Effects of semi-natural habitats on carabids and their potential to control slugs in agricultural landscapes

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Statutory declaration

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Author's contribution

In chapter 2 Moritz S. Fußer collected data in 2014. Sonja C. Pfister collected data in 2013 and 2014. Moritz S. Fußer carried out laboratory work, statistical analysis and led the writing. Jens Schirmel contributed to statistical analysis and writing. Martin H. Entling coordinated the study and contributed to statistical analysis and writing. Sonja C. Pfister, Jens Schirmel and Martin H. Entling participated in the design of the study.

In chapter 3 Moritz S. Fußer carried out field and laboratory work, statistical analysis and led the writing. Jens Schirmel contributed to statistical analysis and writing. Martin H. Entling coordinated the study and contributed to writing. Moritz S. Fußer, Jens Schirmel, Sonja C. Pfister and Martin H. Entling participated in the design of the study.

In chapter 5 Moritz S. Fußer conceived the ideas as well as the design methodology and carried out field work and contributed to writing. Sebastian Wendland participated in the field work, carried out laboratory work as well as statistical analysis and led the writing. Patrick Baudy, Jens Schirmel and Martin H. Entling contributed to statistical analysis and writing.

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In chapter 5 Moritz S. Fußer conceived the ideas as well as the design methodology and carried out field work and contributed to writing. Sebastian Wendland participated in the field work, carried out laboratory work as well as statistical analysis and led the writing. Patrick Baudy, Jens Schirmel and Martin H. Entling contributed to statistical analysis and writing.

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Summary

Carabids, which are frequently distributed in agricultural landscapes, are natural enemies of different pests including slugs. Semi-natural habitats are known to affect carabids and thus, their potential to support natural pest control.

The impact of semi-natural habitats was investigated on carabids and slugs within different non-crop habitats (chapter 2). Most carabids and *Deroceras reticulatum* showed preferences for herbaceous semi-natural habitats, while *Arion* spp. occured mainly in woody habitats. An increase of predatory carabid abundance, which was linked to an inclining amount of semi-natural habitats in the landscape, and a decrease of *Arion* spp. densities, indicated a high potential for slug control in structural rich landscapes.

Effects of semi-natural habitats were investigated on predatory carabids and slugs in 18 wheat fields (chapter 3). Predatory carabid species richness was positively affected by the increasing amount of semi-natural habitats in the landscape, whereas predatory carabid abundance was neither influenced by adjacent habitat type nor by the proportion of semi-natural habitats in the landscape. The target pest species showed divergent patterns, whereas *Arion* spp. densities were highest in structural poor landscapes near woody margins. *D. reticulatum* was not affected by habitat type or landscape, reflecting its adaptation to agriculture. Results indicate an increased control of *Arion* spp. by carabids in landscapes with a high amount of semi-natural habitats.

Effects of semi-natural habitats and the influence of farming system was tested on carabid distribution within 18 pumpkin fields (chapter 4). Carabid species richness generally increased with decreasing distance to the field margins, whereas carabid abundance responded differently according to the adjacent habitat type. Farming system had no effect on carabids and landscape heterogeneity only affected carabids in organic pumpkin fields.

Slug and slug egg predation of three common carabid species was tested in single and double species treatments in the laboratory (chapter 5). Results show additive and synergistic effects depending on the carabid species. In general, semi-natural habitats can enhance the potential of slug control by carabids. This counts especially for *Arionid* slugs. Semi-natural habitats can support carabid communities by providing shelter, oviposition and overwintering sites as wells as complementary food sources. Therefore, it is important to provide a certain amount of non-crop habitats in agricultural landscapes.

Zusammenfassung

In Agrarlandschaften zählen Laufkäfer zu den weit verbreiteten Fressfeinden verschiedener Schädlinge, wie etwa von Nacktschnecken. Einflüsse von naturnahen Randstrukturen auf Laufkäfer und deren Potenzial zur natürlichen Schädlingsbekämpfung sind bekannt.

Der Einfluss von naturnahen Randstrukturen wurde auf randstrukturbewohnende Laufkäfer und Schnecken untersucht (Kapitel 2). Die Mehrzahl an Laufkäfern sowie *Deroceras reticulatum* präferierten Krautsäume, wohingegen *Arion* spp. vor allem in Gehölzen vorkam. Steigende Abundanzen von räuberischen Laufkäferarten und abnehmende Zahlen von *Arion* spp., gefördert durch einen hohen Anteil an Randstrukturen, lassen auf ein erhöhtes Potenzial zur Schneckenbekämpfung in strukturreichen Landschaften schließen.

Der Einfluss von naturnahen Randstrukturen wurde auf räuberische Laufkäfer und Schnecken in 18 Weizenfeldern getestet (Kapitel 3). Der Artenreichtum an karnivoren Laufkäfern stieg zusammen mit dem Anteil an Randstrukturen in der Landschaft, wobei deren Abundanz von kleinräumigen Effekten unbeeinflusst blieb. Die beiden Schädlinge zeigten unterschiedliche Muster, wobei Dichten von *Arion* spp. an Gehölzen in strukturarmen Landschaften am höchsten waren. *D. reticulatum* wurde weder durch lokale noch von großräumigen Effekten beeinflusst, was auf ihre Anpassung an Agrarlandschaften zurückzuführen ist. Die Ergebnisse lassen auf eine gesteigerte Kontrolle von *Arion* spp. durch Laufkäfer in strukturreichen Gebieten schließen.

Effekte von Randstrukturen und Bewirtschaftung wurden auf die Verteilung von Laufkäfern in 18 Kürbisfeldern getestet (Kapitel 4). Der Artenreichtum stieg mit Nähe zu den Randstrukturen, wobei Laufkäferabundanzen je nach Habitattyp unterschiedlich beeinflusst wurden. Die Bewirtschaftungsart hatte keinen Einfluss auf Laufkäfer und Landschaftsheterogenität beeinflusste nur Laufkäfer in ökologisch bewirtschafteten Feldern.

Prädationsexperimente von Schnecken und deren Eiern durch drei Laufkäferarten wurden im Labor in Einzel- und Zweierkonstellationen durchgeführt (Kapitel 5). Je nach Art wurden synergistische und additive Effekte gemessen. Generell erhöhen naturnahe Randstrukturen das Potenzial zur Schneckenbekämpfung durch Laufkäfer, was vor allem für Schnecken der Gattung *Arion* zählt. Es ist wichtig, einen bestimmten Anteil an naturnahen Randstrukturen in Agrarlandschaften bereitzustellen, da sie als Rückzugs-, Eiablage- und Überwinterungsorte fungieren und komplementäre Nahrungsressourcen bereitstellen.

Chapter 1 Introduction

1.1. Natural pest control as an ecosystem service

Natural pest control is an important ecosystem service, which can lead to yield enhancement (Bommarco et al. 2013) by a reduction of the use of pesticides (Pickett & Bugg, 1998). The estimated value of natural pest control in the USA is US $ 13.6 billion annually, whereas the value of pest control by insects alone is US $ 4.5 billion per year (Losey & Vaughan 2006). Sandhu et al. (2015) calculated an economic value of natural pest control of US $ 68 – 200 ha^{-1} yr^{-1} in organic farming systems.

In conventional farming systems a larger chemical input is needed compared to organic arable farming (Sandhu et al. 2008, 2015). In 2012, worldwide pesticide market was worth US $ 49.94 billion dollars and pesticide use was 2.25 million metric tons (Peshin & Zhang, 2014). Although pesticides are one profitable way to maintain global food production, their use has negative effects on human health, natural resources like groundwater and surface water, non-target species like pollinators and natural enemies and it can lead to the development of pesticide resistance (Pimentel et al. 1992, 1995; Pimentel & Peshin 2014). Furthermore, pesticides cannot completely prevent crop losses by pests (Pimentel & Pershin 2014). Nevertheless, a 2.4- to 2.7-fold increase in pesticide use is expected by the year 2050 due to a growing world population, which leads to further losses of ecosystem services and species extinctions (Tilman et al. 2001). The challenge is to supply future food demands by enhancing the productivity of agroecosystems in a sustainable way (Sandhu et al. 2015) and without the negative impacts of chemical pesticide use (Bianchi et al. 2006). However, knowledge about the interactions between natural enemies, pests and their environment is still scarce and scientific studies are uncertain or controversial (Bianchi et al. 2006). Thus, further investigations are needed to elaborate general conclusions so that natural pest control will at last be accepted by farmers as a basic principle (Bianchi et al. 2006).

Although the role of biodiversity in connection with natural pest control is little known (Bianchi et al. 2006, Tscharntke et al. 2005), the loss of biodiversity caused by agricultural intensification is meant to affect natural pest control and other ecosystem services in a negative way (Ricketts et al. 2004, Thies & Tscharntke 1999, Tscharntke et al. 2005, Symondson et al 2002). Pest control is positively linked to species richness among natural enemy communities (Letourneau et al. 2009, Griffin et al. 2013) and thus, predation rates are higher in systems with a higher enemy richness (Chang 1996). This higher enemy richness can lead to complementation and facilitation among predators, where e. g. foliar foraging predators can cause droppings of aphids from plants to the ground, so that ground foraging predators can use them as a complementary food resource (Losey & Denno 1998, Tscharntke et al. 2005). However, a higher species richness can also lead to intraguild predation, which can have negative effects on pest regulation (Tscharntke et al. 2005). Further investigations are needed to analyse the role of biodiversity as well as the impacts of agricultural intensification on natural pest control.

1.2. Carabids as slug control agents

Carabids are considered as predators of different pests, whereas evidence is much based on tests in the laboratory (Kromp, 1999), but also on field data (Hof & Bright 2010), on analysis of the gut content (Kromp, 1999) and on protein antigens (Bohan et al., 2000) of captured carabid beetles. Recently, more studies deal with the control of pest slugs by carabids as an alternative to molluscicides (Symondson, 1994; Cross et al., 2001). These studies mostly focus on one or a few carabid species, especially on species with a larger body size, e. g. *Pterostichus melanarius* (Foltan, 2004; Paill, 2004; Oberholzer & Frank, 2003; Oberholzer et al., 2003), *P. niger* (Pakarinen, 1993), *P. madidus* (Ayre, 2001; Mair & Port, 2001) and *Abax parallelipepidus* (Symondson, 1989, 1994; Asteraki, 1993; Symondson & Lidell, 1993). Larger carabids are considered to overcome the production of alarm mucus as a defence mechanism of slugs and the tough skin as protection of *Arionid* slugs (Foltan, 2004). A consumption of smaller slug individuals and slug eggs by smaller carabid species has also been demonstrated in the laboratory (Hatteland et al., 2010; Mair & Port, 2001; Oberholzer & Frank, 2003). However, results of investigations with alternative prey in the laboratory and the variable slug percentage consumption in carabids by serological tests for slug remains, show that carabids do not feed exclusively on slugs, but on a variety of prey sources (Mair &

Port, 2001). Nevertheless, slug eggs as well as slugs of all size classes are available nearly all year around (Haynes et al., 1996; Mair & Port, 2001) and thus, are important prey sources for carabids (Mair & Port, 2001).

1.3. Slugs as major pests in agriculture

Slugs are major pests in agri- and horticulture of temperate regions (South, 1992). Especially the occurrence of *Deroceras reticulatum* and *Arion vulgaris* in fields can lead to massive damages and yield loss (Eggenschwiler et al., 2012; Frank, 1998a, b; Godan, 1983; Speiser & Niederhauser, 1997). Crops spotted with slime, excrements and feeding traces, which can additionally be infected with bacteria and fungi, are not marketable and can lead to further damages during storage (Godan, 1983). As invasive species, *D. reticulatum* can now be found around the globe and *A. vulgaris* expanded from the Iberian peninsula to the north and east through Europe. The dispersal capacity of both slug species can lead to serious problems in pest management programs (Grimm & Paill, 2001; Grimm et al., 2000; Hommary et al. 1998). Mechanical (tillage) and chemical (molluscicides) inputs are used to control slug populations in fields. In conventional farming systems, molluscicides containing methiocarb and metaldehyde are often used (Howlett et al., 2008), whereas methiocarb was banned in Europe in 2015 because of the negative effects on non-target species. Although metaldehyde is also known to have side effects (Bates et al., 2012), it is still used in agri- and horticulture. Hence, alternative ways have to be established to manage slug populations in fields in a sustainable way without the negative effects on biodiversity.

1.4. Importance of semi-natural habitats to support pest control

Semi-natural habitats are non-crop habitats (García-Feced et al. 2015), which can be categorised by their shape (linear vs. areal) and vegetation type (herbaceous vs. woody) (Holland et al. 2016). These extensively or non-managed habitats are important refugia for different animal taxa like birds, small mammals and insects (Andersen, 1997; Tscharntke et al., 2005; Smith et al., 2008). Furthermore, semi-natural habitats are used as overwintering, shelter, and oviposition sites for beneficial arthropods (Bianchi et al. 2006; Corbett & Rosenheim, 1996; Landis et al., 2000). They also provide complementary resources like pollen for parasitoids or alternative prey (Bianchi et al., 2006, Holland et al., 2006)). The two different types of semi-natural habitats can have different influences on the community structure of natural enemies (Frank & Reichhart, 2004; Pfiffner & Luka, 2000). For example, herbaceous margins are often used as a nectar or pollen resource (Haaland et al., 2011), whereas woody habitats have a greater benefit as overwintering sites due to their dense vegetational structure as a buffer against unsuitable climate conditions (Sotherton, 1985). But in general, all types of semi-natural habitats can provide both food resources and shelter for arthropods (Bianchi et al., 2006; Holland et al., 2016; Pfiffner & Luka, 2000; Sarthou et al., 2014).

Natural enemies can spill from semi-natural habitats into adjacent fields, where they are able to control different pests (Bianchi et al., 2006; Tschumi et al., 2015). Such immigration processes from non-crop into crop areas or vice versa as well as species exchanges between different non-crop areas are important to support biodiversity, recovery capacity from disturbances, ecosystem stability and are crucial to enhance pest control (Bianchi et al., 2006; Tscharntke et al., 2005). Therefore, agricultural landscapes should be a mosaic of different well-connected habitats (Tscharntke et al., 2005). Especially a rapid colonization of crop areas by natural enemies in the early season is important to keep pest populations under a critical threshold (Bianchi et al., 2006). Landscapes with a high proportion of semi-natural habitats contain a higher abundance of predators and a higher predator richness (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Diekötter et al.; 2010). In structural rich landscapes with well-connected non-crop habitats, those predators are able to colonize greater crop areas and can therefore reduce pests more efficiently, since predator activity can decrease with increasing distance to semi-natural habitats (Bianchi et al., 2006; Holland et al., 2016). However, the operational scale of predators is species-specific and depends on their mobility, whereas generalists generally operate on larger scales than specialists (Tscharntke et al., 2005). Accordingly, specialized predators profit from locally good conditions (1500 m: Tscharntke et al., 2005; 700 m: Chaplin-Kramer et al., 2011) and generalists more from the surrounding matrix at large spatial scales (Tscharntke et al., 2005).

Semi-natural habitats can also harbour agricultural pest species like aphids or herbivorous beetles (Bianchi et al., 2006). Also slugs can be favoured by semi-natural habitats and their occurrence lead to yield losses especially near non-crop margins (Frank, 1998a, b; Speiser & Niederhauser, 1997). There is evidence, that simplified landscapes are tendentially at greater risk for pest pressure (Bianchi et al. 2006).

However, the amount of semi-natural habitats in European landscapes has been declining due to simplification of agricultural landscapes (Robinson & Sutherland, 2002), which has been leading to a reduction of biodiversity and a degradation of linked ecosystem services like pest control (Power, 2010).

1.5. Carabids in agricultural landscapes and the importance of semi-natural habitats

Semi-natural habitats are known to affect carabids in agricultural landscapes (Holland et al., 2009; Kromp, 1999) by providing food sources as well as temporary shelter from field management practices (e. g. pesticide use) or unsuitable climate conditions in open fields (Bianchi et al., 2006; Holland et al., 2009; 2016). Hedges or herbaceous margins often function as important overwintering sites for carabids (Holland et al., 2016). There is evidence, that carabid densities within fields are linked to overwintering densities in the adjacent semi-natural habitats (Coombes & Sotherton, 1986). Plant species richness und structural diversity within the semi-natural habitats are essential factors for successful overwintering by maintaining favourable climate conditions (Bürki & Hausamann, 1993; Collins et al., 2002; Desender, 1982; Holland et al., 2016; Pfiffner & Luka, 2000; Thomas et al., 1991). For example, carabid densities are higher in herbaceous margins or grass margins with tussocky grasses than in simple grass strips (Holland et al., 2016). However, the impacts of different non-crop habitat types on carabids in fields are partially contradictory and uncertain (Holland et al., 2016). Semi-natural habitats can also act as a sink for carabids (Holland et al., 2009) and, especially hedgerows, as barriers (Holland et al., 2016).

The utilisation of different semi-natural habitats by carabids might be species-specific as there are species, which use these habitats either temporarily or permanently (Kromp, 1999; Saska 2007). In general, boundary species are known to use open fields for foraging and distances up to 100 m into the open fields were measured (Holland et al., 2009). However, an increased predation was only documented within a distance of 58 m from a beetle bank (Collins et al., 2002). Boundary species are spring breeders and can colonize fields early in the year (Kromp, 1999; Pfiffner & Luka, 2000), which is important to control pests already in early stages (Kromp, 1999). Also a large amount of carabids overwinter within open fields (Holland et al, 2007) and as autumn breeders, those carabids emerge during summer when abundance of spring breeders are low (Holland et al., 2009), which might have further positive effects on pest regulation in fields.

Most carabids are generalists and are therefore influenced by the surrounding landscape (Tscharntke et al., 2005). An increased carabid species richness has been reported in landscapes with a high amount of semi-natural habitats (Diekötter et al., 2010; Weibull et al., 2003). The variety of habitat types throughout the landscape leads to a greater species pool, an enhanced exchange of carabids between different habitats and land-use types as well as to an increased food availability (Diekötter et al., 2010).

Effects of the farming system on carabids are also quite contradictory, where carabids were either positively affected by organic farming (Basedow, 1994; Hokkanen & Holopainen, Hole et al., 2005) or by conventional management (Weibull et al., 2003). Also an independence of carabids from management regimes has been demonstrated (Purtauf et al., 2005). In general, carabids are affected by a range of management practices (Holland & Luff, 2000) like sowing time and crop type (Purvis et al., 2001) or management intensity (Cole et al., 2005). Especially carabids, which overwinter in fields, are more influenced by management practices and soil cultivation than by non-crop areas (Holland et al., 2007; Holland & Luff, 2000; Kromp, 1999; Kromp & Steinberger, 1992).
To optimize natural pest control, it is crucial to understand the (interactive) effects of all different field parameters on natural enemies like carabids at a local and landscape scale.

