ORIGINAL PAPER

Species' traits influence ground beetle responses to farm and landscape level agricultural intensification in Europe

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Abstract Agricultural intensification may result in important shifts in insect community composition and function, but this remains poorly explored. Studying how groups of species with shared traits respond to local and landscape scale land-use management can reveal mechanisms behind such observed impacts. We tested if ground beetles (Coleoptera: *Carabidae*) divided into trait groups based on body sizes, wing morphologies and dietary preferences respond differently to farming practise (organic and conventional), farming intensity (measured as yield) and landscape complexity (measured as the proportion of arable land within a 1,000 m radius) across Europe. We used data from 143 farms in five regions in northern and central Europe. Organic farms did not differ in abundance or richness of any trait group compared to conventional farms. As farm scale intensity (yield) increased, overall abundance of beetles decreased, but abundances of small and medium sized beetles, as well as that of wingless beetles, were unaffected. Overall species richness was not affected by yield, whereas consideration of traits revealed that phytophagous and omnivorous beetles were less species rich on farms with high yields. Increasing the proportion of arable land in the landscape increased overall beetle abundance. This was driven by an increase in omnivorous beetles. The total species richness was not affected by an increase in the proportion arable land, although the richness of wingless beetles was found to increase. Potential effects on ecosystem functioning need to be taken into account when designing schemes to maintain agricultural biodiversity, because species with different ecological traits respond differently to local management and landscape changes.

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Introduction

Intensified use of the agricultural landscape, both at the local farm scale and on the regional landscape scale, has had substantial and well-documented negative effects on species richness, abundances and distributions of a variety of farmland animals and plants (Tscharntke et al. 2005a; Geiger et al. 2010), but the mechanisms behind these responses are less studied. Moreover, shifts in community composition, brought about by agricultural intensification, appears to have escaped attention because most studies have only measured effects on overall abundance and species richness (Aavik and Liira 2010).

Studying how species with different traits respond to local management and landscape complexity may increase our understanding of the mechanisms behind changes in community composition (Dormann et al. 2007; Bommarco et al. 2010; Öckinger et al. 2010; Jonason et al. 2012). In particular, since species pools differ between geographical regions, large-scale comparisons of trait composition can reveal general ecological responses irrespective of regional differences in species composition. Effects of agricultural intensification or farming practises on trait composition have been studied for functionally and economically important taxa, and these effects can be modified by the surrounding landscape (Burel et al. 2004; Purtauf et al. 2005a; Rundlöf et al. 2008; Tscharntke et al. 2012; Woodcock et al. 2014). However, studies of changes in trait composition which include both agricultural intensification and landscape changes across regions or countries remain rare (but see Schweiger et al. 2005; Clough et al. 2007; Liira et al. 2008).

Ground beetles are useful for investigating these questions, since they have previously been found to be sensitive

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to changes in habitat structure and land use (Vanbergen et al. 2005; Hendrickx et al. 2009), and they respond in comparable ways to similar environmental factors across regions (Schweiger et al. 2005). Some ground beetle species are important natural enemies of arable pests and many are a key food resource for birds (Holland et al. 2009). As a result, ecosystem services and functions such as biological control and food chain maintenance can be affected if ground beetle community composition changes (Flynn et al. 2009; Holland et al. 2009; de Bello et al. 2010).

In a recent pan-European study, we showed that landscape simplification, measured as a higher proportion of arable land at the landscape scale, increased the local abundance of ground beetles, whereas their species richness was unaffected by landscape simplification (Winqvist et al. 2011). Both total species richness and abundance were unaffected by farming practice (organic or conventional). It is, however, possible that the trait community composition has changed as a response to organic farming or landscape complexity without any change in total species richness or abundance. Traits linked to diet, dispersal and body size have been suggested as important determinants for community composition in general (Solbreck 1978; Ewers and Didham 2006) and in arable systems in particular (Ribera et al. 2001; Schweiger et al. 2005; Tscharntke et al. 2005a; Hendrickx et al. 2009).

