1992).

2.3. Ecosystem functions

Soil biological activity was measured using bait-lamina probes. The probes were strips of rigid plastic, 6 mm × 160 mm, bearing a series of 16 holes (Ø 1.5 mm) drilled at 5 mm intervals in the lower half of the strip. Holes were filled with bait made of cellulose, agar-agar, bentonite, and wheat bran (Eisenbeis, 1998) and intended to mimic dead plant material in the soil. Soil organisms feed on this substrate such that the number of bait holes that is intact or completely removed provides an estimate of soil fauna feeding activity (Törne, 1990). Bait-lamina strips were inserted next to each pitfall trap so that the uppermost hole was just below the soil surface. Bait-lamina strips were removed from soil after 14 d of exposure. For analysis, we counted the number of completely pierced holes per strip and averaged this number of holes over all 36 bait-lamina strips per field.

Litter decomposition was assessed using litter bags. Litter bags were made from nylon gauze of different mesh sizes (45 µm and 4 mm) and were 25 cm × 25 cm in size. Each bag was filled with 10 g of wheat straw. In each field litter bags were exposed in two series of two pairs on the ground between two rows of wheat. Pairs of litter bags of the same mesh size within each series were spaced at 1 m distance to pairs of alternative mesh sizes; the two series were spaced at 5 m distance. Litter bags were placed in the field on 19/20 May 2007 and collected from the field on 7/8 June 2007. The remaining wheat straw per bag was oven-dried and weighed afterwards. For analysis, we averaged the weight of remaining wheat straw over the four litter bags of the same type per field. We then calculated the difference between bags of the smallest and largest mesh sizes per field to provide an estimate of soil macro-decomposer activity, excluding litter loss through microbial activity.

Weed seed predation was investigated by using seed cards in enclosure cages (25 cm height, 20 cm diameter). Enclosures were constructed of galvanized metal hardware cloth of differing mesh size. Enclosures had a mesh size of 1.5 mm for invertebrate and vertebrate exclusion and of 12.7 mm for the exclusion of vertebrates. Control cages were of the same type as vertebrate enclosures but had three ground-level openings of 10 cm × 10 cm. All enclosures were fixed 3 cm in the ground at 1 m distance to each other between two rows of wheat. Seed cards, one of which was placed in each enclosure, were made of firm, high quality sand paper (7.7 cm × 14.0 cm, grain size 60) sprayed with repositionable glue (3 M Spray Mount™) after Westerman et al. (2003). The glue ensured that seeds stayed on the cards under normal weather conditions while seed predators were still able to remove seeds. Each card contained 15 seeds of *Crepis biennis* (0.67 mg per seed),

Table 2

Results of permutational analyses of variance on the activity density, species richness and community composition of ground beetles, spiders, macrofauna decomposers (millipedes and woodlice) and entomobryid springtails (only activity density) and on the ecosystem services soil animal feeding activity, litter decomposition and seed predation.

Source	df	Activity density								Ecosystem service					
		Ground beetles		Spiders		Decomposers		Springtails		Feeding activity		Litter decomposition		Seed predation	
		F	P	F	P	F	P	F	P	F	P	F	P	F	P
Farming	1	0.000	0.970	1.380	0.287	0.490	0.511	0.310	0.595	0.79	0.384	0.08	0.765	6.03	0.039
Landscape	1	0.680	0.417	3.610	0.096	2.470	0.155	0.040	0.825	0.44	0.510	0.14	0.712	2.18	0.187
Far × Lan	1	1.350	0.272	2.440	0.165	6.470	0.033	0.070	0.775	0.27	0.632	1.15	0.299	2.68	0.146
Residual	8														

Source	df	Species richness						Community composition					
		Ground beetles		Spiders		Decomposers		Ground beetles		Spiders		Decomposers	
		F	P	F	P	F	P	F	P	F	P	F	P
Farming	1	0.030	0.823	1.240	0.287	0.000	1.000	0.970	0.467	1.500	0.160	0.880	0.489
Landscape	1	2.030	0.206	0.910	0.370	2.000	0.203	1.140	0.311	1.300	0.243	1.460	0.224
Far × Lan	1	5.630	0.047	0.230	0.640	3.130	0.101	1.050	0.414	0.890	0.554	0.440	0.877
Residual	8												

Values in bold are significant.