1.6. Objectives of the thesis

The aim of the thesis was to contribute to the understanding of how semi-natural habitats can affect natural enemies to support natural pest control. In that context, the main objectives were

1. To investigate effects of semi-natural habitats on carabids and slugs.
2. To investigate the potential of carabids to control slugs.
3. To investigate the impact of semi-natural habitats on the potential of carabids to reduce slugs in agriculture.

In **chapter 2** landscape effects on carabids and slugs in different semi-natural habitat types (woody vs. herbaceous; linear vs. areal) were analysed. The investigation should provide information

1. If carabid abundance, species richness and functional group composition differ between different semi-natural habitat types.
2. If slug abundance differs between various semi-natural habitat types.
3. If landscape composition affects slugs and carabids in different semi-natural habitats.
4. If semi-natural habitats affect slug control by carabids within the non-crop habitats.

In **chapter 3** effects of semi-natural habitats at the local and landscape scale on predatory carabids and slugs in wheat fields were analysed. The investigation should provide information

1. If predatory carabids in wheat fields are influenced by adjacent semi-natural habitat types and by the proportion of semi-natural habitats in the landscape.
2. If slugs in wheat fields are influenced by adjacent semi-natural habitat types and by the proportion of semi-natural habitats in the landscape.
3. If the potential of carabids to control slugs in wheat fields is influenced by semi-natural habitats at the local and landscape scale.

In **chapter 4** impacts of semi-natural habitats and farming system on the distribution of carabids in pumpkin fields were observed. We addressed the questions

1. If farming system, distance to adjacent semi-natural habitats, semi-natural habitat type and landscape composition affects carabids within pumpkin fields.
2. If interactive effects of those parameters have an impact on carabids in pumpkin fields.

In **chapter 5** the potential of three widely distributed carabid species to control the pest slug *Deroceras reticulatum* and its eggs was investigated. We addressed the questions

1. If the three carabid species differ in their predation rate.

2. How these three carabid species interact in experiments with multiple predator species.

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Chapter 2 Effects of landscape composition on carabids and slugs in herbaceous and woody field margins

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Highlights

- We investigated habitat and landscape effects on carabid beetles and slugs.
- Herbaceous semi-natural habitats contain higher numbers of carabids than woody ones
- Predatory carabid abundances tended to increase in structurally rich landscapes
- Pest slugs responded differently to semi-natural habitats and landscape composition
- Our results indicate that *Arion* spp. could be controlled by carabids

Abstract

Field margin vegetation can provide shelter and complementary resources for both agricultural pests and their natural enemies. Thus, simplification of agricultural landscapes can either reduce or enhance pest pressure, depending on the habitat preferences and mobility of the relevant organisms. The promotion of field margin vegetation that selectively enhances natural enemies but not pests, would be desirable for the optimization of pest control services.

Unfortunately, the majority of existing studies on the effects of field margins and landscape focussed on either natural enemies or (less often) on pests, but very rarely on both. This study evaluates the influence of herbaceous and woody semi-natural habitats and landscape composition on carabid beetles as natural enemies of the pest slugs *Deroceras reticulatum* and *Arion* spp. We found effects of semi-natural habitats on carabids and slugs at the field and landscape scale. While most carabids and *D. reticulatum* preferred herbaceous over woody habitats, *Arion* spp. oppositely showed highest activity-densities in woody habitats. With increasing amount of semi-natural habitats in the landscape activity-densities of predatory carabids tended to increase while activity-densities of *Arion* spp. decreased. This, and a negative correlative trend between *Arion* spp. and carabid densities indicate favourable conditions for natural slug control by carabids in landscapes with a high amount of semi-natural habitats. Our results confirm that different response of pest and their natural enemies to the landscape context can indeed alter the predator-prey ratio. However, our study also revealed that pests such as *Arion* spp. and *D. reticulatum* prefer different types of field margins, complicating the optimization of agricultural landscapes for pest management.

Keywords

Semi-natural habitats, Landscape composition, Pest control, Carabid beetles, Pest slugs

2.1 Introduction

In agricultural landscapes semi-natural habitats are important for different animal taxa like birds, small mammals and insects (Andersen, 1997; Tscharntke et al., 2005; Smith et al., 2008). However the amount of semi-natural habitats in many European agricultural landscapes has been declining throughout the last decades due to the intensification of agriculture (Robinson and Sutherland, 2002). This decline reduces biodiversity and may cause a loss of important ecosystem functions like pollination and pest control (Power, 2010). Compensation of this degradation by expensive chemical and mechanical methods can have further negative impacts (Giller et al., 1997).

Semi-natural habitats, which consist of perennial non-crop vegetation and are extensively or not managed, are known as refuge habitats and hibernation sites for several beneficial arthropods including natural enemies of pests (Bianchi et al., 2006; Corbett and Rosenheim, 1996; Jmhasly and Nentwig, 1995; Pfiffner and Luka, 2000; Tscharntke et al., 2005). Natural enemies can colonize adjacent fields from semi-natural habitats (Coombes and Sotherton, 1986; Corbett and Rosenheim, 1996; Dennis and Fry, 1992; Thomas et al., 1991), where they are able to regulate pests (Collins et al., 2002; Menalled et al., 1999; Tschumi et al., 2015). However, the type of semi-natural habitat can influence the community structure and functioning of natural enemies (Frank and Reichhart, 2004; Pfiffner and Luka, 2000; Woodcock et al., 2010). For example, Sotherton (1985) suggests that predatory beetles may benefit from hedges more than from grassy margins, because hedges provide a more efficient buffer against unsuitable weather conditions.

Semi-natural habitats can also favour the occurrence of pests like the slugs *Arion vulgaris* and *Deroceras reticulatum*. Both species can be very abundant in fields and lead to massive damages in crops (Eggenschwiler et al., 2012; Frank, 1998a, 1998b; Speiser and Niederhauser, 1997). Also seeds are at risk of consumption by slugs and vegetables spotted with excrements and slime therefore are not marketable. In addition, bacteria and fungi, which established on places were slugs fed, lead to more damages during storage (Godan, 1983).

Carabid beetles are natural enemies of slugs. Bohan et al. (2000) proved that *Pterostichus* melanarius fed on *D. reticulatum* in experimental fields using enzyme-linked immunosorbent assays (ELISA) to detect slug protein antigens in *P. melanarius*. Hof and Bright (2010) found enhanced carabid and reduced slug densities in fields with adjacent grass strips than in fields without grass strips. This result indicates a regulation of slugs by carabid beetles, which are favoured by grassy strips in this case. Also laboratory studies have shown that several carabid beetle species feed on slugs, e.g. *Abax parallelepipedus* (Symondson, 1989, 1994), *Harpalus rufipes* and *Harpalus* affinis (Ayre, 2001), *Nebria brevicollis* (Ayre, 2001; Mair and Port, 2001), *Poecilus cupreus* (Oberholzer et al., 2003a,b), *Pterostichus madidus* (Ayre, 2001; Mair and Port, 2001), *P. melanarius* (Bohan et al., 2000; Oberholzer et al., 2003a,b), and *Pterostichus* niger (Pakarinen 1993). *D. reticulatum* may be more preferred due to its soft skin (Foltan, 2004) and adult *A. vulgaris* with thicker skin may not be killed by carabids (Hatteland et al., 2010).

At a larger spatial scale, a complex surrounding landscape often has a positive effect on the diversity and abundance of beneficial arthropods like carabid beetles (Purtauf et al., 2005; Diekötter et al., 2010; Weibull et al., 2003). In fields, many predators tend to decrease with increasing distances from adjoining semi-natural habitats (Bianchi et al., 2006). Therefore, complex landscapes with a high proportion of semi-natural habitats may allow natural enemies to colonize a greater area of crop habitats and to more efficiently reduce pests (Bianchi et al., 2006). Complex landscapes can also favour a higher pest pressure (Bianchi et al., 2006). However, pest damages seem to be a much greater problem in homogeneous landscapes due to the lower connectivity of semi- natural habitats and lower population sizes of natural enemies (Bianchi et al., 2006; Gardiner et al., 2009; O'Rourke, 2010), as well as due to higher concentration of preferred resources (Root, 1973) However, well replicated studies analysing the (interactive) effects of semi-natural habitat type and landscape composition on both natural enemies and pests are still scarce (but see Picchi et al., 2016). In the present study, we investigated carabid beetles and slugs in 69 semi-natural habitats, which were either herbaceous or woody and differ in their geometric form (linear or areal). The semi-natural habitats were distributed among 18 landscapes with a different composition (proportion of semi-natural habitats in 1 km radius) in southwest Germany. We hypothesized that activity-density, species richness and functional group composi- tion of carabids (i) differed between different semi-natural habitats (woody/herbaceous, linear/areal) and (ii) increased with the proportion of semi-natural habitats in the landscape. Further- more, we expected that slug activity-density (*Arion* spp. and *D. reticulatum*) was affected by (iii) semi-natural habitat type and (iv) would decrease with increasing proportion of semi-natural habitats in the landscape caused by increasing (predatory) carabid activity-density. Finally, we expected that (v) activity-densities of slugs would be negatively correlated with the activity-density of (predatory) carabids.

2.2 Material and methods

2.2.1 Study area

The study area was located in the Upper Rhine valley between Landau, Ludwigshafen and Kandel in Rhineland-Palatinate, Germany. The elevation in this region ranges from 90 to 160 m a.s.l. with a mean annual temperature of 10.5 °C and precipitation of 667 mm (station Landau, German Weather Service) (Appendix A, Table A1). Because of its mild climate, fertile soils and the availability of water from the river Rhine, the region is characterized by intensive agriculture and specialized crop farming such as fruit and vegetable cultivation.

2.2.2 Landscape analysis and semi-natural habitat selection

This study was done in 2013 and 2014 in semi-natural habitats (SNH) within 18 agricultural landscapes representing a gradient in landscape composition. In each landscape we selected four different SNHs according to the predominant vegetation (woody or herbaceous) and their geometric form (linear or areal) with a minimum distance of 200 m from each other. In two landscape sectors not all of the four SNH types were present resulting in a total of 69 sampled SNHs (Appendix A, Table A1). Overall we used grass strips, (semi-) permanent grassland, hedges and woodland as SNH. The minimum size of each SNH was 150 m^2 with a minimum width of 1.5 m and a minimum length of 50 m. Areal SNH were at least 25 m wide. Woody SNH consisted of at least of 30% woody vegetation otherwise they were considered as herbaceous. We only selected SNH, which were adjacent to arable fields.

For each SNH we analysed the landscape composition in 1 km radius by calculating the proportion of permanent SNH area (wood, grassland) using aerial photographs (google earth April 2013). Neighbouring sectors were as different as possible in terms of their proportion of SNH. There was no overlap of the landscape sectors among the 18 agricultural landscapes except for one pair. We used QGIS 1.8 for landscape and SNH selection (aerial photographs, google earth April 2013).

2.2.3 Animal sampling

Carabids and slugs were sampled during four days each in June (3.–9.), July (6.–12.) and September (21.–27.) 2013 as well as in April (7.–13.) 2014. In each SNH, we installed two traps at the edge, 0.5 m from the adjoining field, and two traps in the interior, up to 12.5 m from the edge if the SNH was sufficiently wide. Pitfall traps at the edge and in the interior of the SNH were alternating with a distance of 15 m between traps along the length of the SNH. The traps (plastic cups) were 66 mm in diameter and 70 mm in depth and were filled with a 1:3 propylene-glycol-water solution. Trapped individuals were conserved in 70% ethanol. Carabids and slugs of the genus *Deroceras* were determined to species level according to Mueller-Motzfeld (2006) and Godan (1983). Slugs of the genus *Arion* were only determined to the *Arion ater*-group level (Godan, 1983). Slugs of this group (*A. ater, A. rufus, A. vulgaris*) can only be differentiated by dissecting the genitalia. Because *A. ater* does not occur in this part of Germany and *A. rufus* is displaced by invasive *A. vulgaris* on open grounds and thus largely restricted to forest interior (Kappes et al., 2009), the captured individuals most likely belong to *A. vulgaris*.

2.2.4 Data analysis

Data of the four samplings were combined for statistical analysis. Carabids were assigned as ‘herbivores’, ‘omnivores’ and ‘predators’ according to their predominant feeding type (Homburg et al. 2013). In all models we used ‘SNH type’ (woody/herbaceous), ‘SNH form’ (areal/linear) and ‘landscape composition’ as predictor variables. Because the four semi-natural habitats within one agricultural landscape were spatially not independent, we used generalized linear mixed effect models (glmm, command ‘glmmPQL’ in the R package MASS, Venables and Ripley, 2002). The effects of the predictor variables and the interaction between SNH type and landscape composition on the activity-density and species richness of carabids, predatory carabids, and the activity- density of *Arion* spp. and *D. reticulatum* were tested with glmm with a quasipoisson error structure for count data. Effects on the proportion of predatory carabids were tested with glmm with a quasibinomial error structure (proportion data). The predator-prey ratios were calculated as the ratio of predatory carabids and *Arion* spp. and *D. reticulatum*, respectively. Effects of predictor variables and the interaction between SNH type and landscape composition on predator prey ratios were tested using glmm with a gaussian error structure.

We checked model residuals visually for normality and homogeneity of variances by using diagnostic plots (Zuur et al., 2009). The significance of predictor variables was tested with ANOVA. We used R 3.1.2 for all statistical analysis (R Core Team 2014).

2.3 Results

2.3.1 Effects of semi-natural habitats and landscape composition on carabids

In total 2286 carabid individuals of 128 species were recorded (Appendix A Table A.2). SNH type had a significant effect on carabid activity-density and species richness while SNH form and landscape composition did not have a significant effect (Table 1). Carabid activity-density was almost twice as high and species richness about one third higher in herbaceous than in woody SNH (Fig. 1a,b). SNH type and SNH form significantly affected the proportion (%) of predatory carabids (Table 1). The proportion of predators was about one third higher in woody than in herbaceous (Fig. 1d) as well as in areal than in linear SNH (Fig. 1e). Landscape composition did not have a significant effect on the proportion of predators (Table 1). Also total activity-density of predatory carabids was significantly higher in areal than in linear SNH (Table 1,Fig. 1c) and tended to increase with increasing proportion of SNH in the landscape (Table 1, Fig. 2a). In contrast, SNH type had no effect on predatory carabid activity-densities (Table 1).

Table 1 Effects of habitat type, habitat form and landscape composition on carabid beetles, slugs and predator-prey-ratio. Significance of variables was tested with ANOVA. Significant numbers are printed in bold, trends in italic.

Response	**Explanatory variables**	**DF**	**F Chi^2**	**P**
Carabid activity-density	Type	48	19.2	**<0.001**
	Form	48	1.5	0.225
	Landscape	16	0.3	0.555
	Type x Landscape	48	1.0	0.316
Carabid species richness	Type	48	14.1	**<0.001**
	Form	48	0.4	0.542
	Landscape	16	0.6	0.542
	Type x Landscape	48	0.2	0.642
Predatory carabid activity-density	Type	48	0.3	0.582
	Form	48	4.8	**0.028**
	Landscape	16	3.3	*0.07*
	Type x Landscape	48	0.9	0.344
Proportion predators	Type	48	16.4	**<0.001**
	Form	48	9.8	**0.002**
	Landscape	16	2.1	0.143
	Type x Landscape	48	0.0	0.875
***Deroceras reticulatum* activity-density**	Type	48	15.7	**<0.001**
	Form	48	2.1	0.145
	Landscape	16	0.5	0.467
	Type x Landscape	48	2.0	0.157
***Arion spp*. activity-density**	Type	48	3.6	*0.058*
	Form	48	0.0	0.984
	Landscape	16	4.4	**0.035**
	Type x Landscape	48	1.3	0.250
Ratio predators/*D. reticulatum*	Type	48	3.3	*0.069*
	Form	48	3.4	*0.064*
	Landscape	16	1.2	0.267
	Type x Landscape	48	0.1	0.813
Ratio predators/*Arion spp.*	Type	48	10.0	**0.002**
	Form	48	0.0	0.832
	Landscape	16	0.5	0.488
	Type x Landscape	48	0.1	0.712

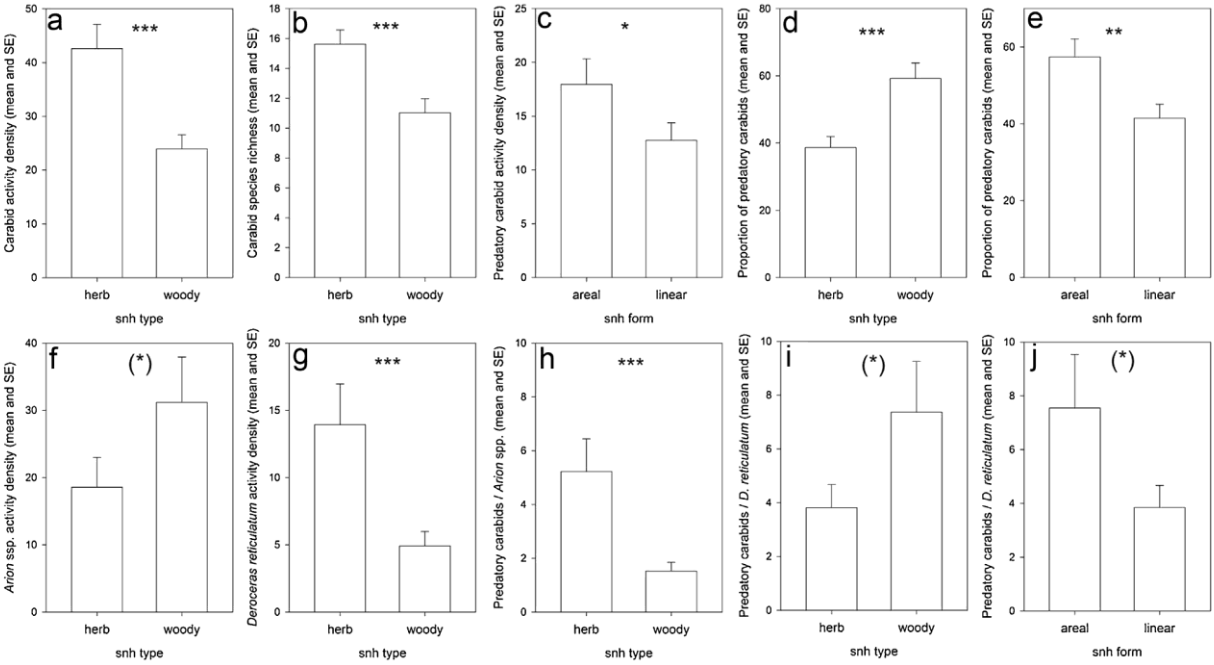

Figure 1 Effects of the type and form of semi-natural habitats on a) carabid activity-density, b) carabid species richness, c) predatory carabid activity-density, d) + e) proportion of predatory carabids, f) Arion spp. activity-density, g) Deroceras reticulatum activity-density, h) predatory carabids/Arion spp., i) + j) predatory carabids/Deroceras reticulatum. Significance was tested with generalized linear mixed models and ANOVA or permutational ANOVA (see Table 1). (*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001

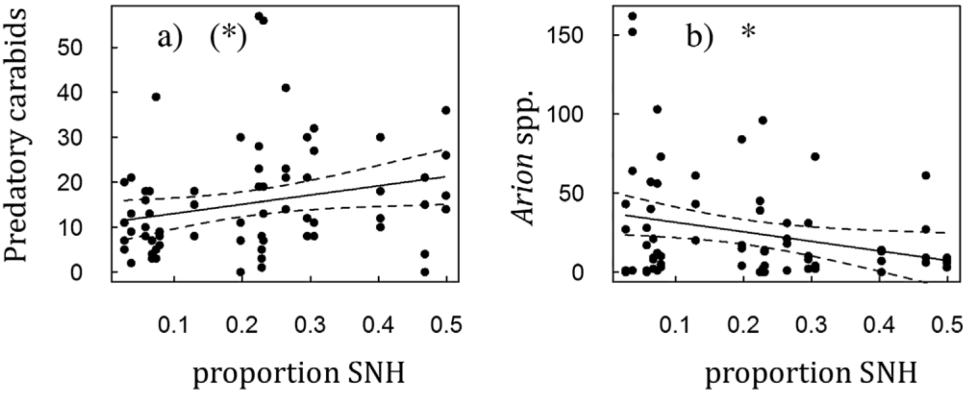

Figure 2 Effects of landscape composition, expressed by the proportion of SNH area in 1 km radius on a) predatory carabid activity-density and b) Arion spp. activity-density. Significance was tested with generalized linear mixed models and ANOVA (see Table 1). (*)P < 0.1, *P < 0.05. Regression lines and 95% confindence intervals are shown.