In this study we used data from 143 farms in five regions across Europe to examine how ground beetles with different diets, wing morphology and body sizes were affected by local management (organic or conventional farming), farming intensity (measured as cereal yield) and regional landscape complexity (measured as the proportion of arable land). We predicted that both the local scale intensity and the regional scale landscape complexity influence the species richness and abundance of ground beetles with the studied traits, due to changes in resource and habitat availability.

Species at higher trophic levels are expected to have larger home ranges and are therefore expected to be more dependent on landscape composition than the quality of the local habitat (Purtauf et al. 2005b). They are also more vulnerable to local disturbances (Kruess and Tscharntke 1994; Purvis et al. 2000), and have been shown to decline more with increasing landscape simplification than phytophagous species (Purtauf et al. 2005b; Ewers and Didham 2006). High mobility allows individuals to track resources and avoid unfavourable conditions both at the local and landscape scale (den Boer 1990). Hence, having a high mobility may be especially favourable in disturbed and changing agricultural landscapes (Hendrickx et al. 2009; Jennings and Pocock 2009). Large bodied species usually have sparser populations, longer life cycles, longer development time and relatively low reproductive rates.

Therefore, their populations are expected to respond more slowly to environmental changes, and large species are expected to be less tolerant to disturbance on the local scale (Blake et al. 1994; Ribera et al. 2001; Burel et al. 2004; Aviron et al. 2005).

Materials and methods

Study region and study sites

The field study was carried out from May to July 2007 in cereal fields on 143 farms in five regions in Europe: Uppland, Sweden (59°51′0″N, 17°37′60″E), Tartu, Estonia (58°21′0″N, 26°34′0″E), Flevoland, the Netherlands (52°32′0″N, 5°43′0″E), Jena (51°6′29″N, 10°38′48″E) in the eastern part and Göttingen (51°32′2″N, 9°56′8″E) in the western part of Germany. Initially we selected 30 farms in each region and on each farm we selected five sampling points from as many cereal fields as possible. Due to sampling failure only 143 farms could be used in the study. Fields on different farms were located at least 1 km apart, and fields within one farm were always closer than 1 km to each other. To reduce spatial auto-correlations and avoid differences in species pools within regions, each study region ranged in size between 30 × 30 km and 50 × 50 km.

Fifty-two of the farms were organically managed with no pesticides or inorganic fertilisers, and 91 farms were conventionally managed. Winter wheat was grown at 80.7 % of the sampling points, spring wheat at 9.8 % and winter rye at 8.8 %, while triticale and winter barley covered <1 %. In Flevoland in the Netherlands most sampled organic fields had spring wheat, whereas conventional fields had winter wheat. Winter wheat yield in the previous year(s) (at 14 % moisture content) was used as a proxy to select farms with different management intensities.

Information about farming practise, yields and management actions such as tillage, fertilizer use and pesticide applications was collected by means of a standardized questionnaire answered by all of the participating farmers (see Geiger et al. 2010; Winqvist et al. 2011), except four from the Göttingen area in Germany.

Landscape measures were calculated in buffer zones with a 1,000 m radius around each sampling point using digital maps or paper maps and definitions from the European Topic Centre for Land Use and Spatial Information (Büttner et al. 2002). We used the Geographical Information System ESRI® ArcMapTM 9.1 (ESRI Inc., Redlands, CA, USA) for the landscape analyses. We used landscape measures estimated at a 1,000 m radius since there was high correlation between 500 m and 1,000 m