20 seeds of *Taraxacum officinale* (0.48 mg per seed), 20 seeds of *Viola arvensis* (0.46 mg per seed), and 40 seeds of *Capsella bursa-pastoris* (0.23 mg per seed). The remaining glue was covered with fine sand to prevent invertebrates from sticking to the glue. Nails were used to secure the seed cards to the ground. Seed cards were laid out on two occasions per field in late May/early June 2007 and collected after 4 d in the field. For analysis, the remaining number of all seeds per seed card was counted, averaged over the two sampling periods and the difference between invertebrate and vertebrate exclosures per field was calculated to provide an estimate of seed predation by soil arthropods.

2.4. Statistical analysis

The fixed factors management type (org. vs. con.) and landscape context (org. vs. con.) and the interaction between both main factors were included in our model. Species richness and abundance of (1) ground beetles (2) spiders and (3) millipedes and woodlice and abundance of entomobryid Collembola were tested with a two-factorial, permutational analyses of variance based on 10,000 permutation runs and Euclidean distances (Anderson, 2001). In case of a small number of possible unique permutation results, Monte-Carlo simulations were used to derive *P*-values. All data were log + 1 transformed prior to analysis. Differences in community composition and ecosystem functions between management or landscape context were tested using the Bray–Curtis statistic as the measure of ordination distance among arthropod communities, because it is one of the most robust statistics for multivariate ecological analysis and is little affected by the presence of rare species (Krebs, 1999).

3. Results

During this study, 34,936 ground beetles, 6986 spiders, 6868 millipedes, 995 woodlice and 13,113 entomobryid springtails were sampled in 12 winter-wheat fields. Whereas ground beetle or entomobryid springtail activity density was neither affected by management type nor landscape context (Table 2), spiders tended to be affected by the landscape context having a 1.4 times higher activity density in a conventional than organic context (Table 2). The combined activity density of macrofauna decomposer species (millipedes and woodlice) was significantly affected by the interaction between farming system and landscape context (Table 2). Millipedes and woodlice were on average 3.5 times less

abundant in conventional fields that were primarily surrounded by other conventional fields than in conventional fields primarily surrounded by organic fields or organic fields with either landscape context (Fig. 1).

In total 8964 ground beetles, 1262 spiders, 5751 millipedes and 872 woodlice were determined to species level resulting in 56 ground beetle, 40 spider, 10 millipede and 9 woodlice species. Ground beetle species richness was significantly affected by the interaction between farming system and landscape context, as carabid communities were on average 3 species poorer in organically managed fields in an organic landscape context than in the other systems (Fig. 2). Spider and decomposer diversity was not significantly affected by farming system or landscape context (Table 2). Community composition of carabids, spiders and decomposers did not differ among fields of differing management type or landscape context (Table 2).

Soil animal feeding activity and litter decomposition did not differ significantly between management type or landscape contexts (Table 2), but feeding activity correlated positively with

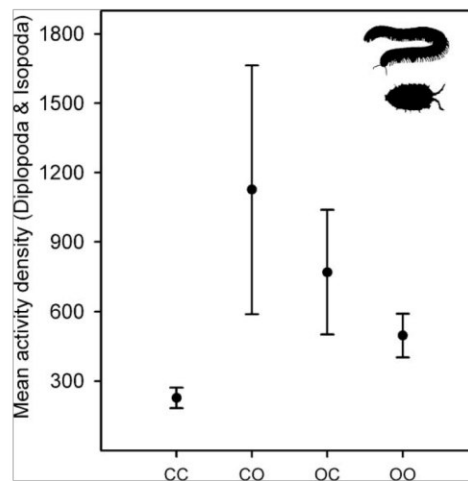


Fig. 1. Mean and standard error of the activity density of macrofauna decomposer species (sum of Diplopoda and Isopoda) depending on the interaction between farming system (first letter: Organic vs. Conventional) and landscape context (second letter: Organic vs. Conventional).