2.3.2. Effects of semi-natural habitats and landscape composition on slugs

In total 2368 slugs were recorded in all SNH, including 1722 individuals of *Arion* spp. and 646 individuals of *D. reticulatum.* As hypothesized, the activity-density of *Arion* spp. is significantly decreased with increasing proportion of semi-natural habitats in the landscape (Table 1, Fig. 2b) and tended to be higher in woody than in herbaceous SNH (table 1, Fig. 1f). In contrast, activity-density of *D. reticulatum* was significantly and about two third higher in herbaceous than in woody SNH (Fig. 1g), but was not affected by landscape composition (table 1). SNH form had no significant effect on slug activity-densities (Table 1).

2.3.3. Predator-prey-ratios

The ratio of predatory carabids to *Arion* spp. was more than twice as high in herbaceous than in woody SNHs (Fig. 1 h, Table 1). Moreover, activity-density of *Arion* spp. tented to decrease with increasing activity-density of carabid beetles (Table 2), but was not correlated with the proportion of predatory carabids. In contrast, the ratio of predatory carabids to *D. reticulatum* tended to be higher in woody than herbaceous (Table 1, Fig. 1i) and in areal than linear SNH (Table 1, Fig. 1j). Unexpectedly, *D. reticulatum* activity-density significantly increased with increasing activity-density of carabid beetles (Table 2). However, *D. reticulatum* activity-density significantly decreased with proportion of predatory carabids (Table 2). We found no significant correlations between the activity-density of predatory carabids and *Arion* spp. or *D. reticulatum* (Table 2).

Table 2 Correlation between slugs and carabid numbers as well as slugs and the proportion of predatory carabids. Significance of variables was tested with ANOVA. Significant numbers are printed in bold, trends in italic.

Response	Explanatory variables	Chi^2	DF	T	P
Arion spp.	Activity-density carabids total	2.9	50	- 1.687	*0.087*
	Proportion predatory	0.1	50	0.221	0.823
	Activity-density predators	1.5	50	- 1.189	0.228
Deroceras reticulatum	Activity-density carabids total	2.8.	50	1.644	*0.095*
	Proportion predatory	9.7	50	- 3.070	**0.002**
	Activity-density predators	0.8	50	- 0.905	0.359

2.4 Discussion

a) Effects of semi-natural habitats and landscape composition on carabid beetles

In our study, carabid activity-density and species richness was higher in herbaceous than woody SNH. The field layer in observed grass strips was denser due to the occurrence of (tussocky) grasses and thus, a more suitable shelter in contrast to woody SNH. Similar to our results, previous studies found more carabid individuals in herbaceous field margins than in woody ones (Hof and Bright, 2010; Pfiffner and Luka, 2000).

Positive effects of herbaceous SNH may be due to their high plant species richness and dense vegetation (especially of tall-growing grasses) as those are essential factors for a successful overwintering (Bürki and Hausamann, 1993; Collins et al., 2002; Desender, 1982; Pfiffner and Luka, 2000; Thomas et al. 1991). Furthermore, grass strips with high plant diversity may offer a variety of prey sources for predatory carabids (Bianchi et al., 2006; Collins et al., 2002). In our study, the activity-density of predatory carabids did not differ between woody and herbaceous SNH, but was higher in areal than linear ones. However, the proportion of predatory carabids was higher in woody and areal semi-natural habitats, which is caused by the small number of herbivore carabids found in the woody margins. Herbivore carabids often occur in herbaceous and crop habitats, which provide more food sources due to the variety of different plants and seeds (Honek et al., 2003).

However, some studies observed the opposite, namely higher carabid activity-densities in woody compared to herbaceous vegetation, which was explained by more favourable microclimate conditions (Sotherton 1985; Varchola and Dunn, 2001). We conclude that herbaceous and woody margins can both be used as shelter habitats as long as the vegetation provides enough buffer against unsuitable weather conditions and offers enough prey sources for carabids.

In contrast to our hypothesis we could not find any influence of landscape composition on carabid species richness and activity- density in semi-natural habitats. This finding is in line with results of Jeanneret et al. (2003), who also found a greater influence of local habitat than landscape effects on carabid beetles. However, predatory carabids were positively influenced by the percentage of SNH in the landscape. Predatory ground beetles are more food limited (Bommarco, 1998), and thus, they have to disperse throughout the landscape matrix to find resources from various habitat types such as crops and woody habitats in the course of the season (Lavandero et al., 2004; Rooney et al., 2008), what leads to an increased sensitivity to landscape structure (e.g. Holt et al., 1999; Kruess and Tscharntke, 1994; Purtauf et al., 2005). However, some studies have shown that overall carabid species richness increased with increasing landscape heterogeneity (Diekötter et al., 2010; Purtauf et al., 2005; Weibull et al., 2003). The explanations are a greater species pool due to different habitats in a landscape, an exchange of species between different habitats and land-use types as well as increased food availability in complex landscapes (Diekötter et al., 2010).

b) Effects of semi-natural habitats and landscape composition on slugs

As hypothesised, we found effects of the SNH type on the main pest slugs *D. reticulatum* and *Arion* spp. The two slug species responded differently: *Arion* spp. occured more often in woody SNH, while *D. reticulatum* preferred herbaceous SNH. *Arion* spp. needs shelter during daytime (Frank, 1998a), because slugs of that genus are not able to hide below ground (Eggenschwiler et al., 2012). In woody SNH, we found a higher cover of forbs, litter and lying dead wood, which is suitable as shelter for *Arion*. In the observed herbaceous SNH the cover of tussocky grasses was high, what may lead to a low activity-density of *Arion* spp. due to its inability to penetrate these grasses (Frank, 1998a). Furthermore simple grasses are also unpalatable for *Arion* spp. (Frank, 1998a). In contrast, we found more *D. reticulatum* individuals in herbaceous SNH. Contrary to *Arion* spp.*, D. reticulatum* feeds on grasses (Frank, 1998a). *D. reticulatum* stays below ground level during daytime and hence does not depend on leaves or wood as shelter. For our study we considered both simple grass and complex herbaceous strips as herbaceous semi-natural habitats, but broadleaved plants occurred in nearly every strip. Only 9 strips were dominated by grasses.

We are not aware of any study analysing landscape effects on slugs. We expected that slug activity-density is reduced in structurally rich landscapes due to a higher predation pressure by natural enemies in these landscapes. Indeed, *Arion* ssp. activity- densities decreased with increasing proportion of SNH in the landscape. This could be a result of a higher predation pressure in structurally rich landscapes (see below). Alternatively, higher activity-densities of *Arion* spp. in landscapes dominated by arable fields could result from a preference for these habitats. Although we did not sample arable fields, the preference of woody over herbaceous habitats by *Arion* makes it unlikely that they can reproduce or show a preference for arable fields. In contrast to our hypothesis, we did not find any effect of landscape composition on *D. reticulatum*.

c) Predator-prey-ratios

Carabids are known to feed on slugs (Ayre, 1995; Oberholzer et al., 2003a,b) and may reduce slug abundances (Bohan et al., 2000; Hof and Bright, 2010). In agricultural landscapes, carabids can benefit from semi-natural habitats on a local and landscape scale (Diekötter et al., 2010; Pfiffner and Luka, 2000; Purtauf et al., 2005; Varchola and Dunn, 2001; Weibull et al., 2003) and functional carabid diversity for pest control is linked to SNH in landscapes (Woodcock et al., 2014). However, our results only partly support the assumptions that the type of SNH and the landscape composition affect the slug control potential of carabids. Our results suggest that *Arion* spp. might be controlled by carabids. The activity-density of *Arion* spp. tended to decrease with increasing activity-density of carabid beetles (but not with predatory carabid activity-density or the proportion of preda- tors). The service of *Arion* spp. control might be especially high in structurally rich landscapes. Although there should be more suitable shelter habitats and food sources in complex landscapes for *Arion* spp. (preference for woody SNH), the activity-density declined with increasing amount of SNH in the landscape while predatory carabid activity-densities tended to increase. Since activity-densities of predatory carabids did not significantly differ between SNH types, the higher ratio of predatory carabid activity-density to *Arion* ssp. activity-density in herbaceous than in woody SNH may reflect the habitat preference of *Arion* for woody SNH rather than a top-down effect. Similarly, the higher ratio of predatory carabid activity-density to *D. reticulatum* activity-density in woody SNH may reflect the preference of *D. reticulatum* for herbaceous SNH. The trend for a positive correlation between total carabid and *D. reticulatum* activity-densities could therefore also result from a preference of *D. reticulatum* for herbaceous SNH, although we cannot rule out that *D. reticulatum* influences populations of all carabids (bottom-up), even predominantly herbivorous carabids as a complementary food source.

2.5 Conclusion

The preference for woody or herbaceous field margins differed between carabids and between the two main pest slug species. Predator-prey ratios were shifted towards carabids in landscapes with high proportions of woody semi-natural habitat, indicating that *Arion* spp. might be controlled by carabids in structurally rich landscapes. The opposite preference of woody and herbaceous field margins in *Arion* spp. and *D. reticulatum* complicates the use of field margins for the management of these agricultural pests.

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2.7 Appendix

Table 3 Coordinates and elevation of the study sites. LS = landscape sector, SNH = semi-natural habitat, ha = herbaceous + areal, hl = herbaceous + linear, wa = woody areal, wl = woody linear

LS	SNH	GPS-N	GPS-E	Elevation
1	ha	49°24'2	8°18'0	110
1	hl	49°24'0	8°18'2	115
1	wa	49°24'4	8°18'3	110
1	wl	49°24'6	8°18'6	105
2	hl	49°29'7	8°18'0	95
2	wa	49°30'1	8°18'1	95

2	wl	49°29'9	8°18'5	95
3	ha	49°27'9	8°19'1	100
3	hl	49°28'2	8°18'8	110
3	wa	49°28'5	8°18'4	110
3	wl	49°28'6	8°19'1	100
4	ha	49°28'8	8°21'8	100
4	hl	49°28'3	8°21'8	100
4	wa	49°28'0	8°21'7	90
4	wl	49°28'7	8°21'4	100
5	ha	49°26'1	8°23'5	95
5	hl	49°25'8	8°22'6	160
5	wa	49°25'8	8°23'1	95
5	wl	49°25'6	8°23'4	120
6	ha	49°24'8	8°22'6	95
6	hl	49°24'2	8°23'8	90
6	wa	49°24'2	8°23'8	95
6	wl	49°24'5	8°22'6	95
7	ha	49°15'5	8°23'2	97
7	hl	49°16'1	8°22'5	115
7	wa	49°15'4	8°23'4	100
7	wl	49°16'1	8°23'4	110
8	ha	49°16'1	8°21'4	120
8	hl	49°16'1	8°21'2	120
8	wa	49°16'0	8°21'4	150
8	wl	49°16'1	8°21'6	135
9	ha	49°18'5	8°19'1	108
9	hl	49°19'0	8°19'1	105
9	wa	49°19'1	8°18'6	110
9	wl	49°18'5	8°18'5	105
10	ha	49°16'5	8°15'2	113
10	hl	49°16'4'	8°15'1	113
10	wa	49°16'2	8°15'3	120
10	wl	49°16'5	8°14'4	113
11	ha	49°14'9	8°14'1	125
11	hl	49°14'8	8°14'8	130
11	wa	49°15'0	8°14'4	125

11	wl	49°15'0	8°14'8	120
12	ha	49°11'0	8°12'1	130
12	hl	49°11'1	8°12'0	128
12	wa	49°11'2	8°12'3	130
12	wl	49°10'5	8°12'1	130
13	ha	49°05'6	8°09'1	130
13	hl	49°05'6	8°10'0	135
13	wa	49°05'8	8°09'6	135
13	wl	49°05'4	8°09'4	135
14	hl	49°04'7	8°05'5	145
14	wl	49°04'4	8°05'6	145
15	ha	49°04'0	8°08'3	130
15	hl	49°04'0	8°08'5	130
15	wa	49°03'8	8°08'0	130
15	wl	49°04'1	8°08'1	130
16	ha	49°04'1	8°11'3	120
16	hl	49°04'6	8°11'2	120
16	wa	49°04'3	8°11'8	120
16	wl	49°04'7	8°11'4	125
17	ha	49°06'3	8°12'3	125
17	hl	49°05'9	8°13'0	125
17	wa	49°06'0	8°12'5	120
17	wl	49°06'0	8°12'2	115
18	ha	49°09'1	8°14'4	120
18	hl	49°09'1	8°14'0	135
18	wa	49°08'4	8°14'3	120
18	wl	49°08'5	8°13'6	117

Table 4 Species list of captured carabid beetles. ha = herbaceous areal; hl = herbaceous linear; wa = woody areal; wl = woody

Species	ha	hl	wa	wl	total
Abax parallelepipedus	8	2	57	19	86
Abax parallelus	1	0	31	2	34
Acupalpus bruneus	0	1	0	0	1
Acupalpus flavipes	1	3	0	2	6

Acupalpus meridionalis	1	0	0	0	1
Agonum emarginatum	4	0	9	3	16
Agonum muelleri	2	1	0	1	4
Agonum viduum	1	0	1	0	2
Amara aenea	8	28	2	5	43
Amara apricaria	1	3	0	2	6
Amara bifrons	2	2	1	1	6
Amara communis	20	20	3	15	58
Amara convexior	7	8	4	7	26
Amara curta	2	2	0	0	4
Amara eurynota	5	5	3	2	15
Amara famelica	3	0	0	0	3
Amara kulti	7	0	0	0	7
Amara litorea	0	0	0	1	1
Amara lunicollis	20	6	1	0	27
Amara majuscula	0	0	1	0	1
Amara ovata	2	14	0	1	17
Amara plebeja	0	9	0	1	10
Amara similata	5	25	3	4	37
Amara tibialis	1	1	2	3	7
Anchomenus dorsali	5	12	2	18	37
Anisodactylus binotatus	71	16	4	7	98
Anisodactylus signatus	0	1	0	0	1
Anthracus consputus	0	3	0	1	4
Asaphidion flavipes	2	4	2	4	12
Badister bullatus	1	0	0	3	4
Badister meridionalis	0	0	0	1	1
Badister unipustulatus	2	1	1	4	8
Bembidion articulatum	0	1	0	0	1
Bembidion biguttatum	2	1	1	6	10
Bembidion femoratum	1	2	12	0	15
Bembidion lampros	59	47	8	28	143
Bembidion properans	5	11	0	0	16
Bembidion pygmaeum	3	1	0	0	4
Bembidion quadrimaculatum	9	7	1	6	23
Bembidion tetracolum	2	4	1	9	16

Brachinus explodens	2	1	1	1	5
Bradycellus harpalinus	2	4	0	0	6
Calathus cinctus	0	2	0	0	2
Calathus erratus	0	0	0	1	1
Calathus ambiguus	6	17	1	5	29
Calathus fuscipes	2	0	0	0	2
Calathus melanocephalus	3	3	1	0	7
Carabus auratus	1	0	9	3	13
Carabus cancellatus	1	1	3	1	6
Carabus coriaceus	1	0	5	1	7
Carabus nemoralis	3	0	21	7	31
Chlaenius vestitus	1	0	0	0	1
Chlaenius nigricornis	2	0	0	0	2
Clivinia fossor	12	1	1	3	17
Demetrias atricapillus	1	0	0	0	1
Diachromus germanus	26	2	0	3	31
Dromius angustus	0	1	0	0	1
Drypta dentata	1	0	0	0	1
Dyschirius globosus	5	3	1	1	10
Harpalus affinis	28	65	3	10	106
Harpalus atratus	0	0	1	1	2
Harpalus attenuatus	0	0	0	1	1
Harpalus dimidiatus	0	1	0	5	6
Harpalus distinguendus	11	6	1	1	19
Harpalus griseus	0	3	0	1	4
Harpalus honestus	0	3	0	3	6
Harpalus latus	4	5	1	10	20
Harpalus luteicornis	13	9	3	8	33
Harpalus marginellus	0	2	1	0	3
Harpalus melancholichus	3	1	0	7	11
Harpalus modestus	0	5	0	0	5
Harpalus pumilus	0	0	0	1	1
Harpalus rubripes	1	2	1	0	4
Harpalus rufipes	65	79	28	76	248
Harpalus serripes	7	1	0	6	14
Harpalus smaragdinus	5	2	0	0	7

Harpalus solitaris	1	0	1	0	2
Harpalus subcylindricus	0	1	0	0	1
Harpalus tardus	2	2	1	0	5
Harpalus zabroides	1	1	0	0	2
Laemostenus terricola	0	0	0	1	1
Lebia marginata	0	1	0	0	1
Leistus ferrugineus	7	0	0	5	12
Leistus fulvibarbis	0	0	1	0	1
Leistus piceus	1	0	0	1	2
Leistus rufomarginatus	0	0	0	1	1
Leistus spinibarbis	0	0	0	1	1
Limodromus assimilis	1	0	6	3	10
Loricera pilicornis	2	12	4	5	23
Microlestes maurus	2	6	0	4	12
Microlestes minutulus	1	7	1	4	13
Molops piceus	1	0	1	0	2
Nberia salina	5	2	1	0	8
Nebria brevicollis	12	3	43	5	63
Notiophilus biguttatus	0	0	16	1	17
Notiophilus palustris	2	0	7	7	16
Oodes helopioides	1	0	0	2	3
Ophonus azureus	8	2	1	5	16
Ophonus laticollis	0	1	0	0	1
Ophonus melletii	0	1	0	0	1
Ophonus puncticollis	0	0	2	0	2
Ophonus rupicola	1	0	0	0	1
Ophonus subsiuatus	1	0	0	0	1
Oxyporus obducens	0	0	1	1	2
Panagaeus bipustulatus	0	0	1	4	5
Paradromius linearis	0	1	0	0	1
Parophonus maculicornis	5	2	1	0	8
Platyderus depressus	1	0	0	0	1
Poecilus cupreus	136	37	11	7	191
Poecilus lepidus	0	1	1	1	3
Poecilus versicolor	79	20	5	23	128
Pterostichus diligens	4	2	4	0	10

Pterostichus macer	1	0	0	0	1
Pterostichus madidus	0	0	1	1	2
Pterostichus melanarius	14	55	4	15	88
Pterostichus niger	17	3	14	1	35
Pterostichus oblongopunctatus	0	0	6	0	6
Pterostichus pumilio	0	0	1	2	3
Pterostichus quadrifoveolatus	0	0	1	0	1
Pterostichus strenuus	9	2	9	12	32
Sphodrus leucophthalmus	0	0	1	0	1
Stenolophus mixtus	0	0	1	0	1
Stenolophus teutonus	2	1	0	0	3
Stomis pumicatus	1	3	6	6	16
Synuchus vivalis	1	1	0	0	2
Trechus obtusus	2	14	2	6	24
Trechus quadristriatus	1	14	3	9	27
Zabrus tenebrioides	0	2	0	1	3
total	792	657	390	447	2286

Chapter 3 Effects of field margin type and landscape composition on predatory carabids and slugs in wheat fields

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Highlights

- Predatory carabids in wheat are positively influenced by landscape composition
- *Arion* spp. densities decrease with increasing landscape composition
- *D. reticulatum* did not respond to local and landscape factors.
- Results suggest control of *Arion* spp. by carabids in structural rich landscapes

Abstract

Semi-natural vegetation can affect the colonization of crop fields by invertebrates as a source habitat and by the supplementation of resources. Such effects have been studied at the scale of field margins or at the wider landscape scale, but rarely in combination. Variation in their response to local and landscape factors between crop pests and their natural enemies can have consequences for biological pest control. We studied *Arion* spp. and *Deroceras reticulatum* as major slug pests in Europe and beyond, and predatory carabids as their potential antagonists.