radius (r = 0.86; $P < 0.0001$; N = 744), and the 1,000 m radius has been shown to be ecologically important for a number of organisms and biological control agents (Thies et al. 2005; Winqvist et al. 2011). The proportion of arable land within 1,000 m from the sampling point was positively correlated with mean field size (Pearson correlation coefficient r = 0.58, $P < 0.0001$, N = 147) and negatively correlated with land cover diversity (r = −0.84, $P < 0.0001$, N = 147). Therefore, we only used the proportion of arable land as a measure of landscape complexity in the statistical models. We selected farms along both a yield and a landscape complexity gradient in each study region. The proportion of arable land showed weak relationships with yield (r = 0.21, $P = 0.0120$, N = 147), and did not differ between farm types (r = -0.076, $P = 0.36$, N = 147), enabling us to use landscape complexity and local intensity in the same model. Yield and farm type were strongly related to each other (r = −0.71, $P < 0.0001$, N = 147), and were therefore not analysed in the same model. Yield was also strongly related to total pesticide use (r = 0.65, $P < 0.0001$, N = 744).

One conventional farm in the Netherlands was omitted from the landscape analyses because it had a very low proportion of arable land in the surrounding landscape, thereby influencing the results disproportionately. One farm in Sweden was omitted when testing for effects of organic farming due to the fact that some fields were managed organically and some fields conventionally on the same farm. Four farms in Göttingen were excluded from yield analyses due to missing management data.

Ground beetle sampling

At each farm, ground dwelling arthropods were sampled twice in five sampling points. The sampling points were situated at the middle of the longest side of the sampled field, 10 meters into the field from the margin. All field margins were dominated by grassy vegetation to standardize the sampling (Dennis and Fry 1992). When farms had fewer than five cereal fields, more than one sampling point was located in the same field. In such cases, sampling points were placed at opposite sides of the field and with a minimum distance of 50 m between them.

The timing of sampling of ground beetles was synchronized across countries using the phenological growth stages (BBCH) of winter wheat (Federal Biological Research Centre for Agriculture and Forestry 2001) as a time reference. Traps were open for 7 days on each of two sampling occasions (Niemelä et al. 1990). The first sampling period started 1 week after the appearance of spikes of winter wheat (BBCH 55) and the second sampling period started at the milk ripening stage of winter wheat (BBCH 75).

The ground beetles were caught with two pitfall traps (90 mm diameter, 150 ml of 50 % ethylene glycol) per sampling point. Roofs made of cardboard were fixed to the ground with needles to prevent flooding of traps by rain. The vegetation and soil surrounding the pitfalls were left unaffected. One randomly selected pitfall trap per sampling point was analysed; the other trap was kept as a backup. The use of pitfall traps has been widely debated for many years (in Baars 1979). Still, pitfall trapping is the most widely used method for catching ground dwelling arthropods in arable landscapes (Lang 2000) and we have no reason to believe that the efficiency of pitfall traps in catching species with certain traits differed between farm types or along the landscape complexity or farming intensity, and thereby biased our analyses.

Invertebrates caught were preserved in 70 % ethanol. All ground beetles were identified to species. In total 63,345 beetles belonging to 150 species were caught. Sixteen farms had one or two samples missing, but we assumed that the estimate of number of species per farm would not be affected. We calculated abundance as average number of individuals per pitfall trap per farm to overcome the problem of missing samples.

Trait information

Information about species' traits was collected from the literature and through collaboration with researchers holding unpublished databases (see Acknowledgements). A complete list of species with traits is given in Table S1 in Supporting Information. Ground beetle body lengths were separated into three groups: small (<6 mm), medium (6–10 mm), and large (>10 mm). The cut-off points between body size groups used were set to obtain a similar number of species in each group (Barbaro and van Halder 2009). Analyses were also conducted using body size as a continuous variable, and the results did not change (data not shown). Dispersal mode was separated into macropterous species with wings and wing muscles, brachypterous species without wings or wing muscles, and wing dimorphic species having individuals of both types (Barbaro and van Halder 2009). Diet was separated into three groups: carnivorous, phytophagous and omnivorous (Purtauf et al. 2005b; Schweiger et al. 2005). We acknowledge that these separations are simplifications, but that they still serve the purpose of studying possible shifts in community composition. We found no correlation between diet and wing morphology (r = 0.03, P = 0.74, N = 122) or body size (r = 0.11, P = 0.22, N = 125). Wing morphology and body size were only weakly correlated (r = −0.35, P < 0.0001, N = 126).