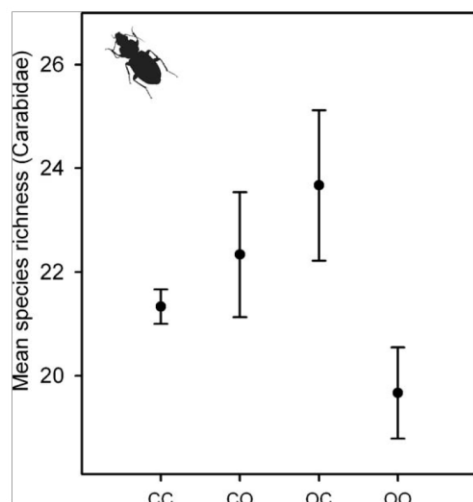


Fig. 2. Mean and standard error of species richness of ground beetles depending on the interaction between farming system (first letter: Organic vs. Conventional) and landscape context (second letter: Organic vs. Conventional).

the activity density of macrofauna decomposer species ($N = 12$, Spearman's $R = 0.65$, $P = 0.022$). In contrast, seed predation differed between management types, with seed removal being significantly higher in organically managed fields (Table 2).

4. Discussion

Agricultural management at the local scale has been shown to affect a variety of soil organisms such as earthworms (Birkhofer et al., 2008a), ground beetles (Döring and Kromp, 2003; Purtauf et al., 2005b) and spiders (Birkhofer et al., 2008b). Congruent with the majority of studies included in a meta-study by Bengtsson et al. (2005), these studies revealed positive effects of organic farming on the abundance or richness of soil organisms. In contrast, a main effect of agricultural management could neither be revealed on activity density, species richness nor community composition of either taxon of soil arthropods in our study. Yet, consistent with our hypothesis we were able to show that even for soil taxa an effect of local management may only become apparent once the landscape context is taken into consideration. This significant management–landscape interaction affected the activity density of macrofauna decomposers and the species richness of ground beetles.

The species richness or activity density of woodlice is known to be largely affected by local management (Paoletti and Hassall, 1999; Dauber et al., 2005) and associated habitat characteristics, such as soil humidity (Dauber et al., 2005), pesticide application or tillage operations (Paoletti and Hassall, 1999). Previously the diversity of woodlice was also shown to be affected by an interaction of local and regional land use (Dauber et al., 2005). The cover of arable land in the vicinity was found to have no effect on species richness in arable fields, whereas it had a positive effect in grassland and a negative effect in fallow land. The local species richness of diplopods was best explained by the proportion of forest in the surrounding landscape but not by local management (Dauber et al., 2005). This effect of regional factors on species richness and the newly revealed landscape effect on decomposer activity density suggest that macrofauna decomposers are also affected by resource complementation. Like other taxa (e.g. Haynes et al., 2007; Holzschuh et al., 2008), in our study, macrofauna decomposer activity density was highest in situations with

complementary resources like in conventional fields with an organic context or in organic fields with a conventional one (Dunning et al., 1992). Surprisingly, the higher macrofauna decomposer activity did not affect rates of soil fauna feeding activity or litter removal. Most likely, other organism groups that were not sampled contributed to those processes and likely masked any effect of diplopods and woodlice. Earthworms and enchytraeids, for example, are known to significantly contribute to bait-lamina feeding and litter removal (Curry and Byrne, 1994; Helling et al., 1998).

The availability of alternative food resources, shelter or places for hibernation in the proximity of a specific habitat element such as a wheat field seemingly increased not only the activity density of woodlice and diplopods but also the species richness of ground beetles. These results concord with findings of Weibull et al. (2003) and Purtauf et al. (2005b) in which the local species richness of ground beetles increased with landscape heterogeneity or the percent cover of grassland in the surrounding, respectively. Bengtsson et al. (2005) proposed that positive effects of organic farming on species richness will be larger in intensively managed agricultural landscapes than in small-scale diverse landscapes with many non-crop biotopes. Positive effects of organic farming indeed only increased abundance and species richness in homogeneous but not in heterogeneous landscapes in butterflies (Rundlöf and Smith, 2006) and bumblebees (Rundlöf et al., 2008). Here, focusing on less mobile species, we were able to confirm these results. The species richness of ground beetles was highest in organically managed wheat fields that were situated in a conventional landscape context and second highest in the opposite situation whereas it was lowest in organic fields in an organic context.