Predatory carabids and slugs were sampled in 18 wheat fields bordered by different habitat types (arable fields, woody or herbaceous semi-natural vegetation) along a gradient of landscape composition (amount of semi-natural habitats in 1 km radius). Species richness of predatory carabids increased with the amount of semi-natural habitats in the landscapes around wheat fields. No effects of landscape composition or adjacent habitat type were observed for predatory carabid activity-density and *Deroceras reticulatum.* In contrast, *Arion* spp. had highest numbers in structurally poor landscapes, but only if fields were bordered by woody vegetation. Thus, *Arion* spp. thrived best in situations where predatory carabid species richness was lowest, indicating that carabids may contribute to the natural control of slug populations. The divergent patterns between carabids and the two slug species demonstrate that more studies of multiple pest species are needed in order to develop comprehensive landscape management strategies for conservation biological control.

Keywords

Carabids, Landscape composition, Ecosystem services, Semi-natural habitats, Natural pest control

3.1 Introduction

Biological pest control by natural enemies is an important ecosystem service to agriculture. It provides several environmental and economic benefits, because it can reduce the need for pesticides (Pickett and Bugg, 1998), while yields can be enhanced (Bommarco et al., 2013). The economic importance of biological pest control in the US was estimated with an annual value of 4.5 billion US dollars (Losey and Vaughan, 2006). However, agricultural intensification and the associated loss of biodiversity in agricultural landscapes may decrease important ecosystem services like pest control (Power, 2010). Compensation of this degradation by expensive chemical and mechanical methods can have further negative impacts (Bommarco et al., 2013).

Conserving and optimizing biological pest control as an ecosystem service in agricultural management schemes requires knowledge of the interaction between pests and their antagonists and of the impact of different environmental parameters at the local and landscape scales. Semi-natural habitats are important refuge habitats and hibernation sites for several beneficial arthropods, from which they can move to crop areas and regulate pests (Bianchi et al., 2006; Holland et al., 2016). Those natural enemies are influenced by local and landscape parameters at different spatial scales depending on their ability to disperse (Tscharntke et al., 2005; Bianchi et al., 2006). Small and specialized natural enemies like egg parasitoids operate on smaller scales and are mainly affected by local parameters (Bianchi et al., 2006). Generalist predators like carabids (Coleoptera: Carabidae) are often strongly influenced by the surrounding landscape due to their high dispersal and colonization capacity (Tscharntke et al., 2005; Chaplin-Kramer et al., 2011). To enhance natural pest regulation, successful immigration into non-crop and crop areas by natural enemies is essential (Tscharntke et al., 2005; Bianchi et al., 2006). To ensure the exchange of beneficial arthropods, the spatial arrangement of semi- natural habitats within the agricultural matrix is important (Tscharntke et al., 2005). Thereby, complex landscapes with a high amount of semi- natural habitats should allow natural enemies to colonize fields from a greater non-crop area, which can lead to an enhanced biological regulation of pests (Bianchi et al., 2006).

Besides natural enemies, also pest species can benefit from semi-natural habitats at the local and landscape scale (Bianchi et al., 2006; Fusser et al., 2016). However, Chaplin-Kramer et al. (2011) did not find a significant overall influence of the landscape on pests in their meta-analysis, which could be due to the low number of studies that related pest densities to the landscape context, so far. In Europe, slugs of the genus *Arion* (Férussac, 1819) and *Deroceras* (Rafinesque, 1820) are major pests in agricultural landscapes, leading to massive damages in a variety of different crops where they occur (Godan, 1983; Frank, 1998a,b). These slugs profit from semi-natural habitats (Speiser and Niederhauser, 1997; Frank, 1998a,b, 2013; Fusser et al., 2016), however, benefits are species-specific and can vary between semi-natural habitat types and landscapes (Fusser et al., 2016).

Many carabids are generalist predators and important natural enemies of slugs (e.g. Symondson 1989, 1994; Ayre 1995). Carabids in arable crops are influenced by landscape composition (Weibull et al., 2003; Purtauf et al., 2005; Diekötter et al., 2010; Fusser et al., 2016) and also locally by the adjacent semi-natural habitats (Kromp, 1999; Pfiffner and Luka, 2000). However, results about the effects of different semi-natural habitat types on carabids are quite contradictory and studies found positive effects of either woody or herbaceous habitat types (Varchola and Dunn, 2001; Hof and Bright 2010; Fusser et al., 2016). The combined and possible interactive effects of semi-natural habitats adjacent to fields and at the landscape scales on field densities of carabids and slugs have to our knowledge never been tested. We investigated the interactive effects of local and landscape factors on predatory carabids, slugs and the potential for natural pest control of slugs by carabids in wheat fields. As local factor we considered the adjacent habitat type (arable fields, woody or herbaceous semi-natural vegetation) and we considered the proportion of semi-natural habitats in 1 km radius as a landscape factor.

We hypothesized that (i) species richness and abundance of predatory carabids in wheat fields are influenced by the adjacent habitat type, (ii) species richness and abundance of predatory carabids increased with the proportion of semi-natural habitats at the landscape scale, (iii) slug activity-densities are influenced by the adjacent habitat, and (iv) slug activity-densities are lowest in landscapes rich in semi- natural habitats due to higher predatory carabid densities.

3.2 Material and methods

3.2.1 Study area

The study area was located in the Upper Rhine region between Ludwigshafen, Landau and Kandel in Rhineland-Palatinate, Germany. With annual mean temperatures around 10.5 °C, this region is one of the warmest in Germany. The elevation in this region ranges from 90 to 160 m NN, and annual precipitation is 667 mm (station Landau, German Weather Service). Its climate and fertile soils lead to an intensive agricultural land use with specialized crop farming like fruit and vegetable cultivation.

3.2.2 Site selection

The study was done in 2014 in 18 winter wheat fields. Six fields were bordered by herbaceous semi-natural habitats (SNH) and six by a woody SNH. Woody SNH consisted of at least 30% woody vegetation cover, otherwise SNH were considered as herbaceous. Field margin selection was done irrespective of their orientation in order to be representative for the study region. There was no significant effect of woody margin orientation on any of the dependent variables. We also included six control fields, which bordered another arable field (no SNH). The wheat fields were located in six regions of different landscape composition, expressed as the percentage of SNH in 1 km radius (ranging from ~5 to 50% SNH). The amount of SNH in the landscapes was digitized from aerial photographs (QGIS 2.6., google earth, accessed on

April 2013) and ground-truthed by field inspection. Neighbouring landscape sectors were as different as possible in terms of their percentage of SNH in order to avoid spatial non-independence. The minimum distance between wheat fields within one region was 200 m. The length of each field was at least 52 m.

3.2.3 Animal sampling

Carabid and slug activity-density (in the following only ‘density’) was assessed with pitfall traps for one week each at the end of May and June in 2014 (Griffiths et al., 1998). Two transects were installed in each field 10 m apart from each other, so that they divided each field lengthwise into half. Transects reached 26 m into the investigated fields (half the minimum length of the field). In each transect, one pitfall trap was placed at four positions (2 m, 10 m, 18 m, 26 m; N = 8 traps per field). The traps (plastic cups) were 66 mm in diameter and 70 mm in depth and were filled with a 1:3 propylene-glycol-water solution. Trapped individuals were conserved in 70% ethanol. Carabids and slugs of the genus *Deroceras* were determined to species level according to Mueller-Motzfeld (2006) and Godan (1983), *Arion* spp. only to genus level (Godan, 1983) without dissection.

3.2.4 Data analysis

We used R 3.1.2 for all statistical analysis (R Development Core Team, 2014). We combined the data of the 8 pitfall traps per field and the two sampling dates for statistical analysis. Carabids were classified as predators according to Homburg et al. (2013).

We used ‘habitat type’ (factor with three levels: woody, herbaceous, field), ‘landscape composition’ (continuous: % semi-natural habitats in 1 km radius) and their interaction as predictor variables in all models. We tested for effects of predictor variables on log10(x + 1) transformed data of densities of predatory carabids, predatory carabid species richness, densities of *Arion* spp. and *D. reticulatum* as well as on pre- dator-prey ratios with linear mixed effect models (command ‘lme’ in R package nlme; Pinheiro et al., 2016). Because fields were nested within the six landscapes, we included ‘landscape’ as a random effect (using the command ‘lme’ in the R package MASS, Venables and Ripley, 2002). We checked model residuals for normality and homogeneity of variances by using diagnostic plots (Zuur et al., 2009). The significance of predictor variables was tested with ANOVA (command ‘Anova’, R package car; Fox and Weisberg, 2010) or permutational ANOVA (command

‘PermTest’, in R package pgirmess; Giraudoux and R Core Team, 2016, if model assumptions were violated).

We used permutational multivariate analysis of variance using the Bray-Curtis distance as a distance measure to test for effects of the predictor variables on the species composition on predatory carabids, whereas fields were nested within one region using ‘strata’ and the command ‘adonis’ in the R package vegan (Oksanen et al., 2016).

3.3 Results

3.3.1 Predatory carabids

We sampled 973 predatory carabids of 25 species (Table 8 in Appendix). Dominant species were *Pterostichus melanarius, Poecilus versicolor* and *Bembidion lampros*, which are typical species of arable landscapes. In contrast to our hypothesis, the adjacent habitat type had no significant effect on density and species richness of predatory carabids (Table 5). In line with our hypothesis, species richness of predatory carabids significantly increased with the amount of semi-natural habitats in the landscape, whereas density of predatory carabids was not significantly affected (Table 5, Fig. 3). The interaction between adjacent habitat type and amount of SNH in the landscape was not significant for predatory carabid species richness and density (Table 5 Fig. 8 Appendix). The species composition of predatory carabids was significantly related to the adjacent habitat type and the amount of semi-natural habitats in the landscape (Table 6, Fig. 4).

The ratio of predatory carabids and *Arion* spp. was significantly affected by the adjacent habitat type and highest in field-to-field situations (Table 5, Fig. 5b). Moreover, we found a significant interaction between the adjacent habitat type and the amount of semi-natural habitats in the landscape (Table 5). In field-to-field situations the ratio of predatory carabids and *Arion* spp. strongly increased with increasing amount of semi-natural habitats in the landscape while this pattern was much less obvious in fields bordering woody or herbaceous habitat types (Fig. 5). We found no significant effects of habitat type and landscape on the ratio of predatory carabids and *D. reticulatum* (Table 5).

Table 5 Effects of adjacent habitat type and landscape (% SNH area in 1 km radius) on predatory carabids and predator-prey ratios in wheat fields. Significance was tested with ANOVA. Significant numbers are printed in bold

Response	Explanatory variables	DF	Chi^2	P
Predatory carabid density	Habitat type	8	2.90	0.234
	Landscape	4	2.11	0.146
	Habitat type: landscape	8	5.08	0.079
Predatory carabid species richness	Habitat type	8	2.35	0.309
	Landscape	4	4.51	**0.034**
	Habitat type: landscape	8	5.09	0.078
Ratio predatory carabids/*Arion* spp.	Habitat type	8	11.38	**0.003**
	Landscape	4	0.84	0.361
	Habitat type: landscape	8	11.13	**0.004**
Ratio predatory carabids/*D. reticulatum*	Habitat type	8	1.88	0.391
	Landscape	4	1.57	0.210
	Habitat type: landscape	8	3.12	0.210

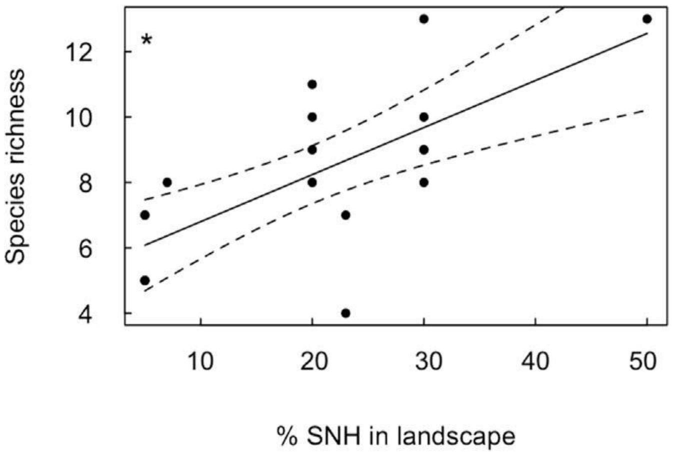

Figure 3 Effects of landscape (% SNH area in 1 km radius) on predatory carabid species richness in wheat fields. Significance was tested with linear mixed models and ANOVA (see Table 1). * P < 0.05. Regression lines and 95% confidence intervals are shown.

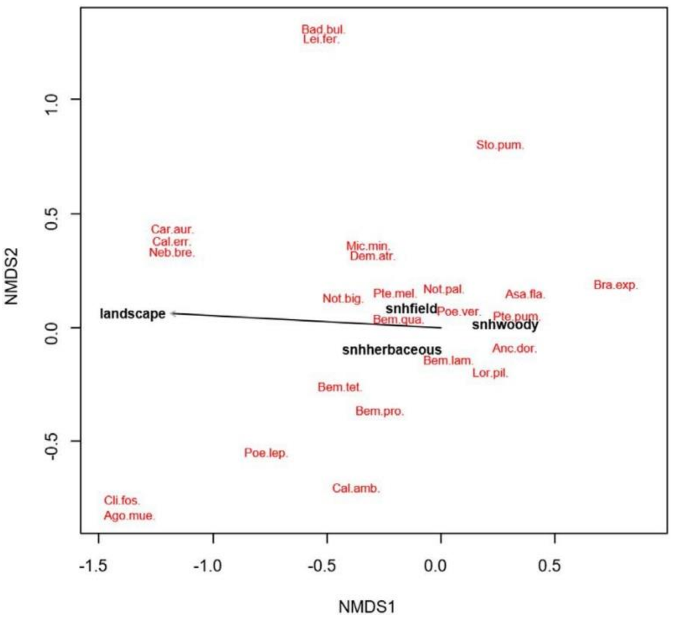

Figure 4 Ordination of species composition of predatory carabids in wheat fields. Significance of predictor variables (SNH type, amount of SNH in landscape and their interaction) was tested with permutational multivariate analysis of variance using distance matrices. Ago.mue = Agonum muelleri, Anc.dor. = Anchomenus dorsalis, Asa.fla. = Asaphidion flavipes, Bad.bul. = Badister bullatus, Bem.lam. = Bembidion lampros, Bem.pro. = Bembidion properans, Bem.qua. = Bembidion quadrimaculatum, Bem.tet. = Bembidion tetracolum, Bra.exp. = Brachinus explodens, Cal.amb. = Calathus ambiguous, Cal.err. = Calathus erratus, Car.aur. = Carabus auratus, Cli.fos. = Clivina fossor, Dem.atr. = Demetrias atricapillus, Lei.fer. = Leistus ferruginosus, Lor.pil. = Loricera pillicornis, Mic.mau. = Microlestes maurus, Mic.min. = Microlestes minutulus, Neb.bre. = Nebria brevicollis, Not.big. = Notiophilus biguttatus, Not.pal. = Notiophilus palustris, Poe.lep. = Poecilus lepidus, Poe.ver. = Poecilus versicolor, Pte.mel. = Pterostichus melanarius, Pte.pum. = Pterostichus pumilio, Sto.pum. = Stomis pumicatus.

Table 6 Effects of adjacent habitat type and landscape (% SNH area in 1 km radius) on species composition of predatory carabids in wheat fields. Significance was tested with permutational multivariate analysis of variance using distance matrices. Significant results are printed in bold.

Explanatory variables	DF	F-Model	R^2	P
Habitat type	2	1.73	0.170	**0.026**
Landscape	1	2.25	0.110	**0.017**
Habitat type: landscape	2	1.35	0.132	0.162

3.3.2 Slugs

We found 46 *Arion* spp. and 70 *D. reticulatum* individuals. Density of *Arion* ssp. was related to the adjacent habitat type and highest in wheat fields bordered by woody SNH, while lowest densities were found adjacent to another field (Fig. 5a). We observed an interactive effect of habitat type and amount of SNH in the landscape on *Arion* spp. (Table 7). Density of *Arion* spp. adjacent to woody SNH decreased with increasing amount of SNH in the landscape while their densities were always low in fields adjacent to herbaceous SNH or another field (Fig. 6). Density of *D. reticulatum* in wheat fields was not affected by bordering SNH type, landscape or their interaction (Table 7).

Table 7 Effects of adjacent habitat type and landscape on slugs in wheat fields. Significance was tested with permutational ANOVA. Significant results are printed in bold.