The number of species and individuals in the different trait groups is shown in Table S2. The large, omnivorous and wing dimorphic *Pterostichus melanarius* Illiger was the most common species (ca 60 % of the catches). Other abundant species were *Poecilus cupreus* Linnaeus (7.4 %), *Pterostichus niger* Schaller (6.7 %), *Anchomenus dorsalis* Pontoppidan (5.4 %) and *Harpalus rufipes* DeGeer (4.9 %).

Statistical analyses

We tested for effects of local intensity and landscape complexity by analysis of covariance (ANCOVA) using SAS PROC MIXED based on normal error distributions in SAS 9.1 for Windows (Littell et al. 2006, SAS Institute Inc., Cary, NC, USA). *Post hoc* tests using SAS PROC MIXED were conducted to assess differences in responses between trait categories. As dependent variables we used the species richness or mean abundance of a group of species sharing a certain trait. Ground beetle trait mean abundance, species richness and yield were log transformed [log10 (x + 1)] to achieve normal distribution of variables. Analyses were conducted with data pooled at the farm level. Effects of yield levels and farming practise were analysed in separate models.

We used landscape complexity, farming practise (organic or conventional farming), trait, and all two- and three-way interactions as fixed factors. As random factors we included region, farm nested within region, region*trait, region*farming practise*trait, and region*landscape complexity*farming practise*trait. We allowed the regression slopes to vary between regions by including slope (region*farming practise*landscape, and complexity*trait) in the random structure. We selected this random structure because we were mainly interested in the overall effect of farming practise and landscape complexity on traits across regions. Specific regional differences in the responses to organic farming and landscape complexity were not considered in this study.

Model simplification was done in a stepwise backward model selection procedure by removing non-significant interactions. The random part of the model was not reduced in any analysis.

When analysing the effect of yield and landscape complexity, we used the same model set up, with the difference that yield was analysed as a continuous variable, and the random structure included region*landscape complexity and landscape complexity*trait.

All statistical analyses were performed with landscape complexity as a continuous variable, but estimates of species richness and abundance for different trait groups are presented at 40 % arable land (complex landscapes) in comparison to 90 % arable land (simple landscapes). Yield was also analysed as a continuous variable, but in post hoc comparisons we present the estimated species richness and abundance at 3,000 kg/ha (low yield) and 7,000 kg/ha (high yield).

Figures were created by plotting the model estimates plus the residual values from the full model including the random terms per sampling point along the landscape gradient, as follows:

y = x + Variable + z + residual;

where x is the model estimate for farming practice (the intercept), Variable is the proportion arable land or yield, z is the model estimate for landscape complexity or yield (the slope) and residual is the model residual.

Results

Effects of farming practice

The overall species richness and abundance of ground beetles did not differ between organic and conventional farms, which was shown in a previous study (Winqvist et al. 2011).

We did not find an effect of farming practice on species richness or abundance of any of the studied trait groups (data not shown). This means that all trait groups responded in a similar way to organic farming as did the overall species richness or abundance.

Effects of yield

Overall, carabid species richness was not significantly related to yield ($F_{1,4} = 3.62$, $P = 0.13$), whereas carabid abundances decreased with increasing yield ($F_{1,4} = 25.91$, $P = 0.0070$).

The species richness of ground beetles in the three diet groups showed different responses to increasing yield (Table 1). The number of phytophagous and omnivorous species declined with increasing yield ($F_{1,139} = 10.68$, $P = 0.0014$ and $F_{1,121} = 4.51$, $P = 0.036$, respectively), whereas carnivorous species richness was unaffected ($F_{1,139} = 0.08$, $P = 0.77$) (Table 2, Fig. 1a). The species richness of phytophages decreased from 1.8 species on low yield farms (3,000 kg/ha) to 1.1 species on high yield farms (7,000 kg/ha). Species richness of omnivores declined from 5.4 species at low yields to 4.8 species at high yields (SE = 0.16, d.f. = 8 for all measures).