Higher numbers of species in a heterogeneous landscape situation with contrasting local and regional management types may be explained by a higher species pool in complex than simple landscapes (Schweiger et al., 2005) and the exchange among land-use types of species that use multiple habitats during their life cycle (Pfiffner and Luka, 2000; Tschamntke et al., 2008). Likewise the observed pattern in macrofauna decomposers, higher species richness in a heterogeneous landscape may also indicate that ground beetles frequently move between land-use types as they may benefit from resource complementation not only at different stages during their life cycle but also within the same stage (cf. Bommarco and Fagan, 2002; Diekötter et al., 2005; Haynes et al., 2007; Holzschuh et al., 2008). Predaceous carabid species may benefit from an increased availability of potential herbivore prey in highly productive conventionally managed wheat fields (Siemann, 1998; Weibull and Ostman, 2003) and may later shift to organic fields, as they offer ample seeds and prey due to their diversity of arable weeds (Gabriel et al., 2006).

Seeds of arable weeds provide food to many species of ground beetles (Lovei and Sunderland, 1996) and thus seed predation is an ecosystem service that is strongly associated with this taxon (Honek et al., 2003). Although no main effect of management on the species richness, activity density or community composition of ground beetles was apparent in our study, we were able to reveal a significantly higher seed predation in organically than conventionally managed wheat fields. Thus, besides providing resources to one of the most abundant and ecologically meaningful taxa of agricultural landscapes, agro-environmental schemes that aim at an increased floral diversity in agricultural fields seem to similarly foster the biological control of arable weeds.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2010.01.008.

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Landscape and management effects on structure and function of soil arthropod communities in winter wheat (2010) Agriculture, Ecosystems & Environment 137, 108-112
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Appendix List of spider, carabid, millipede and woodlice species caught in each of three wheat fields under either organic (O) or conventional (C) management (first letter) with either organic (O) or conventional (C) landscape context (second letter).

Species	CC	CO	OC	OO
<i>Araeoncus humilis</i>			+	+
<i>Argenna subnigra</i>	+	+	+	+
<i>Aulonia albimana</i>	+		+	
<i>Bathypantes gracilis</i>	+		+	+
<i>Diplocephalus picinus</i>			+	
<i>Diplostyla concolor</i>	+			
<i>Enoplognatha thoracica</i>	+	+	+	+
<i>Eperigone trilobata</i>	+		+	+
<i>Erigone atra</i>	+	+	+	+
<i>Erigone dendipalpis</i>	+	+	+	+
<i>Euryopis flavomaculata</i>			+	
<i>Hahnia nava</i>				+
<i>Leptyphantes tenuis</i>				+
<i>Mangora acalifa</i>	+	+		
<i>Meioneta rurestris</i>	+	+	+	+
<i>Micaria pulicaria</i>	+			+
<i>Micrargus herbigradus</i>			+	
<i>Microlinyphia pusilla</i>	+	+		+
<i>Milleriana inerrans</i>	+	+	+	+
<i>Oedothorax apicatus</i>	+	+	+	+
<i>Oedothorax sp.</i>	+	+		+
<i>Ozyptila simplex</i>		+	+	+
<i>Pachygnatha clercki</i>	+	+	+	+
<i>Pachygnatha degeeri</i>	+	+	+	+
<i>Pardosa agrestis</i>	+	+	+	+
<i>Pardosa lugubris</i>				+
<i>Pardosa palustris</i>	+	+	+	+
<i>Pardosa prativaga</i>	+	+	+	+
<i>Pardosa pullata</i>	+	+		
<i>Pirata piraticus</i>				+
<i>Porrhomma microphthalmum</i>	+	+	+	+
<i>Tenuiphantes tenuis</i>	+	+	+	+
<i>Theridion bimaculatum</i>	+			
<i>Trochosa rucicola</i>	+	+	+	+
<i>Trochosa terricola</i>		+	+	+
<i>Walkenaeria dysderoides</i>		+	+	+
<i>Walkenaeria nudipalpis</i>	+			
<i>Xysticus kochi</i>	+	+	+	+