Response	Explanatory variables	P
Arion spp. density	Habitat type	**0.032**
	Landscape	0.244
	Habitat type: landscape	**0.040**
D. reticulatum density	Habitat type	0.241
	Landscape	0.269
	Habitat type: landscape	0.494

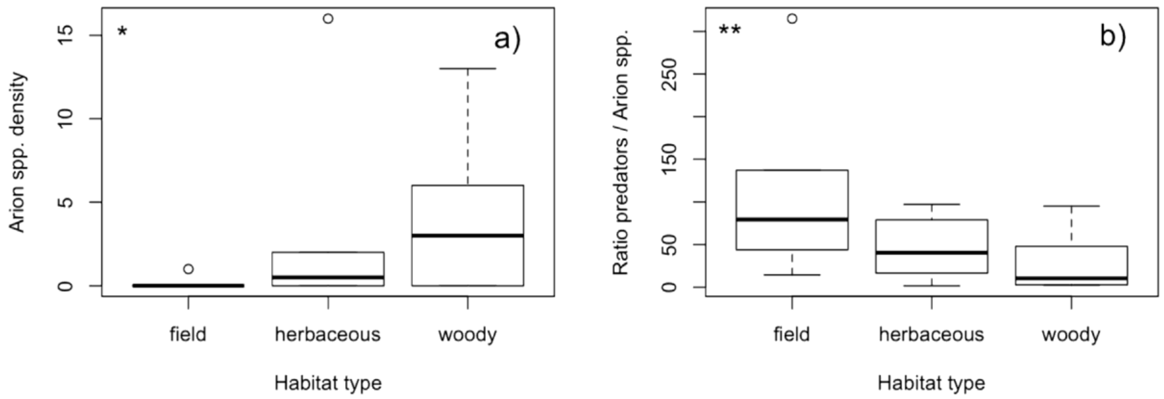

Figure 5 Effects of adjacent habitat type on a) Arion spp. activity-density and b) the ratio of predatory carabids and Arion spp in wheat fields. Significance was tested with linear models and ANOVA or permutational ANOVA (see Tables 1 and 2). * $P < 0.05$, ** $P < 0$

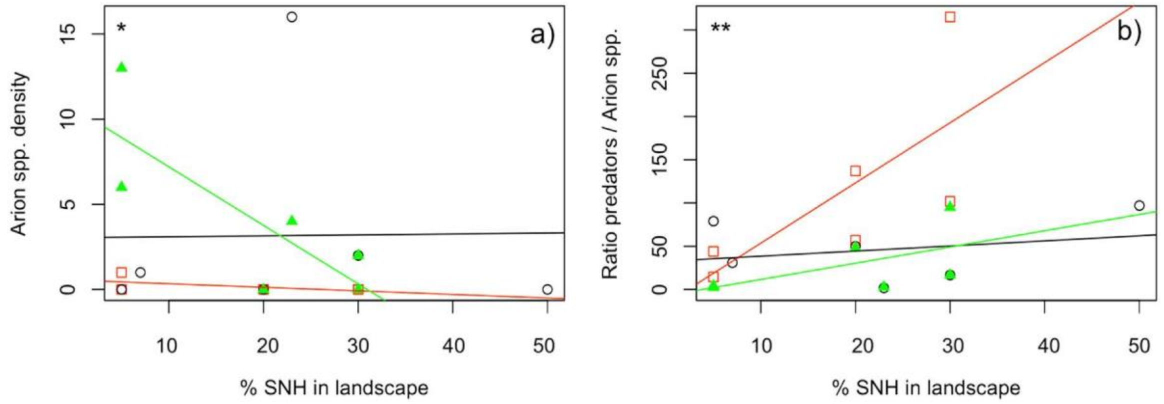

Figure 6 Interactive effect of landscape (% SNH area in 1 km radius) and adjacent habitat type on a) Arion spp. activity-density and b) predator-prey ratio (carabids/Arion spp.) in wheat fields. Significance was tested with linear models and ANOVA or permutational Anova (see Tables 1 and 2) * $P < 0.05$, ** $P < 0.01$. □ = field, ▲ = woody, O = herbaceous SNH.

3.4 Discussion

Our results show that local and landscape parameters affect predatory carabids and *Arion* spp. in wheat fields. Species richness of predatory carabids within fields increased with increasing amount of SNH in the landscape. In contrast, adjacent habitat type did not affect species richness or activity-density of predacious carabids. This is in accordance to findings of Fusser et al. (2016) in the same study region, where density of predatory carabids within SNH increased with amount of SNH in the landscape, but SNH type had no effect. High trophic level species are generally expected to respond to resource distribution at large spatial scales (Holt et al., 1999), because they are more food limited (Bommarco, 1998) and have larger home ranges to track resources in space and time than herbivores (Holt 1996; Lavandero et al., 2004; Rooney et al., 2008). Furthermore, generalist predators with higher dispersal ability, like many carabids, are more strongly influenced by the landscape compared to specialist predators with a limited mobility (Tscharntke et al., 2005). Thus, simplification of the landscape matrix can have negative impacts on predatory carabid diversity (Purtauf et al., 2005) possibly reducing their potential for pest control. We found differences in the species composition of predatory carabids among fields with different adjacent habitats and in relation to the amount of semi-natural habitats in the surrounding landscape. These findings reflect differences in habitat preference of the different predacious carabid species. In general, SNH function as hibernation sites for carabids and adjacent fields can be colonized after over-wintering periods (Kromp 1999; Pfiffner and Luka, 2000). Some carabid species exclusively overwinter within the open fields and thus, their occurrence does not depend on non-crop field margins (Kromp and Steinberger, 1992; Holland et al., 2007). Also other parameters such as sowing time of crops and crop type (Purvis et al., 2001), vegetation cover (Eyre and Leifert, 2011), management intensity (Cole et al., 2005) and orientation of the margins (Sarthou et al., 2014) are known to potentially affect beneficial arthropods including carabids in fields. Numbers of the pest slug *Arion* spp. were affected by adjacent habitats and by the amount of SNH in the landscape. In general, semi-natural habitats can favor pests like aphids and herbivore beetles (Bianchi et al., 2006; Rusch et al., 2012) and also *Arion* spp. (Frank 1998b; Fusser et al., 2016). We found most *Arion* spp. individuals in wheat fields adjacent to woody field margins and lowest numbers in fields without adjacent SNH, which is in line to highest *Arion* spp. densities within woody field margins in the study area (Fusser et al., 2016). *Arion* spp. lives above ground and needs shelter habitats during daytime (Frank, 1998a). Furthermore *Arion* spp. do not feed on grasses (Frank, 1998a). Thus, the distribution of *Arion* spp. in fields is limited by the proximity to the favored field margins. This supports findings of Eggenschwiler et al. (2013) and Frank (1998b) who found more *Arion vulgaris* nearby field margins than in the field center. Interestingly, *Arion* spp. did not benefit from a high amount of SNH at the landscape scale. Highest densities of *Arion* spp. were observed in wheat fields adjacent to woody SNH and with low amounts of SNH in the surrounding landscape. This pattern was not found in fields adjacent to herbaceous SNH or to an- other field, but densities adjacent to these structures were generally very low. As *Arion* spp. densities in woody SNH are high, the decrease of *Arion* spp. individuals with increasing amounts of SNH in the landscape cannot be explained by an avoidance of those habitats. Instead, the high densities of *Arion* spp. in simple landscapes could be a result of reduced densities and species richness of predatory carabids, and hence reduced predation pressure in those landscapes. This within field pattern is also congruent to the pattern in field margins (Fusser et al., 2016), where enhanced *Arion* spp. numbers and reduced carabid numbers occurred in simple landscapes. In- creasing predator-prey ratios of predacious carabids and *Arion* spp. along woody habitats with increasing amount of SNH in the landscape also indicate a control of this slug species.

Our results suggest that simple agricultural landscapes are at greater risk of damages by *Arion* spp., especially when primarily woody SNH occur in those landscapes. Also Rusch et al. (2016) found reduced pest control in simple landscapes, where the simplification (increase from 2% to 100% of cultivated land in the landscape) reduced aphid control by 46%. However, our findings are contrary to Chaplin-Kramer et al. (2011), who could not find a relationship between pest abundance and landscape complexity. But it has to be taken into account that only few studies considering pest densities were included in that meta-analysis, and none of them dealt with slugs (Chaplin-Kramer et al., 2011).

In contrast to *Arion* spp., density of *D. reticulatum* in wheat fields was not affected by adjacent habitats. The spatial distribution of *D. re-ticulatum* depends more on agricultural practices, where no-tillage systems as well as direct-drilling favor the occurrence of *D. reticulatum* (Frank 1998b; Glen and Symondson 2002). During daytime *D. reticulatum* buries in the soil and can survive soil cultivation (Eggenschwiler et al., 2013), thus making it more independent of perennial and undisturbed vegetation than *Arion* spp. Densities of *D. reticulatum* within field margins were higher in herbaceous than in woody semi-natural habitats, underlining its adaptation to agricultural habitats (Fusser et al., 2016). Because we could not find any impact of habitat type and landscape on *D. reticulatum,* we assume that densities might be bottom-up regulated by factors not included in this study.

The different results for *Arion* spp. and *D. reticulatum* show that there is no single strategy in habitat management to cope with the two pests. However, compared to other studies the divergent patterns for *Arion* spp. and *D. reticulatum* may be rather exceptional. Schüepp et al. (2014) showed that natural control of two different pests (aphids, herbivorous beetles) was similarly affected by adjacent semi-natural habitats. Also pollination services by different wild bees can benefit in a similar manner by the proximity of forest (Ricketts et al., 2008), and predation pressure and pollination may even show parallel increases with habitat connectivity (Farwig et al., 2009). However, studies about effects of non-crop habitats on pests are still scarce and investigations about effects on natural enemies alone are not sufficient to understand natural pest control in agricultural landscapes (Chaplin-Kramer et al., 2011). More studies combining multiple pest and beneficial species are needed to understand if certain landscape management strategies have overall positive effects on conservation biological control.

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3.6 Appendix

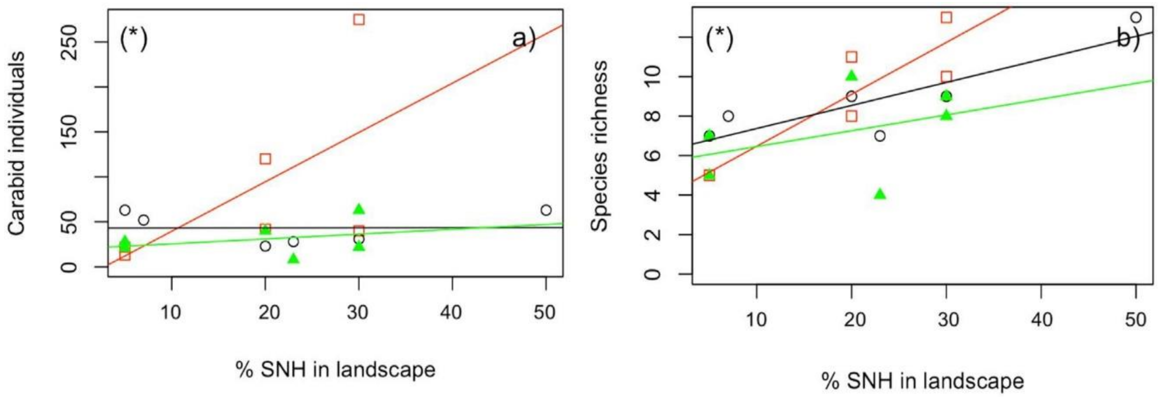

Figure 7 Interactive effect of landscape (% SNH area in 1 km radius) and adjacent habitat type on a) activity-density and b) species richness of predatory carabids in wheat fields. Significance was tested with linear models and ANOVA (see Table 1) (*) P < 0.1. □ = field, △ = woody, O = herbaceous SNH.

Table 8 Species list of captured carabids, including predators, omnivores and herbivores

Species	**total individual numbers**
Agonum muelleri	1
Amara aenea	5
Amara bifrons	1
Amara communis	5
Amara convexior	1
Amara eurynota	5
Amara similata	7
Anchomenus dorsalis	84
Anisodactylus binotatus	7
Anisodactylus signatus	1
Asaphidion flavipes	16
Badister bullatus	2
Bembidion lampros	154
Bembidion properans	22
Bembidion quadrimaculatum	98
Bembidion tetracolum	32

Brachinus explodens	1
Calathus ambiguus	9
Calathus erratus	1
Carabus auratus	1
Clivina fossor	1
Demetrias atricapillus	1
Diachromus germanus	3
Harpalus affinis	47
Harpalus dimidiatus	2
Harpalus distinguendus	3
Harpalus latus	5
Harpalus rubripes	1
Harpalus rufipes	103
Harpalus signaticornis	3
Harpalus tardus	1
Leistus ferruginosus	1
Loricera pillicornis	47
Microlestes maurus	0
Microlestes minutulus	11
Nebria brevicollis	1
Notiophilus biguttatus	1
Notiophilus palustris	1
Ophonus azureus	2
Ophonus puncticeps	0
Paradromius linearis	14
Parophonus maculicornis	1
Poecilus cupreus	17
Poecilus lepidus	6
Poecilus versicolor	135
Pterostichus melanarius	345
Pterostichus pumilio	1
Stomis pumicatus	1
Trechus obstusus	11
Trechus quadristriatus	53

Chapter 4 Interactive effects of local and landscape factors on farmland carabids

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Abstract

1. As a result of migration and spillover from noncrop habitats, predacious insects in agricultural fields respond locally to adjacent field margins and on a larger spatial scale to habitats in the surrounding landscape. However, the relative importance of local and landscape effects and their possible interactions have rarely been studied.
2. We studied carabids in 18 pumpkin fields bordered by different field margins, along a gradient from simple to structural rich landscapes. Carabids were caught in pitfall traps along transects from the adjoining semi-natural habitat towards the field centre.
3. Although estimated species richness generally increased towards the field edges, carabid abundance increased towards adjacent woody margins and other crop fields. By contrast, abundance decreased towards adjacent herbaceous margins. Estimated carabid species richness in organically managed fields increased with increasing

landscape heterogeneity, whereas this effect was absent in conventional fields. However, estimated species richness did not differ between organic and conventional fields.

4. The differential response of carabid abundance to distance from the field edge in accordance with the type of field margin may explain the variability of patterns reported in the literature. The results of the present study show that both local and landscape parameters must be taken into account to promote carabids as natural enemies of crop pests.

Keywords

agri-environment schemes, carabids, natural pest control, semi-natural habitats, species richness, within-field distribution

4.1 Introduction

Natural pest control requires sufficient densities of generalist predators to prevent pest outbreaks. Such beneficial arthropods can be enhanced by semi-natural habitats, which provide important resources, such as shelter, hibernation and oviposition sites, or alternative prey (Root, 1973; Letourneau, 1990; Bianchi *et al.*, 2006; Holland *et al.*, 2016). Carabids (Coleoptera: Carabidae) are abundant predators in crop fields and prey on a wide variety of pests (Sunderland, 2002).

Carabid species vary in the way in which they utilize semi-natural habitats in agricultural landscapes. Some species use them purely for overwintering or aestivation, whereas others are more or less permanent residents, although they may forage in the nearby crop (Kromp, 1999; Pfiffner & Luka, 2000; Varchola & Dunn, 2001; Hof & Bright, 2010). In addition, large numbers of carabids also overwinter within fields and must be taken into account when evaluating the effectiveness of landscape features (Holland *et al.*, 2007). However, positive local effects of semi-natural habitat types on carabids in adjoining crop fields are partly contrasting depending on the habitat type (Holland & Luff, 2000; Varchola & Dunn, 2001; Holland *et al.*, 2007, 2016; Hof & Bright, 2010). More recently, studies conducted at larger spatial scales have investigated the effects of semi-natural habitats on carabids (Woodcock *et al.*, 2014; Fusser *et al.*, 2016). Thereby, a high proportion of semi-natural habitats in the surrounding landscape (or a low proportion of arable fields) has been shown to increase carabid species richness as a result of a larger species pool, an exchange between different habitats and resource complementation (Weibull *et al.*, 2003; Purtauf *et al.*, 2005; Diekötter *et al.*, 2010).

The crop farming system also affects field arthropods and organically managed fields often contain higher abundances and species richness than conventionally managed fields (Hole *et al.*, 2005; Puech *et al.*, 2014; Rusch *et al.*, 2014), although not always (Winqvist *et al.*, 2011). Arthropods are considered to benefit from the reduced use of synthetic pesticides and the often more heterogeneous vegetation structure in organic fields, which led to a more beneficial microclimate and increased food availability (Hole *et al.*, 2005). However, knowledge about the interactions of the farming system and semi-natural habitats at the local and landscape scale on carabids and subsequent effect on their distribution within fields is limited (Rusch *et al.*, 2014, Winqvist *et al.*, 2011).

Carabid numbers often decline with increasing distance from semi-natural habitats towards the center of adjacent fields (Hol- land *et al.*, 2005, 2009; Saska *et al.*, 2007; Anjum-Zubair *et al.*, 2010). Such distribution patterns are also known to occur with other beneficial arthropods (Coombes & Sothertons, 1986; Bianchi *et al.*, 2006). The reasons for this include spillover into fields from adjacent habitats, more suitable microclimatic conditions and higher food availability near the margins (Bianchi *et al.*, 2006). Landscape effects on the within-field distribution of carabids are unclear and there is also a lack of knowledge on how different farming systems affect the within-field distribution of carabids. So far, studies have shown that farming systems can affect carabids in agricultural fields, although the results are more contradictory regarding the most beneficial farming system (Hol- land *et al.*, 2002; Hole *et al.*, 2005). Importantly, possible inter- active effects between local farming and landscape composition on carabids are unclear. For spiders, positive effects of landscape heterogeneity on species richness are limited to fields with conventional farming system whereas organic fields have generally high spider richness (Schmidt *et al.*, 2005). Similar patterns can be expected for carabid beetles.

In the present study, we investigated the effects of the type of semi-natural habitats at the local scale (i.e. semi-natural habitat type adjacent to a crop field) and the landscape scale (i.e. the amount of semi-natural habitats in a landscape) on the within-field distribution of carabids in pumpkin fields. Moreover, we tested whether these effects differed between organic and conventional fields.

We hypothesized that (i) carabid abundances and species richness in fields would increase with proximity to the field edge, with an increasing proportion of semi-natural habitats in the landscape and with organic compared to conventional farming system. In addition, we expected that (ii) landscape effects on carabids would be stronger in conventional than in organic fields. Furthermore, we expected edge effects on carabid abundance and species richness to differ (iii) between the type of semi-natural habitat; (iv) between farming systems with a greater contrast between field edge versus field interior in conventional fields; and (v) between landscapes with different proportions of semi-natural habitats.