Abundances in each of the feeding mode groups decreased with increasing yield (Table 2, Fig. 1b). Phytophages declined with around 50 % from on average 0.5 individuals per trap to 0.26 ($F_{1,139} = 12.18$, $P = 0.0006$) when yields increased from 3,000 to 7,000 kg/ha. Similarly, the abundance of omnivores declined by nearly 50 % from 24.4 individuals to 12.7 individuals ($F_{1,138} = 19.83$, $P < 0.0001$) in response to the increase in yield. Carnivores decreased by ca 35 %, from 6.7 individuals to 4.4

individuals (SE = 0.29, d.f. = 8 for all measures) ($F_{1,138} = 8.08$, $P = 0.0052$). The significant yield*diet interaction (Table 1) indicates that even though all feeding groups decreased in abundance with increased yield, they differed slightly in their responses.

The abundance of ground beetles in different dispersal groups showed different responses to increasing yield (Tables 1 and 2, Fig. 1c). Winged and dimorphic beetles decreased in abundance when yields increased from 3,000 to 7,000 kg/ha ($F_{1,139} = 32.55$, $P < 0.0001$ and $F_{1,138} = 11.81$, $P = 0.0008$), from 16.5 to 7.9 and from 13.5 individuals per trap to 7.9 (SE = 0.30, d.f. = 8 for all measures), respectively, whereas the abundance of wingless beetles was unaffected by yield ($F_{1,138} = 0.13$, $P = 0.72$). Yield did not affect the species richness in groups with different dispersal modes (data not shown).

Yield also affected the abundance of ground beetles in the different body size categories differently (Tables 1 and

Table 1 Statistical analyses of the relationships between farming practice (organic or conventional) or yield, landscape complexity (percentage of arable land in a 1,000 m radius buffer zone) on the species richness and abundance of ground beetles having different traits (diet, dispersal mode or size)

Diet		
Species richness		
Yield	$P = 0.0227$	$F_{1,8} = 7.92$
Diet	$P = 0.1116$	$F_{2,8} = 2.92$
Yield*diet	$P = 0.0124$	$F_{2,8} = 7.99$
Abundance		
Yield	$P = 0.0010$	$F_{1,8} = 25.33$
Landscape	$P = 0.0192$	$F_{1,8} = 8.55$
Diet	$P = 0.0108$	$F_{2,8} = 8.40$
Yield*diet	$P = 0.0457$	$F_{2,8} = 4.65$
Landscape*diet	$P = 0.0428$	$F_{2,8} = 4.80$
Dispersal mode		
Species richness		
Landscape	$P = 0.4411$	$F_{1,18} = 0.62$
Dispersal	$P = 0.0002$	$F_{2,8} = 32.08$
Landscape*disp	$P = 0.0016$	$F_{2,18} = 9.40$
Abundance		
Yield	$P = 0.0028$	$F_{1,8} = 18.01$
Dispersal mode	$P = 0.0017$	$F_{2,8} = 15.81$
Yield*disp	$P = 0.0091$	$F_{2,8} = 8.95$
Size		
Abundance		
Yield	$P = 0.0245$	$F_{1,8} = 7.64$
Size	$P = 0.0012$	$F_{2,8} = 17.45$
Yield*size	$P = 0.0046$	$F_{2,8} = 11.37$

Only models with significant trait-interactions are shown. d.f. = the approximate denominator degree of freedom from the mixed model analysis

Table 2 Summary of the results per trait group for farming practise, landscape complexity and yield