<i>Zelotes lutetianus</i>	+	+	+	+
<i>Zelotes pusillus</i>		+	+	+
<i>Abax ovalis</i>			+	
<i>Acupalpus meridianus</i>	+	+	+	+
<i>Agonum muelleri</i>		+	+	
<i>Amara aenea</i>		+	+	
<i>Amara eurynota</i>	+			+
<i>Amara familiaris</i>			+	+
<i>Amara lunicollis</i>	+			+
<i>Amara montivaga</i>		+	+	
<i>Amara ovata</i>				+
<i>Amara plebeja</i>		+	+	+
<i>Amara similata</i>	+	+	+	+
<i>Amara tricuspidata</i>			+	+
<i>Anchomenus dorsalis</i>	+	+	+	+
<i>Anisodactylus binotatus</i>	+		+	
<i>Anisodactylus signatus</i>		+		+
<i>Asaphidion flavipes</i>	+	+	+	
<i>Badister bullatus</i>				+
<i>Badister sodalis</i>	+			+
<i>Bembidion guttula</i>				+
<i>Bembidion lampros</i>	+	+	+	+
<i>Bembidion obtusum</i>	+	+	+	+
<i>Bembidion properans</i>	+			
<i>Bembidion tetracolum</i>		+		
<i>Brachinus crepitans</i>		+		+
<i>Brachinus explodens</i>		+	+	
<i>Calathus ambiguus</i>		+		
<i>Calathus fuscipes</i>	+			+
<i>Carabus auratus</i>	+	+	+	+
<i>Carabus granulatus</i>	+			+
<i>Carabus nemoralis</i>	+	+	+	+
<i>Demetrias atricapillus</i>	+	+	+	+
<i>Harpalus affinis</i>	+	+	+	+
<i>Harpalus atratus</i>		+		+
<i>Harpalus dimidiatus</i>	+	+		
<i>Harpalus distinguendus</i>	+	+	+	+
<i>Harpalus latus</i>	+			
<i>Harpalus luteicornis</i>	+		+	+
<i>Harpalus rubripes</i>		+	+	+
<i>Harpalus rufipes</i>	+	+	+	+
<i>Harpalus signaticornis</i>	+		+	
<i>Harpalus tardus</i>			+	+
<i>Loricera pilicornis</i>	+	+	+	
<i>Microlestes maurus</i>			+	
<i>Microlestes minutulus</i>			+	+
<i>Nebria brevicollis</i>	+	+	+	+
<i>Nebria salina</i>	+	+	+	+
<i>Notiophilus aesthuans</i>	+			

<i>Notiophilus biguttatus</i>	+	+	+	+
<i>Notiophilus palustris</i>	+			+
<i>Poecilus cupreus</i>	+	+	+	+
<i>Poecilus versicolor</i>		+		+
<i>Pterostichus melanarius</i>	+	+	+	+
<i>Pterostichus oblongopunctatus</i>	+			+
<i>Pterostichus vernalis</i>	+	+		
<i>Stomis pumicatus</i>	+		+	+
<i>Trechus quadristriatus</i>	+	+	+	+
<i>Brachyiulus pusillus</i>	+	+	+	+
<i>Cylindroiulus caeruleocinctus</i>	+	+	+	+
<i>Diplopoda morphospec. 1</i>	+	+	+	+
<i>Glomeris marginata</i>			+	
<i>Melogona voigti/gallica</i>				+
<i>Polydesmus denticulatus</i>	+		+	
<i>Polydesmus superus</i>	+			
<i>Polydesmus spec.</i>	+	+	+	+
<i>Tachypodiulus niger</i>		+		
<i>Unciger foetidus</i>	+	+	+	+
<i>Armadillium nasatum</i>		+	+	
<i>Armadillium pictum</i>	+	+		
<i>Armadillium pulchellum</i>		+		+
<i>Armadillium vulgare</i>				+
<i>Ligidium hypnorum</i>		+	+	
<i>Oniscus asellus</i>		+		
<i>Philoscia muscorum</i>	+	+	+	+
<i>Porcellio scaber</i>	+	+		
<i>Trachelipus rathkei</i>	+	+	+	+