4.2 Materials and methods

4.2.1 Study site selection

The study was conducted in 2014 between Ludwigshafen, Landau and Kandel in Rhineland-Palatinate, Germany (Fig. 8). This region is characterized by intensive agricultural land-use as a result of its fertile soils and the relatively mild climate, with a mean annual temperature of 10.5 ∘C and precipitation of 667 mm (station Landau, German Weather Service). We selected 18 different pumpkin fields on sandy to loamy soils, which bordered either a woody semi-natural habitat (SNH) ($n = 6$), a herbaceous SNH ($n = 6$) or, as a control, another field ($n = 6$) (Fig. 1). Nine of the fields were under organic and conventional farming, respectively. Woody SNH consisted of at least of 30% woody vegetation (i.e. hedges, tree lines, abandoned fields with more than 30% shrub/tree canopy cover); otherwise, they were considered as herbaceous (i.e. field margins, grass strips, semi-natural grassland). Most studied hedges and tree lines were interspersed with or bordered by herbaceous vegetation. The most common weed was *Atriplex patula* (found in 15 out of 18 fields), followed by *Polygonum persicaria* (eight fields) and *Stellaria media* (seven fields).

The side of the pumpkin fields at which the sampling took place was at least 52 m long. The fields were situated in 18 different landscapes. For each landscape, we measured its composition within a radius of 1 km by calculating the pro- portion of SNH area (area of permanent semi-natural woody and herbaceous elements, see above) using aerial photographs (QGIS, version 2.6, https://download.qgis.org; Google Earth, https://earth.google.com, accessed April 2013). Fields and SNH area were ground-truthed by field inspection. The 18 landscapes represented a gradient from 5% to 50% SNH.

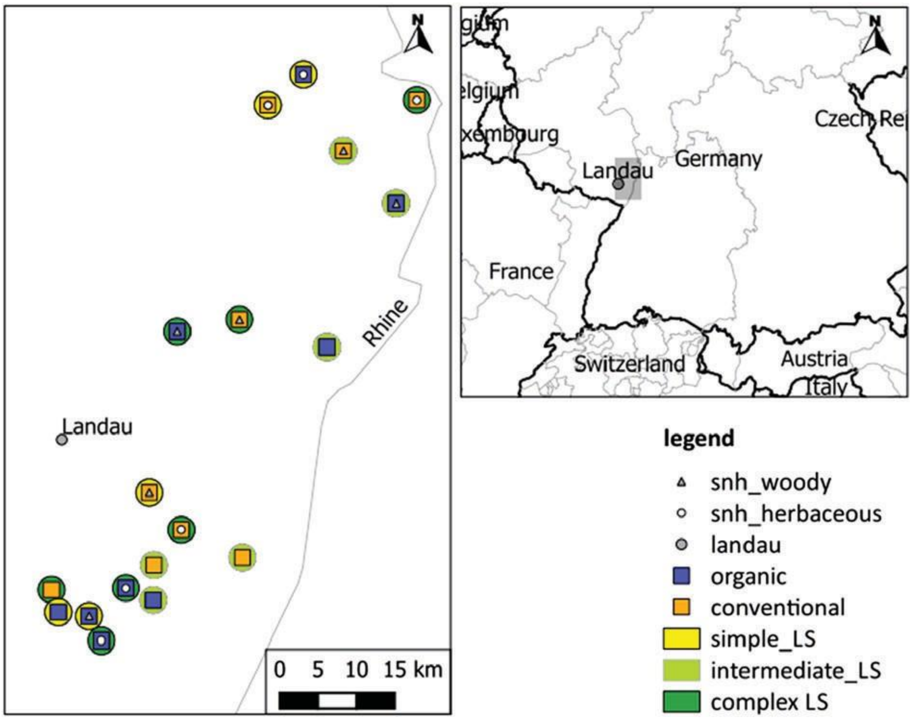

Figure 8 Study area and location of the study fields near landau in Rhineland-palatinate, Germany. Control fields bordering another field = no symbol for snh_woody or snh_herbaceous. [Colour figure can be viewed at wileyonlinelibrary.com].

4.2.2 Carabid sampling

Carabids were sampled using pitfall traps (diameter 66 mm, depth 70 mm), half filled with a 1:3 propylene-glycol-water solution. In each pumpkin field, the traps were installed along two transects at four distances (2, 10, 18 and 26 m) from the adjoining SNH or neighbouring field. The two transects were placed 10 m apart from each other and located centrally with the field edge that was at least 52 m long. The trapped carabids were conserved in 70% ethanol. We determined carabid species according to Mueller-Motzfeld (2006). The sampling took place for 1 week each at the end of May and at the end of June 2014.

4.2.3 Statistical analysis

We used r, version 3.1.2 for all statistical analysis (R Development Core Team, 2014). Data from each distance of two transects and sampling periods per field were combined. The Chao index was used to compare species richness across levels of explanntory variables (Chao &

Jost, 2012). We used the Chao 1 estimator, which accounts for species abundance data. As a result of terms of simplification, we refer to ‘species richness’ throughout the present study rather than ‘estimated species richness’.

The abundance and species richness of carabids was related to predictor variables with generalized linear mixed models with negative binomial error structure (command ‘glmer.nb’ in r-package lme4; Bates *et al.*, 2015). Because traps were nested within the fields, we included ‘field’ as a random effect. In all models, we used the predictor variables ‘SNH type’ (factor with three levels: woody, herbaceous, field), ‘farming system (factor with two levels: organic, conventional), ‘distance’ (continuous: four sampling points along transects), ‘landscape composition’ (continuous: % semi-natural habitats in 1 km radius) and their interactions. Model performance was checked visually using diagnostic plots (Zuur *et al.*, 2009). Waldchi-squared tests were used to test for the significance of predictor variables (command ‘Anova’, library ‘car’; Fox & Weisberg, 2010).

We used permutational multivariate analysis of variance using the Bray– Curtis distance as a distance measure to test for effects of the predictor variables (SNH type, landscape, farming system, SNH × landscape, SNH × farming system, landscape × farming system) on the carabid assemblage [command ‘adonis’ in the r-package vegan, Oksanen *et al.* 2016]. We combined data of all distances per field (= assemblage of the entire field) to avoid data loss, because several traps caught no beetles.

4.3 Results

In total, we found 1434 carabid individuals and 47 carabid species. 736 carabids belonging to 35 carabid species were trapped in organic fields and 698 individuals belonging to 34 carabid species were trapped in conventional fields (Table 11 in appendix). The most frequent species were *Harpalus rufipes* (29% of the catch), *Bembidion tetracolum* (24% of the catch) and *Bembidion quadrimaculatum* (11% of the catch).

For carabid abundance, the interaction between distance and the SNH type was significant (Table 9). Carabid abundance in pumpkin fields increased towards adjacent woody SNH (from 30 to 42 individuals) or other crop fields (from eight to 18 individuals), whereas it decreased towards adjacent herbaceous SNH from 25 to 15 individuals (Fig. 9). By contrast, landscape composition and farming system had no significant effects on carabid abundance.

Table 9 Effects of semi-natural habitat (SNH) type, distance, farming system and landscape composition on carabid activity-density and carabid species richness

Response variables	Explanatory variables	d.f.	χ^2	*P*
Abundance	SNH type	2	2.25	0.325
	Distance	1	3.27	*0.071*
	Farming system	1	0.06	0.800
	Landscape	1	0.25	0.619
	Distance × Farming system	1	1.77	0.184
	Landscape × Farming system	1	3.26	*0.071*
	Distance × Landscape	1	1.30	0.253
	Distance × SNH type	2	10.50	**0.005**
Species richness	SNH type	2	8.04	**0.018**
	Distance	1	6.74	**0.009**
	Farming system	1	3.81	*0.051*
	Landscape	1	6.60	**0.010**
	Distance × Farming system	1	1.42	0.233
	Landscape × Farming system	1	15.27	**<0.001**
	Distance × Landscape	1	0.01	0.944
	Distance × SNH type	2	0.78	0.678

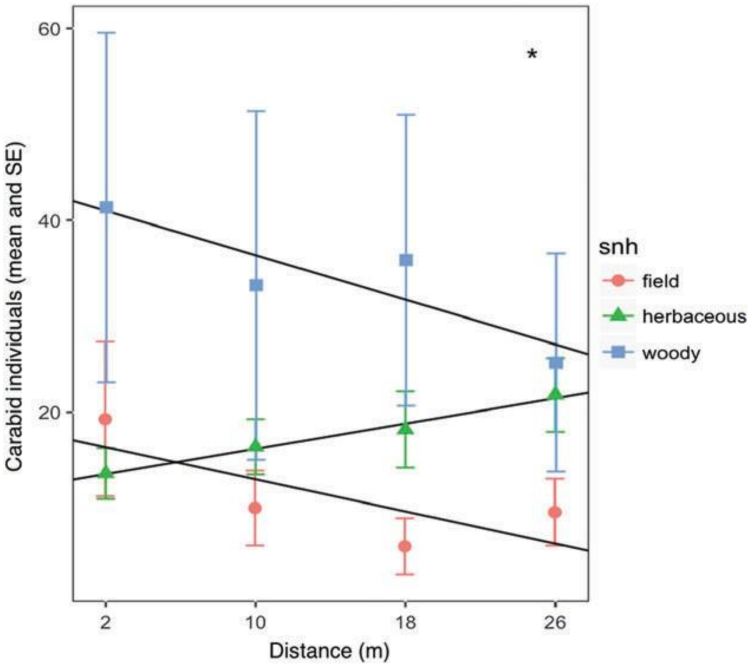

Figure 9 Effects of distance from field margin on carabid activity-density (mean ± SE) in pumpkin fields. For test statistics, see Table 1. *P < 0.05. Regression lines are shown. , woody; , herbaceous; , field

Carabid species richness significantly decreased from the field edge towards the field centre (Fig. 10 and Table 9). Moreover, species richness increased with increasing percentage SNH in 1 km radius (Table 9). However, we also found a significant interactive effect of farming system and landscape composition on species richness (Fig. 11 and Table 9). In organic pumpkin fields, species richness increased from approximately three to 15 species with an increase in the percentage SNH in a 1-km radius of 25%, whereas landscape composition had no effect on species richness in conventional fields (Fig. 11). Carabid richness was affected by adjacent SNH type, with the lowest species richness in fields without adjacent SNH. By contrast, species richness showed no significant response to farming system or to the interaction between distance and farming system or with landscape composition. Carabid species composition did not differ between SNH type, landscape and farming system (Table 10).

Table 10 Effects of semi-natural habitat (SNH) type, landscape and farming system on carabid assemblages. Significance was tested with permutational multivariate analysis of variance using distance matrices

Explanatory variables	d.f.	F-Model	r^2	*P*
SNH type	2	0.80	0.10	0.750
Landscape	1	0.44	0.03	0.947
Farming system	1	1.41	0.09	0.166
SNH x Landscape	2	1.09	0.14	0.364
SNH × Farming system	2	1.01	0.13	0.478
Landscape × Farming system	1	0.82	0.05	0.668

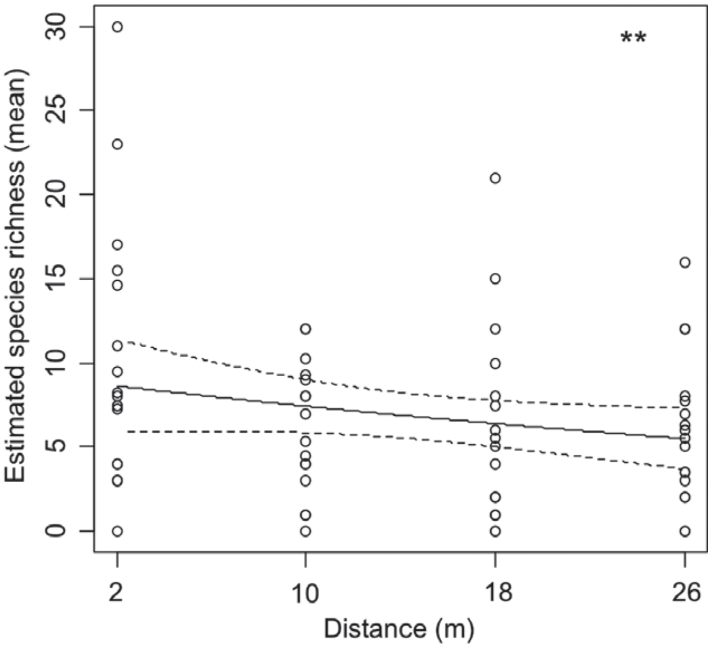

Figure 10 Effects of distance from field margin on carabid species richness in pumpkin fields. For test statistics, see Table 1. **P < 0.01.

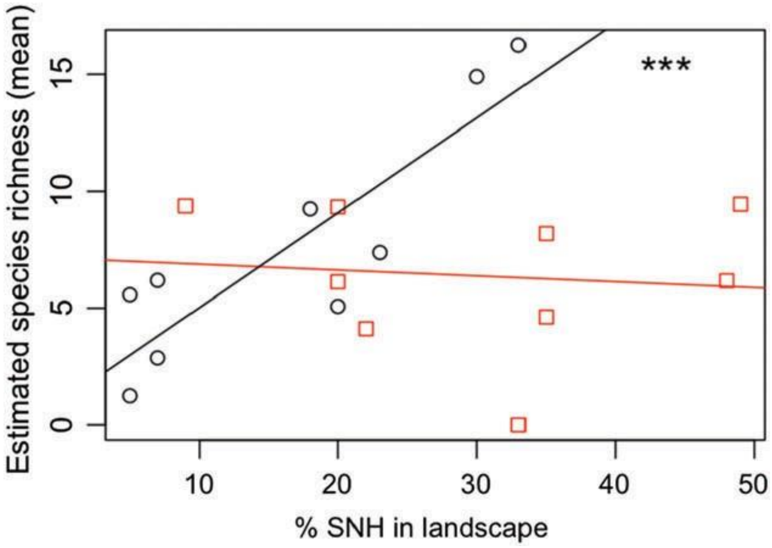

Figure 11 Species richness of carabids (mean) increased with the percentage of semi-natural habitats in the surrounding landscape in organic but not in conventional fields. For test statistics, see Table 1. ***P < 0.001. Regression lines are shown. □ conventional; o organic.

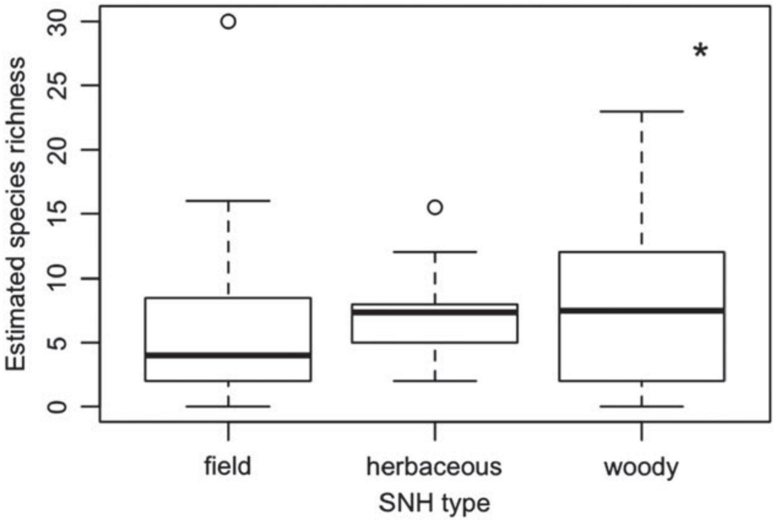

Figure 12 Effects of semi-natural habitat (SNH) type on carabid species richness. *P < 0.05.

4.4 Discussion

4.4.1 Effects of distance from field margin depend on the type of SNH

The results of the present study show that the within-field distribution of carabids depends on the adjacent SNH type but not on the farming system (conventional versus organic) of pumpkin fields. We found highest carabid species richness and abundance at field edges adjoining semi-natural habitats, with both decreasing towards the field centre. This finding supports the results of prior studies in other crops, which also found increased species richness and abundance towards field edges (Kromp & Stein- berger, 1992; Lys & Nentwig, 1992; Lys *et al.*, 1994; Reddersen, 1997; Saska *et al.*, 2007; Holland *et al.*, 2009; Anjum-Zubair *et al.*, 2010). These results likely represent the migration and spillover of carabids from semi-natural habitats such as hibernation sites and shelters towards the open field (Honek & Kocian, 2003). However, decreases of carabid activity towards field centres only apply for fields adjacent to woody margins and in crop-to-crop situations. By contrast, fields with adjacent herbaceous semi-natural habitats contained lower carabid abundances near the edges than in the field centres. Other studies also showed higher carabid abundances in the field interior than near grassy or herbaceous margins (Batary *et al.*, 2012; Birkhofer *et al.*, 2013; Anjum-Zubair *et al.*, 2015). Anjum-Zubair *et al.* (2015) concluded that this pattern might be a result of higher prey densities in the field interior because of higher plant productivity by fertilizers (Siemann, 1998; Haddad *et al.*, 2000) or by a promotion of especially ‘field-interior’ species, although they only investigated different herbaceous margins (wildflower versus grassy strips). Another reason might be that herbaceous margins are more attractive than the field interiors so that carabids remain in the beetle banks in summer (Thomas *et al.*, 2001). In our case, the contrasting results between fields with woody and herbaceous margins may be explained by an enhanced overwintering success and higher prey abundances in and near the woody margins (Nazzi *et al.*, 1989; Letourneau, 1990), the provision of alternative food sources such as slugs of the genus *Arion* along woody SNH (Fusser *et al.*, 2016), and more suitable microclimatic conditions near the woody SNH, which may offer protection against strong winds or sunshine during hot and dry summer months, as commonly occur in the study region. Reduced carabid abundance near the herbaceous SNH can also be a result of predator avoidance or avoidance of interference, especially with wolf spiders (Anjum-Zubair *et al.*, 2010), which are often more abundant near herbaceous field edges (Clough *et al.*, 2005). However, it also needs to be taken into consideration that higher numbers near woody SNH may also be a result of low food resources around those margins, which may lead to higher carabid activity rates because of increased hunger levels (Thomas *et al.*, 2002).

Higher abundance towards other crops may be a result of the neighbouring crop types, which were winter crops and hence sources of crop-inhabiting carabids for the spring-sown pumpkin fields during the sampling period. We suggest that this pattern could be the result of an edge effect, where carabids might benefit from a greater supply of food and different microclimate conditions at the transition of different crops. Such effects have been partially shown for parasitoids across an artificial resource gradient (Tylianakis *et al.*, 2004). It is also possible that some carabids are able to overwinter in small strips at the borders of different fields, where the soil is less disturbed by mechanical management compared with the field interior. Another reason could be an impact of the movement of carabids by different vegetation densities of the two different crops (Thomas *et al.*, 2006).