Traits	Farming practise		Increased yield		Landscape simplification	
	Abundance	Species richness	Abundance	Species richness	Abundance	Species richness
Diet						
Phytophagous	NS	NS	–	–	NS	NS
Carnivorous	NS	NS	–	NS	NS	NS
Omnivorous	NS	NS	–	–	+	NS
Dispersal						
Wingless	NS	NS	NS	NS	NS	+
Winged	NS	NS	–	NS	NS	NS
Dimorphic	NS	NS	–	NS	NS	NS
Size						
<6 mm	NS	NS	NS	NS	NS	NS
6–10 mm	NS	NS	NS	NS	NS	NS
>10 mm	NS	NS	–	NS	NS	NS

NS non significant

+ or −: a significant ($P < 0.05$) increase or decrease in species richness or abundance for that group along the landscape complexity or yield gradient, or between farming practices. Boxes highlight differences in response between trait categories

2, Fig. 1d). Large beetle abundances declined as yields increased ($F_{1,138} = 25.75$, $P < 0.0001$), from 24.6 individuals per trap on low yield farms (3,000 kg/ha) to 12.2 individuals (SE = 0.35, d.f. = 8 for all measures) on high yield farms (7,000 kg/ha). The abundances of small and medium sized beetles on the other hand were not affected by changes in yield ($F_{1,137} = 0.04$, $P = 0.85$ and $F_{1,139} = 0.20$, $P = 0.65$, respectively). The species richness of the different size groups did not differ along the yield gradient (data not shown).

Effects of landscape complexity

The complexity of the surrounding landscape did not affect the overall species richness of ground beetles, but ground beetle abundances increased with an increase in the proportion of arable land (Winqvist et al. 2011).

The abundance of different feeding groups differed in their response to landscape simplification (Table 1). Omnivorous beetles increased in abundance with increasing proportion of arable land ($F_{1,121} = 7.04$, $P = 0.0090$) (Table 2, Fig. 2a), from 11.9 individuals per trap in complex landscapes to 22.2 individuals in simple landscapes (SE = 0.32, d.f. = 8). The abundances of phytophages ($F_{1,66.5} = 0.22$, $P = 0.64$) and carnivores ($F_{1,99.9} = 1.56$, $P = 0.21$) was not influenced by landscape complexity. Landscape complexity did not affect the species richness of beetles depending on their diets (data not shown).

Effects of landscape complexity on species richness depended on dispersal mode (Table 1, Fig. 2b). There were more wingless species in homogeneous landscapes, on average 1.3 wingless species per farm compared to 0.8 species (SE = 0.21, d.f. = 8) in complex landscapes ($F_{1,80.6} = 7.37$, $P = 0.0081$). Species richness of winged and of dimorphic species were not significantly affected the by degree of

landscape complexity ($F_{1,73.1} = 3.01$, $P = 0.087$ and $F_{1,138} < 0.01$, $P = 0.98$, respectively). The abundance of ground beetles in different dispersal groups was not affected by landscape complexity (data not shown).

Neither the abundance nor the species richness of ground beetles belonging to different size groups did differ along the landscape complexity gradient (data not shown).

Discussion

We show that there are general effects of agricultural intensification and landscape structure on ground beetle community trait composition, when comparing across regions differing in underlying species pool and climate. Our results support previous findings that species richness and overall abundance measures often are too crude to reveal actual differences between communities (Clough et al. 2007; Liira et al. 2008).

Many of our findings do not support, or even contradict, general fragmentation or disturbance theories (Ewers and Didham 2006). These theories may, however, not be valid if communities are supported via immigration (source-sink dynamics or mass effects; Pulliam 1988; Leibold et al. 2004) and in systems far from equilibrium (Holt et al. 1999), which might often be the case in agricultural landscapes. Results from this and similar studies may be useful when developing new theories, better suited to highly disturbed ecosystems with great variation in species richness and abundance between years.