Zusammenfassung

Der Landnutzungswandel und die Intensivierung in der Landwirtschaft haben in den letzten Jahrzehnten in starkem Maß zu einem Rückgang der Artenvielfalt geführt. Gleichzeitig fehlen noch viele Erkenntnisse hinsichtlich des Einflusses der umgebenden Landschaft auf Artenreichtum, Artenzusammensetzung und ökosystemare Funktionen von Lebensgemeinschaften. Als eine zahlenmäßig sehr bedeutende taxonomische Gruppe sind auch Laufkäfer von den Entwicklungen in der Agrarlandschaft betroffen. Durch die verschiedenen ökologischen Ansprüche der einzelnen Arten ermöglichen sie die Einteilung funktioneller Gruppen, mit deren Hilfe verschiedene Fragestellungen der Landschaftsökologie beleuchtet werden können. Diese Dissertation hat das Ziel, den Einfluss landschaftlicher Steuergrößen auf die Diversität und die Artenzusammensetzung von Laufkäfern und ihrer funktionellen Gruppen, ihre Ausbreitung in der Agrarlandschaft und ihre ökosystemaren Dienstleistungen abzuschätzen. Als Untersuchungssysteme wurden Ackerflächen und Wirtschaftsgrünland herangezogen, die den höchsten Anteil an ackerbaulich genutzter Fläche in Deutschland ausmachen und die sich hinsichtlich ihres Arteninventars und der Auswirkungen landwirtschaftlicher Intensivierung voneinander unterscheiden. In den ersten beiden Studien konnte gezeigt werden, dass die Heterogenität lokaler Habitat- und Managementfaktoren und regionaler Landschaftskompositionen zu stark heterogenen Laufkäfergemeinschaften auf Wirtschaftsgrünland führte, bei denen die Unterschiede der Artenzusammensetzung zwischen den Flächen den größten Teil der regionalen Artenvielfalt ausmachte. Es zeigte sich aber auch, dass die Effektrichtung und Effektstärke der verschiedenen Einflussfaktoren, sowie der Beitrag zu den Komponenten der regionalen Diversität sich für die unterschiedlichen funktionellen Gruppen unterschieden. In den nächsten beiden Studien wurde der Einfluss naturnaher Landschaftsstrukturen auf die Kolonisation von Ackerflächen nach der Überwinterung, bzw. auf die Auswirkung von Habitatisolierung bei Wirtschaftsgrünland für funktionelle Gruppen mit unterschiedlichem Ausbreitungspotential untersucht. Hier konnte nachgewiesen werden, dass die funktionelle Gruppe mit höherem Ausbreitungspotential gar nicht, oder nur schwach auf den Einfluss der Landschaft reagierte, die funktionelle Gruppe mit niedrigem Ausbreitungspotential hingegen sehr stark. Naturnahe Rand- und Uferstrukturen verzögerten für Laufkäfer mit niedrigem Ausbreitungspotential die Geschwindigkeit der Besiedlung von Äckern im Frühjahr, verminderten aber für diese funktionelle Gruppe auch den negativen Einfluss der

Habitatisolierung auf die Artenzahl auf Grünland. Überdies wurde eine starke räumliche und zeitliche Abhängigkeit des Landschaftseinflusses nachgewiesen. Diese Ergebnisse unterstreichen die Bedeutung funktioneller Gruppen und verdeutlichen die Notwendigkeit einer hohen zeitlichen und räumlichen Auflösung bei der Untersuchung ökologischer Prozesse, um Effekte nachweisen zu können, die auf verschiedenen Skalen divergieren. In der letzten Studie wurde der Einfluss lokaler und regionaler Bewirtschaftung auf die Diversität und ökosystemare Dienstleistungen von Laufkäfern und anderen Taxa untersucht. Lokale ökologische Bewirtschaftung erhöhte die Predation von Wildkräutersamen auf den Untersuchungsflächen und die Interaktion lokaler und regionaler Bewirtschaftung erhöhte die Diversität der Laufkäfer. Diese Untersuchung verdeutlichen die Bedeutung des Bewirtschaftungssystems auf die Heterogenität der Agrarlandschaft und die wirtschaftliche Bedeutung des Landschaftsmanagements für die Erhaltung der ökosystemaren Dienstleistungen. Insgesamt betonen die vorliegenden Studien die Bedeutung einer höheren Auflösung von taxonomischen Gruppen bei landschaftsökologischen Untersuchungen. Da ökologische Prozesse zwischen den Arten bzw. funktionellen Gruppen variieren, ist die Diversität der Laufkäfer als alleinige Messgröße in vielen Fällen für die Beantwortung ökologischer Fragestellungen unzureichend. Daher sollte eine hohe zeitliche und räumliche Auflösung von Landschaftseinflüssen auf die unterschiedlichen funktionellen Gruppen der Laufkäfer in die Analysen mit aufgenommen werden, wenn der Focus von Untersuchungen auf dem Erhalt von Biodiversität und ökosystemarer Dienstleistung in Agrarlandschaften liegt.