4.4.2 Independence of within-field distribution from the surrounding landscape

By contrast to our hypothesis, we found no significant interac-tions between distance from the field edge and landscape composition. This indicates that the within-field distribution pattern of carabids is more strongly influenced by local effects of the adjacent semi-natural habitats and that landscape effects play only a minor role. Although species richness and abundance of generalists such as carabids are known to be often influenced by landscape composition (Tscharntke *et al.*, 2005), their distribution within fields might only be related to small scale effects, as shown in the present study (Rusch *et al.*, 2014). The direct availability of shelter habitats adjacent to crops is more important for their distribution within fields than the proportion of shelter habitats in the surrounding landscape because of their limited propensity to disperse (Holland *et al.*, 2004; Griffiths *et al.*, 2008). Such patterns would be also expected for specialist biocontrol agents such as parasitoids, which are strongly influenced by small scale effects (Tscharntke *et al.*, 2005) and are known to be more abundant near field margins (Bianchi *et al.*, 2006).

4.4.3 Positive effects of landscape heterogeneity only in organic fields

As expected, we found interactive effects of the farming system and landscape composition on carabid species richness. How- ever, carabid species richness increased with the amount of SNH in the surrounding landscape only in organic fields, whereas species richness in conventional fields was unaffected by the surrounding landscape. These findings are in agreement with those of Winqvist *et al.* (2011), who only found effects of predation in organic fields, with the highest predation rates in organic fields situated in complex landscapes. However, our findings were in contrast to our expectations and those of other studies, emphasizing the importance of the landscape composition for generalist predator diversity only in conventional fields (Weibull *et al.*, 2003; Purtauf *et al.*, 2005; Schmidt *et al.*, 2005). Also, Bengtsson *et al.* (2005) proposed that positive effects of organic farming are greater in simple landscapes than in heterogeneous landscapes. Diekötter *et al.* (2010) found the highest carabid species richness in organic fields situated in a conventional landscape matrix, whereas species richness was lowest in fields situated in landscapes that always had the same field management practices. However, the preferences of the farming system differ between carabid species. For example, *Harpalus* spp. prefers organic fields and *Trechus quadristiatus* prefers conventional fields (Hole *et al.*, 2005). In the present study, carabid species composition did not significantly differ between fields and landscapes, although some carabid species showed a slight preference for either one or the other farming system (Appendix A1). This demonstrates that single carabid species respond differently from farming system and landscape composition and thus we assume that this could lead to different distribution patterns among landscapes with different composition and farming systems, depending on the respective carabid species pool.

We found no effects of the farming system as a main effect on carabid abundance and species richness, which is in agreement with the findings of Purtauf *et al.* (2005). This is in contrast to many studies, where carabids in organic fields benefitted from higher food sources from weeds and other invertebrates as prey (Hokkanen & Holopainen, 1986; Basedow *et al.*, 1994), as well as from favourable microclimate conditions (Hole *et al.*, 2005). However, there are some studies reporting higher numbers in conventionally managed fields (Weibull *et al.*, 2003; Hole *et al.*, 2005). Carabids are affected by a whole range of different farming practices (Holland & Luff, 2000; Hance, 2002); therefore, differences between farming systems are likely variable (Puech *et al.*, 2014). Contrasting results may also be related to varying sampling periods across studies and complex spatio-temporal pattern of species distribution, as shown for *P. melanarius* (Vasseur *et al.*, 2013). Explanations for the absence of negative effects of conventional farming in the present study might include (i) the absence of pesticide applications in conventional pumpkin fields between planting and carabid sampling;

(ii) the similar cover of weeds between conventional and organic managed fields; (iii) the higher intensity of mechanical weeding in organic farming systems (Sonja Pfister, unpublished data); and (iv) higher levels of fertilization in conventional fields leading to a higher plant productivity, which could have positive effects on carabids (Siepel *et al.*, 1989; Siemann, 1998; Soderstrom *et al.*, 2001).

4.5 Conclusions

The results of the present study confirm the importance of semi-natural habitats for the within-field distribution of carabids. The observed interactive effects between adjacent habitat type and within-field distribution of carabid activity may explain some of the variability found in the results of previous investigations. The absence of differences between farming systems emphasizes the specificity of organic farming benefits to crop types. Overall, our results show that both local and landscape parameters must be taken into account to promote carabids as natural pest control agents.

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4.7 Appendix

Table 11 Trapped carabid individuals, conv. = conventional, org. = organic

Species	**Conv.**	**Org.**	**Field**	**Herb**	**Woody**	**Total**
Acupalpus meridionalis	3	0	3	0	0	3
Agonum muelleri	1	0	0	1	0	1
Amara aenaea	3	2	2	3	0	5
Amara bifrons	8	9	0	11	6	17
Amara communis	4	0	0	4	0	4
Amara convexior	2	0	0	2	0	2
Amara eurynota	2	1	1	1	1	3
Amara similata	1	0	0	0	1	1
Anchomenus dorsalis	4	2	2	2	2	6
Anisodactylus binotatus	2	1	0	0	3	3
Anisodactylus signatus	3	10	5	2	6	13
Asaphidion flavipes	0	1	1	0	0	1
Badister bullatus	0	1	0	0	1	1
Bembidion lampros	80	29	28	22	59	109
Bembidion properans	19	6	4	6	15	25
Bembidion quadrimaculatum	86	74	44	64	52	160
Bembidion tetracolum	266	73	44	71	224	339
Broscus cephalotes	1	33	3	0	31	34
Calathus ambiguus	3	13	5	0	11	16
Calathus erratus	0	1	0	0	1	1

Clivina fossor	5	0	0	4	1	5
Harpalus affinis	51	33	27	34	23	84
Harpalus dimidiatus	0	1	0	0	1	1
Harpalus distinguendus	2	9	1	0	10	11
Harpalus griseus	0	2	0	1	1	2
Harpalus latus	1	0	0	1	0	1
Harpaus luteicornis	0	1	0	0	1	1
Harpalus pumilus	0	1	0	0	1	1
Harpalus rufipes	68	340	79	77	252	408
Harpalus tardus	0	1	0	0	1	1
Laemostenus terricola	0	1	0	0	1	1
Loricera pillicornis	6	3	5	1	3	9
Microlestes maurus	2	0	0	0	2	2
Microlestes minutulus	6	10	1	7	8	16
Notiophilus pallustris	1	0	0	1	0	1
Ophonus azureus	0	2	0	0	2	2
Ophonus puncticeps	1	0	0	1	0	1
Paradromius liearis	3	0	2	0	1	3
Poecilus cupreus	0	6	0	4	2	6
Poecilus lepidus	21	2	4	3	16	23
Poecilus versicolor	15	20	5	9	21	35
Pterostichus mellanarius	10	32	20	10	12	42
Pterostichus pumilio	0	1	1	0	0	1
Stomis pumicatus	1	1	0	0	2	2
Trechus obtusus	0	7	1	0	6	7
Trechus quadristriatus	16	7	15	8	0	23
Zabrus tenebrioides	1	0	1	0	0	1
Total	698	736	304	350	780	1434

Chapter 5 Contrasting predation pressure of different ground beetles on slugs and their eggs

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Abstract

Slugs such as Deroceras reticulatum Müller (Pulmonata: Agriolimacidae) cause crop losses in temperate regions worldwide. Numerous species of ground beetles (Coleoptera: Carabidae) feed on slugs, but possible interactive effects are poorly known. Here, we compared predation pressure on slug eggs and slug immatures among Abax parallelepipedus PILLER & Mitterpacher, Pterostichus niger SCHALLER, and Pterostichus melanarius Illiger. The latter was most effective against slug eggs but least effective against immature slugs compared to the other species, demonstrating some specificity of ground beetle predation on life stages. Slug egg predation of P. niger in combination with both other species was synergistic, with up to twice as many eggs consumed as for single species treatments. The effect of species combinations on immature slugs showed no differences from expectations based on single species treatments. Our results indicate that combinations of ground beetle species are favourable for the suppression of slugs in early life stages.

Keywords

Carabidae, *Deroceras reticulatum*, slug predator, slug egg, biological pest control

5.1 Introduction

Slugs (Pulmonata: Agriolimacidae) are voracious agricultural pests in humid and temperate regions all over the world (South 1992). The surface-active grey field slug *Deroceras reticulatum* Müller, indigenous in northern Europe, invaded North and South America, Asia, Australia, and New Zealand where it causes severe crop losses of arable land and in horticulture by consuming seeds and plants in the early development stages (Douglas and Tooker 2012; Howlett 2005; Renkema et al. 2014; South 1992; Speiser et al. 2001). Moreover, this slug species also occurs in gardens, hedgerows, and grasslands and is the most damaging pest slug worldwide (South 1992; Speiser and Kistler 2002).

Agricultural practices to control these organisms are tillage (Roger-Estrade et al. 2010) and the application of molluscicide pellets containing the active ingredients iron phosphate (Speiser and Kistler 2002) or in conventional agriculture methiocarb and metaldehyde (Howlett et al. 2008). Even though the usage of the latter two products has increased during the last decades (Howlett 2005), the efficacy as well as their side effects on non-target species were debated vigorously (Henderson and Triebskorn 2002; Howlett 2005; Iglesias et al. 2002; Langan et al. 2004). The European Commission ultimately prohibited the application of pellets containing methiocarb in 2015 (European Commission, Regulation No.187/2014). However, metaldehyde is still in use, although this substance can cause adverse effects on aquatic (e.g. oysters; Treilhou et al. 2015) and terrestrial (e.g. dogs and mice; Bates et al. 2012) non-target organisms. Generally, pesticide-based crop cultivation systems may have reached a critical point, as the adverse effects on beneficials could exceed the increased yield (Vasseur et al. 2013).

One of the most important natural enemy groups in agroecosystems are ground beetles (Coleoptera: Carabidae), who play a major role in suppressing slugs (Kromp 1999; Symondson et al. 2002). The generalist species *Pterostichus melanarius* Illiger (Hatteland et al. 2010; Oberholzer and Frank 2003) and *Abax parallelepipedus* Piller & Mitterpacher are effective slug predators, where *A. parallelepipedus* can be as effective against slugs as compared to the molluscicide methiocarb (Asteraki 1993). Moreover, *Pterostichus niger* Schaller consumes different pest slugs including *D. reticulatum* (Hatteland et al. 2010; Pakarinen 1994). The two *Pterostichus* species also feed on the eggs of *D. reticulatum*, which highlights their importance for slug control (Hatteland et al. 2010; Oberholzer and Frank 2003).

Ground beetles are usually hunting through random search (Lövei and Sunderland 1996), where individuals likely encounter potential competitors (Sih et al. 1998). For such encounters between two predator species different scenarios are possible (Losey and Denno 1998): First, both predators do not harm each other acting only on the prey. Summing up the predators' individual impacts on the prey therefore leads to an additive predator-predator effect. Second, interference between predators such as intraguild predation results in an antagonistic effect, where less prey is consumed than the sum of the individual effects. Finally, if predators together have higher foraging success on a prey than the sum of their individual impacts, a synergistic effect occurs. Thereby, the interaction between predators enhances the individual impact of at least one species.

We studied the potential of the ground beetles *A. parallelepipedus*, *P. niger* and *P. melanarius* for the control of the pest slug *D. reticulatum* and its eggs in two experiments. We thereby analysed the impacts of individual predator species as well as combinations of two species. We addressed the following research questions: Do the three ground beetle species differ in their predation rate on the slug eggs of *D. reticulatum*? How do the three species differ in predation rate on immature slugs? Are the ground beetle predation rates (on both eggs and immature slugs) additive, synergistic or antagonistic in experiments with multiple predator species? Our results showed that the investigated ground beetles differed in their effectiveness to control slugs and their eggs, thus complementing each other in the presence of multiple pest stages. Moreover, we found additive effects of species combinations on slug predation and synergistic effects on egg predation.

5.2 Material and methods

5.2.1 Animal collection and maintenance

The ground beetles and slugs were collected with dry pitfall traps and hand catches in different habitats such as orchard meadows, woodland and hedgerows between May and October 2015 near Landau/Palatinate, Germany (49°19'82"N, 8°11'22"E). Ground beetles species and slugs were separately kept in plastic boxes (36 x 21.5 x 13.5 cm^3) filled with regularly moistened soil from the field in a climate chamber at 15 °C day and 12 °C night temperatures, with a 12:12 h light:dark photoperiod. Ground beetles were fed every second day with cat food (REWE Beste Wahl Katzenfutter Junior mit Geflügel, Zooroyal GmbH, Aachen, Germany). The slugs were mainly fed with lettuce (*Lactuca sativa* L.) and small amounts of cat food to cover their protein requirements. Prior to the experiments, ground beetles were starved for 3 days in plastic boxes without any food or food remnants. During this period the climate chamber was adjusted to 18 °C day and 15 °C night temperature.

During the weekly cleaning processes of the slug boxes, the eggs of the slugs were collected and transferred to plastic boxes (36 x 21.5 x 13.5 cm^3) for obtaining the eggs for the egg predation experiment. The boxes were filled with moistened soil (Compo BIO Universal, Compo GmbH, Münster, Germany) to prevent desiccation and were kept under the same conditions as the ground beetles and slugs.

5.2.2 Egg predation experiment

The egg predation experiment took place in an experimental chamber illuminated by daylight at the Institute for Environmental Sciences, University of Koblenz-Landau between the 6th and the 7th of November 2015. The temperature was measured every ten minutes by a HOBO Temp/Light logger UA-002-64. We used plastic containers (78.5 x 47.0 x 31.5 cm^3) filled with a thin layer of potting soil (Compo BIO Universal, Compo GmbH, Münster, Germany). They were arranged in a randomised block design. Six blocks with a distance of 20 cm to each other, each containing one replicate of each treatment and one control. In a block the containers were placed in a distance of 10 cm to each other. We established six treatments differing in ground beetle species with six replicates each. Thereby, the initial total biomass of the ground beetles was kept constant in the containers (each 0.4 g of beetles), to obtain a comparable predator density among treatments (Evans 1991). Single species treatments were: two *A. parallelepipedus,* four *P. melanarius,* two *P. niger.* Two-species treatments were: one *A. parallelepipedus* and two *P. melanarius*, one *A. parallelepipedus* and one *P. niger,* two *P. melanarius* and one *P. niger*. In the control only eggs were added in order to quantify the egg survival at the end of the experiment.

To measure egg predation we stuck ten eggs on a small wooden slat (3 cm length each). The eggs were treated with a drop of tap water to prevent desiccation. In each container we inserted four wooden slats (N=40 eggs per container) at a distance of 10 cm to each corner. Eggs of two slats were uncovered while eggs of the remaining two slats were covered with 20 ml of soil to investigate possible differences in aboveground and below ground egg predation among ground beetles.

After 24 hours all slats were removed from the containers and the soil around the slats was searched so that detached eggs could be recovered. The eggs were counted and examined under a stereomicroscope. Eggs with damaged egg-envelope, causing yolk coming out if slight pressure was applied with a blunt-nosed tweezer, as well as untraceable eggs were considered as eaten.

5.2.3 Slug predation experiment

The slug predation experiment was conducted in the field near Landau/Palatinate in Germany (49°19'72"N, 8°12'47"E), beginning on the 5th and ending on the 12th of October 2015. For the experiment we used plastic containers (78.5 x 47.0 x 31.5 cm^3), painted with a hydrophobic, citric acid-based antislug paste (IRKA Schneckenabwehrpaste, C&C Gartenbedarf, Meitingen, Germany) at a height of 20 cm on the inside walls to prevent the escape of the test slugs as well as the entry of slugs from the outside. Preliminary tests confirmed that the slugs do not cross this barrier and that their survival was not negatively affected. Each container was filled up to 10 cm with potting soil (Compo BIO Universal Erde, Compo GmbH, Münster, Germany) and two rows of four lamb's lettuce *(Valerianella locusta)* seedlings were planted as food for the slugs. Two pieces of pine bark were washed and dried to remove alternative food sources (each ~300 cm^3) and put between the two rows of lettuce serving as shelters for the animals. Each container was covered with gauze (Voile: 100% polyester) to prevent external influences (e.g. birds or cats). Before the experiment started the containers were watered for 10 seconds using a watering can with a spray head, to create favourable conditions for the slugs (South 1992). We monitored the moisture by visual inspection of the soil surface. During the trial the weather was rainy and the air humidity was sufficient to keep the soil moist so that no addition of water was necessary. A scaffold construction was installed, and a tarp used to cover the experiment during strong rain in order to prevent flooding of the containers.

In each container we inserted ten slugs from three weight classes (4 small < 0.25 g, 4 medium-sized > 0.25 g < 0.5 g and 2 large > 0.5 g). We established the same six treatments differing in ground beetle species with six replicates each as in the egg predation experiment. For the control we inserted only slugs without beetles (N=6) to obtain information about the survival of slugs experiencing no predation pressure. In the field the containers were arranged in a randomised block design (six blocks with a distance of 50 cm to each other, each containing one replicate of each treatment and one control, all with 15 cm of space between them). To minimise the influence of abiotic factors (e.g. light conditions), the blocks were moved clockwise from one position to the next every day.

After six days all ground beetles (dead or alive) and slugs were recovered. For the removal of the remaining hidden slugs a further three days were needed. The searching ended when no more mucus traces could be seen at the soil surface in the treatments and all slugs from the control were retrieved. Slugs not recovered at this point were considered as eaten.

5.2.4 Data analysis

All statistical analyses were done using the free software R 3.2.2 (R Development Core Team 2016). Treatment effects on slug egg predation (% missing eggs) and slug predation (% missing slugs) were tested with generalised linear models (GLM) with binomial error structure (link="logit") for proportional data. We used binomial distribution because prey consumption had an upper (the number of prey introduced) and a lower limit (zero). To account for overdispersion we corrected standard errors using a quasi-GLM. Significance of explanatory variables were analysed using F-statistics with ANOVA (library "car", Fox and Weisberg 2011). Five containers were excluded from the analysis of the slug predation experiment because dead ground beetles occurred.

Because of the few soil covered eggs recovered (3.6% ± 0.97) a separate analysis was not appropriate and due to the experimental design corresponding to an exposure of slug eggs in a heterogenous way we pooled eggs of both wooden stick types. If the treatment effect was significant ($p < 0.05$), multiple comparisons of means were performed by Tukey's test, using the "multcomp" package (Hothorn et al 2008).

In order to identify additive, synergistic or antagonistic effects on slug and egg predation, observed predation rates in the combined treatments were compared to expected predation rates. Expected predation rates were calculated by halving the respective single species treatments' average observed predation rates and summing them up according to the respective combination. To test whether the observed results deviated significantly from the respective expected value, we subtracted the expected value from the observed value and then performed a t-test to see if the intercept of the observed values was significantly different from zero.

5.3 Results

5.3.1 Egg predation

The numbers of eggs were significantly reduced by the ground beetles ($F_{6,35}$ = 18.88, p < 0.001). Most eggs were consumed in the treatment with only *P. melanarius* (Pm; 40%) followed by the combinations of *P. melanarius* and *P. niger* (Pm/Pn; 35%), *A. parallelepipedus* and *P. melanarius* (Ap/Pm; 29%), and *A. parallelepipedus* and *P. niger* (Ap/Pn; 28%) (Tukey test: all *p* < 0.001; Fig. 13). The fewest eggs were consumed in the treatments with only *A. parallelepipedus* (Ap; 11%) and *P. niger* (Pn; 14%) where egg predation rates did not significantly differ from the control treatment.

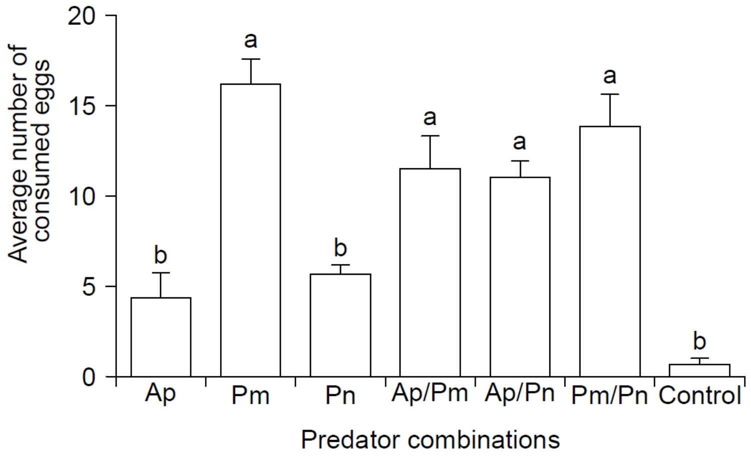

Figure 13 The proportion of consumed eggs in all treatments (means +SE). Bars sharing the same letter are not significantly different for pairwise comparison with the control (Tukey's test, p > 0.05). Ap = *Abax parallelepipedus*, Pm = *Pterostichus melanarius*, Pn = *Pterostichus niger*

5.3.2 Slug predation

Five containers were excluded from the evaluation because dead beetles were found: in the two-species treatments of *A. parallelepipedus* and *P. melanarius* three beetles of *A. parallelepipedus* and one *P. melanarius* were recovered dead. One dead *P. melanarius* was found in the single species treatment and one in the two species treatment of *P. melanarius* and *P. niger*.

Slugs were significantly reduced by the ground beetles ($F_{6,30} = 5.99$, $p < 0.001$). Three treatments showed significant differences compared to the control where *A. parallepipedus* consumed the most slugs (51%; Tukey test: $p < 0.001$) followed by the combination of *A. parallelepipedus* and *P. niger* (Ap/Pn; 43%; Tukey test: $p < 0.001$) and the treatment with only *P. niger* (Pn; 38%; $p = 0.007$) (Fig. 14). In contrast, *P. melanarius* consumed only 26% of the slugs and all treatments containing *P. melanarius* did not significantly differ from the control without predators.

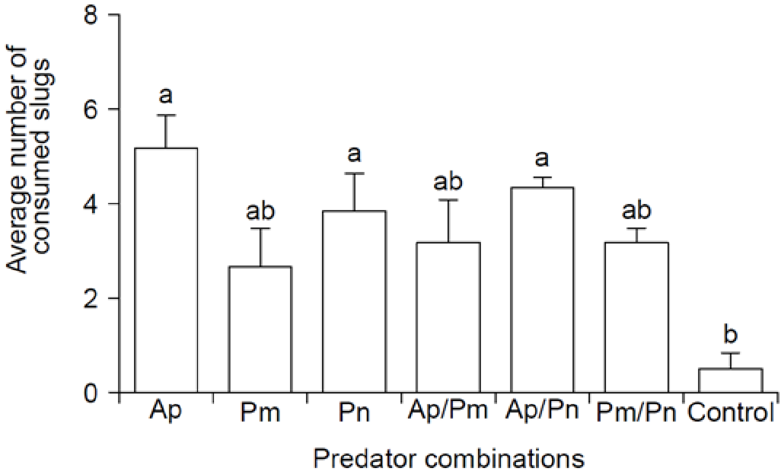

Figure 14 The proportion of consumed slugs (means +SE) in the treatments. Bars sharing the same letter are not significantly different for pairwise comparison with the control (Tukey's test, p > 0.05). Ap = *Abax parallelepipedus*, Pm = *Pterostichus melanarius*, Pn = *Pterostichus niger*

5.3.3 Interactive predation effects

In the egg predation experiment the observed egg predation rate in the treatment with *A. parallelepipedus* and *P. niger* (Ap/Pn) was almost twice as high compared to the expected egg predation rate ($t_5 = 6.445$, $p < 0.001$) (Fig. 15a). The observed egg predation rate of the treatment with *P. melanarius* and *P. niger* (Pm/Pn) was also significantly higher compared to the expected predation rate ($t_5 = -28.065$, $p < 0.001$). No significant difference was found by comparing the expected and observed egg predation rates in the treatment with *A. parallelepipedus* and *P. melanarius* (Ap/Pm). In contrast, in the slug predation experiment, all comparisons of the expected combined predation effects and the observed combined predation rates revealed no significant differences (Fig. 15b).

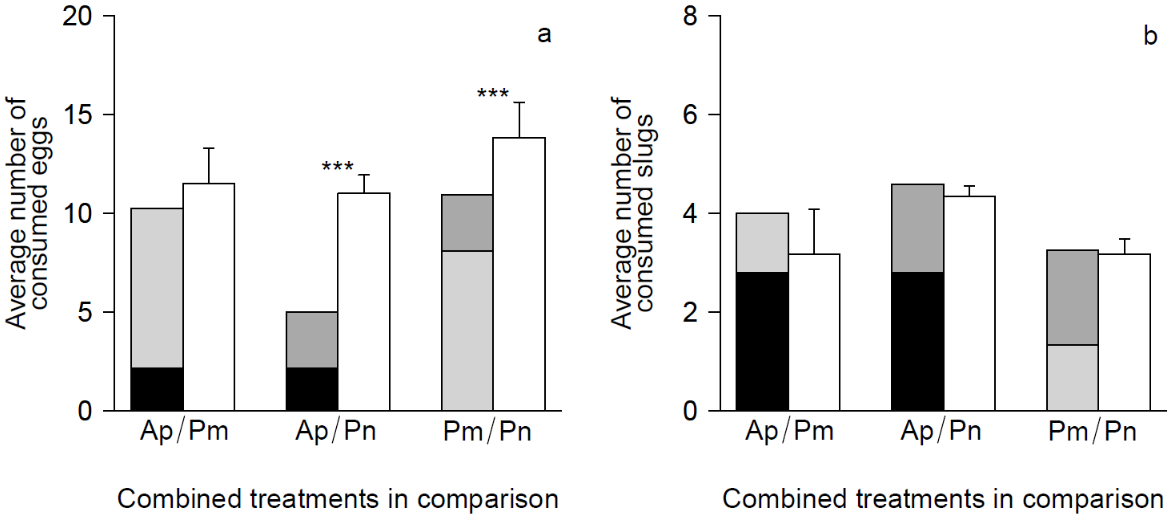

Figure 15 The observed consumption of slug eggs (a) and slugs (b) of the combined ground beetle treatments (white bars: means +SE) compared to the expected consumption. Expected values were created by halving the results of corresponding single species treatments' average feeding rate and adding them up according to the respective combination. The two different shades of the expected value bars show the proportion of the single species treatment (Black = A. parallelepipedus (Ap), dark grey = P. niger (Pn), light grey = P. melanarius (Pm)). Asterisks show significant differences between expected and observed results obtained by one sample t-tests.

5.4 Discussion

The three investigated ground beetle species differed strongly in their predation of slug eggs. Interestingly, effectiveness of species occurred in reversed order compared to the predation of immature slugs. *P. melanarius* was by far the most effective egg predator (compared to *A. parallelepipedus* and *P. niger*), but least effective against immature slugs. Eggs of *D. reticulatum* are a suitable prey for *P. melanarius* and are often preferred to alternative prey (aphids, crickets, dipteran larvae) (Oberholzer and Frank 2003). Surprisingly, *P. melanarius* was a much more effective egg predator than *P. niger* and consumed about three times more eggs. This contrasts findings of a field study by Hatteland et al. (2010) where *P. niger* showed similar predation rates on eggs as *P. melanarius*. However, eggs in this field study were exposed multiple times longer to the predators than in our 24 h experiment. A longer exposure of the eggs to the predators could probably result in higher egg consumption for *P. niger* and *A. parallelepipedus*, due to their larger body mass and their capacity to consume their own body mass in prey each day (Lövei and Sunderland 1996).

Regarding the immature slug predation experiment the three ground beetle species differed in their predation rates on *D. reticulatum*. Thereby, *A. parallelepipedus* and *P. niger* (and also their combination) influenced *D. reticulatum*'s survival substantially (> 40% predation rate) and predation rates were much higher than in treatments with *P. melanarius*. The more effective slug control of *A. parallelepipedus* and *P. niger* might be caused by their larger body size (Jones 1979; Rouabah et al. 2014) and stronger mandibles which helps to overcome the mucus of the slugs (McKemey et al. 2001; Pakarinen 1994). However, Hatteland et al. (2010) summarised that *P. melanarius* is an effective slug predator both in field situations and in laboratory experiments. Importantly, all used slugs in our experiment were heavier than 100 mg and we observed a preference of *P. melanarius* for smaller slugs. Also Paill (2004) found *P. melanarius* to prey effectively only on small slugs with a body mass up to about 100 mg. Hence, predation rates revealed from our experiment may underestimate the true slug control potential of *P. melanarius* in the field (McKemey et al. 2001), where it mainly occurs between July and September, a period with a high proportion of juvenile and small slugs.

The combined species treatments analysed in the immature slug predation experiments showed additive predation effects, i.e. the observed slug predation rates of the mixed treatments did not differ from the expected predation rates based on the predation rates obtained from the single species treatments. Hence, it seems that two co-occurring ground beetles neither interfere (e.g. intra-guild predation) nor facilitate each other (Sih et al. 1998).

However, in four containers with two co-occurring species we found dead ground beetles. All of these containers contained *P. melanarius* and recorded deaths might have been caused by intraguild predation. Possibly, prey density for *P. melanarius* was limited (as slugs were mainly able to survive the predators' attacks because of their size; see above) which may lead to either a higher intraguild interferences (Lucas et al. 1998) or starvation. In the field such starving circumstances are probably less common, because of their polyphagous habits and ability to consume a wide range of prey (Ayre 1995; Rouabah et al. 2014). This was found in a previous study by Rouabah et al. (2014) where *P. melanarius* and *A. parallelepipedus* did not kill each other in the same treatment when enough alternative food was available. Moreover, in the egg predation experiment with lots of accessible slug eggs no dead ground beetle was found.

Interestingly, we found synergistic egg predation of *P. niger* in combination with either of the other ground beetle species. We can only speculate about the mechanism of this synergistic predation. It may have resulted from different search strategies, which could lead to higher egg discovery of species combinations compared to multiple conspecifics that apply the same strategy. No emergent impact of multiple predators was observed on slug immatures. This indicates that differences between ground beetle species are less relevant for predation of slug immatures. Possibly, the exposure of slug immatures to ground beetles is generally higher than for eggs. Thus, differences in hunting strategies may be less relevant. Given the predator defence abilities of immature slugs (e.g. excretion of mucus), prey handling is likely more limiting to consumption rates than prey discovery when compared to the egg stage.

Our results suggest that the diversity of generalist predator species can improve biological pest control. The investigated ground beetle species showed contrasting effectiveness regarding the control of slugs and their eggs, thus complementing each other in the presence of multiple pest stages. Moreover, we found additive effects of species combinations on slug predation and even synergistic effects on egg predation. Such effects of ground beetle combinations deserve further investigation, to fully assess the potentially beneficial effect of combined species on slug predation.

However, the presented results are based on laboratory and mesocosm experiments. In the field additional biotic and abiotic factors influence natural enemies in natural situations (Barbosa 1998). Recently, Rusch et al (2016) found that landscape simplification has a negative effect on biological pest control and that especially generalist predators respond positively to landscape complexity (Chaplin-Kramer et al. 2011). In addition, organic farming with low chemical input is recommended to favour ground beetles and reduce slug damage (Douglas and Tooker 2012; Kromp 1999). Furthermore, enhancing crop diversity (Douglas and Tooker 2012), establishing beetle banks and annual flower strips with connected field boundaries could strengthen the natural enemy communities (Landis et al. 2000; Tschumi et al. 2015). These methods of enhancing conservation biological control could allow a reduction of chemical control of slugs.

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Chapter 6 General discussion and outlook

6.1. Effects of woody semi-natural habitats

Semi-natural habitats can support carabids in agricultural landscapes as results show. Carabid abundance and species richness were high near woody semi-natural habitats, which underlines the importance of hedges and woodlands as shelter habitats and overwintering sites due to a denser vegetation and buffer against unsuitable climatic conditions (Sotherton, 1985). In general, a variety of natural enemies can benefit from woody habitats, because they are less disturbed than herbaceous margins, offer beneficial climate conditions and they provide alternative prey as well as floral resources e. g. for parasitoids (Bianchi et al., 2006; Holland et al., 2016; Orford et al., 2016). However, woody semi-natural habitats can also inhibit dispersal of carabids and can support pests like aphids (Holland et al., 2016) or, as our investigations show, slugs of the genus *Arion*. Highest densities of *Arion* spp. were measured within and near to woody semi-natural habitats, which could lead to serious pest pressure in fields adjacent to woody margins.

This problem of a higher pest pressure by *Arion* spp. in fields near woody margins might only occur in simple landscapes due to an increase of predatory carabid richness and a tendency in the increase of abundances of predacious carabids in heterogeneous landscapes. In landscapes with a higher amount of semi-natural habitat, this increase could lead to an enhanced control of *Arion* spp. within woody margins and in fields adjacent to this semi-natural habitat type.

6.2. Effects of herbaceous semi-natural habitats

Herbaceous semi-natural habitats can also harbour carabids, as we found higher carabid abundances and species richness within herbaceous margins than in woody habitats. This type of semi-natural habitat is the most common in agricultural areas and especially grassy strips are often the only semi-natural habitat type in simple landscapes (Holland et al., 2016). Herbaceous semi-natural habitats can also be utilised as shelter or overwintering sites as long as they provide specific climatic conditions due to a high plant species richness and a dense vegetation, especially by tussock grasses (Collins et al., 2002; Holland et al., 2016; Pfiffner &

Luka, 2000). Previous studies found higher carabid numbers and higher densities of further natural enemies in grassy and herbaceous margins than in fields (Holland et al., 2016). Especially wildflower strips can enhance natural enemy diversity and densities more than simple grass strips, i. a. by providing floral resources (Holland et al., 2016).

Effects of herbaceous semi-natural habitats on natural enemies in adjacent crop fields are quite contradictory (Holland et al., 2016). We found less carabid numbers near herbaceous habitats than within the interior field underlining the possibility that herbaceous semi-natural habitats can act as sink habitats (Thomas et al., 2001).

Herbaceous semi-natural habitats can also harbour different pests (Bianchi et al., 2006), especially aphids (Holland et al., 2016). We found high densities of *Deroceras reticulatum* within this habitat type, but we could not find any evidence for the control of this slug species by carabids.

6.3. Effects of semi-natural habitats on a landscape scale

Generalists like many carabid species are considered to be more or less mobile and are therefore affected by the landscape (Tscharntke et al., 2005). The results show that predatory carabid richness in wheat fields can be negatively affected by the simplification of landscapes and this can probably lead to a reduced control of *Arionid* slugs in fields and within adjacent semi-natural habitats (see also chapter 6.1.). There is also a tendency that predatory carabids within field margins react to their surrounding landscape. However, we found no effects of landscape on the distribution of carabids in pumpkin fields. There are many carabid species, which hibernate in the field and are more independent of semi-natural habitats as overwintering habitats (Holland et al., 2009; Kromp, 1999). But our results show that the direct availability of shelter habitats is more important for the distribution of carabids within fields than the amount of semi-natural habitats in the landscape. There is a variety of different factors that affect carabids in agriculture like sowing time as well as crop type (Purvis et al., 2001) or management (Cole et al., 2005) and the overall impact of these factors is yet poorly understood (Holland & Luff, 2000). Different carabid species respond in different ways to their environment leading to various distribution patterns (Winqvist et al., 2011). Our results on interactive effects of landscape and management regime might also be explained by species-specific responses. Also carabids within semi-natural habitats were not affected by the landscape. A reason might be that semi-natural habitats are stable habitats in comparison to fields and some carabid species, which are less mobile, are therefor bound to non-crop habitats (Saska 2007).

6.4. Conclusion

Semi-natural habitats are important for carabid beetles in agricultural landscapes, but utilisation of non-crop habitats by carabids is species- or group-specific. Predatory carabids are generally more influenced by the proportion of semi-natural habitats in the landscape, whereas some carabid species are influenced by semi-natural habitats at a local scale. Furthermore, different semi-natural habitat types can affect carabids differently. This fact must be taken into consideration for the development of agri-environmental schemes and both local and landscape parameters must be taken into account to support carabids as natural enemies.

Differences in the responses of the common pest slugs *D. reticulatum* and *Arion* spp. to local and landscape factors will lead to challenges in controlling slugs by carabids. However, our results show that pest pressure is greater in simple landscapes, especially by *Arionid* slugs when woody habitats are the only non-crop habitats.

A provision of a higher amount of different types of semi-natural habitats in simple landscapes, the conservation of the diversity of semi-natural habitats in heterogeneous landscapes as well as the promotion of the connectivity of non-crop habitats should be aim to support slug control by carabids as well as natural pest control in general.

6.5. Future research

Further investigations should focus more on interactive effects of landscape and local parameters on carabids, because carabids are influenced by a variety of factors (Winqvist et al., 2011). For natural pest control, it is important to know what factors mainly control their distribution (Holland & Luff, 2000). However, many carabids overwinter in fields and other species are only found within non-crop margins (Holland et al., 2009; Saska 2007) making it difficult to draw general conclusions about the influence of semi-natural habitats. Therefore, future studies should also include impacts on species level (e.g. field margin species vs. open field species) and they should also address the questions:

- What is the optimal ratio of woody and herbaceous semi-natural habitats in the landscape to support carabids?
- How can negative effects of semi-natural habitats like impingement (e.g. for field carabids) or sink effects (e.g. for margin species) be minimized?
- How can alternative prey and/or other natural enemies (e.g. rove beetles) affect the potential of carabids for natural slug control?

The last point is from great interest, because interactions between natural enemies can lead either to an enhanced pest control as our results from the laboratory partly show or to an interruption, for example by the preference of carabids for slugs infected by nematodes (Foltan & Puza, 2009; Hatteland et al. 2013). Such interactions must be identified between single species or, to analyse overall effects of natural pest control, between the whole enemy community. Further studies should also focus on the influence of pest control on yield (Rusch et al, 2016) and on local and landscape effects on different pests (Chaplin-Kramer et al., 2011). Here it is important to determine factors, which affect the distribution of different pests, especially when single pest species seem to be hardly controlled by natural enemies (e.g. *Deroceras reticulatum* by carabids).

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