Summary

The change in land-use and the intensification in agricultural production are identified as major drivers for the loss of biodiversity in the last decades. In addition, there is a lack of knowledge about the impact of the surrounding landscape on diversity, community composition and ecosystem services of species communities in agricultural landscapes. Ground beetles are highly affected by agricultural development as they are represented by a high number of species and individuals in agricultural landscapes. They can be divided into functional groups due to their varying species traits, which can be a helpful tool in dealing with issues of landscape ecology. Thus, in this cumulative dissertation, the impact of landscape variables on the diversity and composition of ground beetles and their functional groups, their dispersal, colonisation and ecosystem service was studied. Agricultural crops and permanent grasslands make up the largest part of agricultural landscapes and harbour varying compositions of ground beetles species. As the effect of agricultural intensification also differs between these two systems, analyses were conducted in both systems to amplify the knowledge of landscape impacts on ground beetles in agricultural landscapes. The heterogeneity of local habitat and management factors and landscape composition led to highly heterogeneous ground beetle communities, which was shown with the first two studies. The differences among the species composition of different grasslands accounted for the largest share of the regional diversity. Additionally, it was demonstrated that effect size and effect direction of the analysed variables varied for different functional groups as well as the degree to which they contribute to the regional diversity. The third and fourth study analysed the impact of semi-natural landscape elements on the colonisation of crop fields in spring and the impact of habitat isolation on managed grassland on functional groups, respectively, differing in their dispersal ability. It was documented that ground beetles with high dispersal ability were not or only weakly affected whereas ground beetles with low dispersal ability were strongly affected by landscape variables. Semi-natural boundaries and banks delayed the speed of crop colonisation in spring of ground beetles with low dispersal ability but also diminished the negative impact of habitat isolation on their species number on managed grassland. Furthermore, a strong spatial and temporal dependency of landscape impacts could be demonstrated. These results pointed out the meaning of functional groups as a powerful tool for analysing ecological questions and the need for a high temporal and spatial resolution in studies that focus ecological processes as they might diverge at different scales. The last

study dealt with the local and regional impact management on the diversity and the ecosystem services of ground beetles and other taxa. It could be shown that organic management at the local scale enhanced the predation of weed seeds on the study sites whereas the interaction of local and regional management enhanced the diversity of ground beetles. These results demonstrated the relevance of including different management systems to preserve the heterogeneity of agricultural landscapes and the importance of landscape management for the maintenance of ecosystem services.

In conclusion, the results of the dissertation show the necessity of a higher resolution of taxonomic groups for research in landscape ecology. As ecological processes vary between species and functional groups, respectively, species diversity of ground beetles as sole measure for solving ecological questions is usually insufficient. Therefore, a high temporal and spatial resolution of landscape impacts on different functional groups of ground beetles should be taken into account if studies focus on biodiversity and ecosystem function and services in agricultural landscapes.

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Publikationen

- Wamser S**, Dauber J, Birkhofer K, Wolters V (2011) Delayed colonisation of arable fields by spring breeding ground beetles (Coleoptera: Carabidae) in landscapes with a high availability of hibernation sites. *Agriculture, Ecosystems & Environment* 144, 235-240.
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- Öberg S, **Mayr S**, Dauber J (2008) Landscape effects on recolonisation patterns of spiders (Araneae) in arable fields. *Agriculture, Ecosystems & Environment* 123, 211-218.
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Tagungsberichte

- Wamser S**, Birkhofer K, Dörner T, Wolters V, Diekötter T (2011) Organic farming effects on fitness and seed predation of phytophagous carabids. *Verhandlungen der Gesellschaft für Ökologie* 41.
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(Sabine Wamser)

Ort, Datum