As was expected, both farm scale land use intensity, measured as yield, and regional scale landscape complexity, measured as the proportion of arable land, influenced the species richness and abundance of ground beetle species with different traits. Surprisingly, farming practice did not affect any of the studied traits, although organic farming has
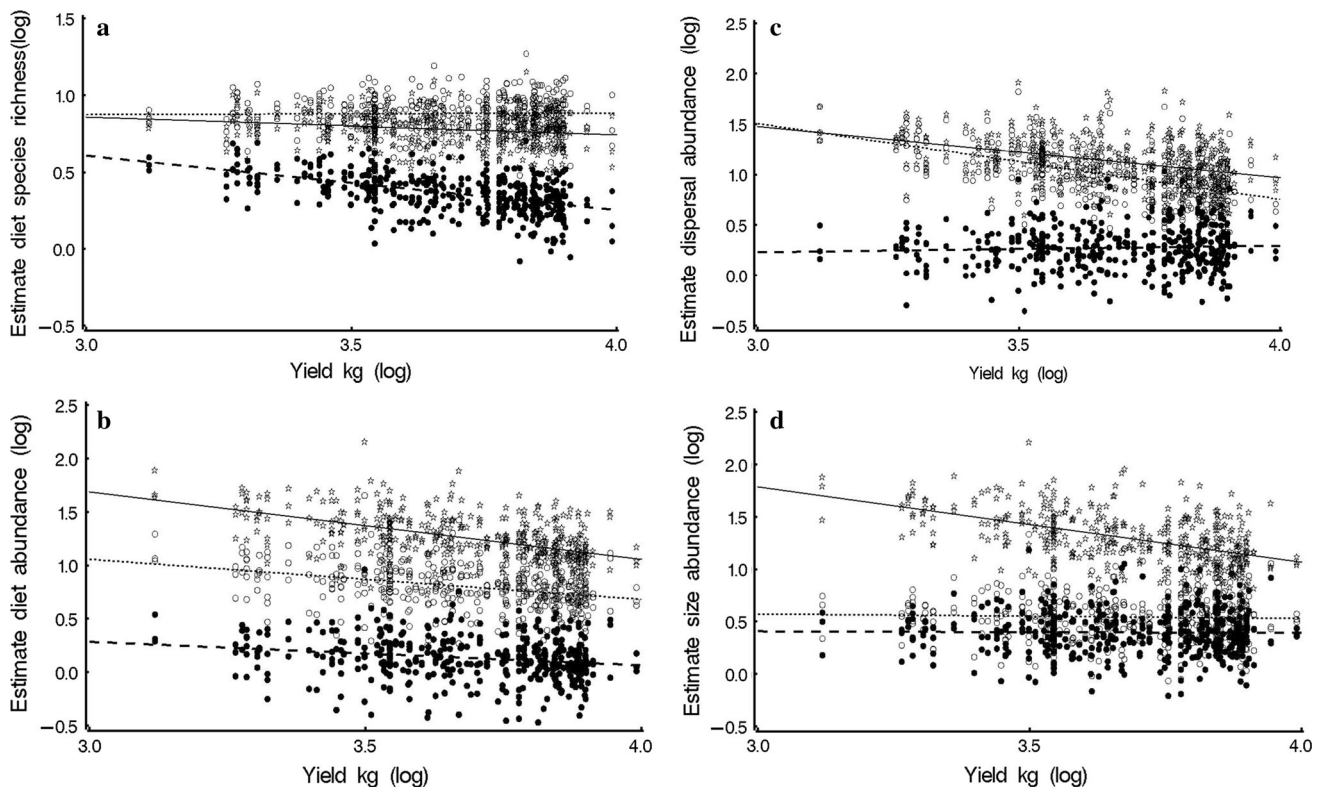
Fig. 1 a The relationship between species richness of ground beetles (Carabidae) in different diet groups (model estimates and residuals) and yield (from ca 1,000 to 7,000 kg/ha). *Black dots* and *broken line* = phytophagous beetles, *open dots* and *stippled line* = carnivorous beetles, stars and *solid line* = omnivorous beetles. **b** The relationship between abundance of ground beetles (Carabidae) in different diet groups (model es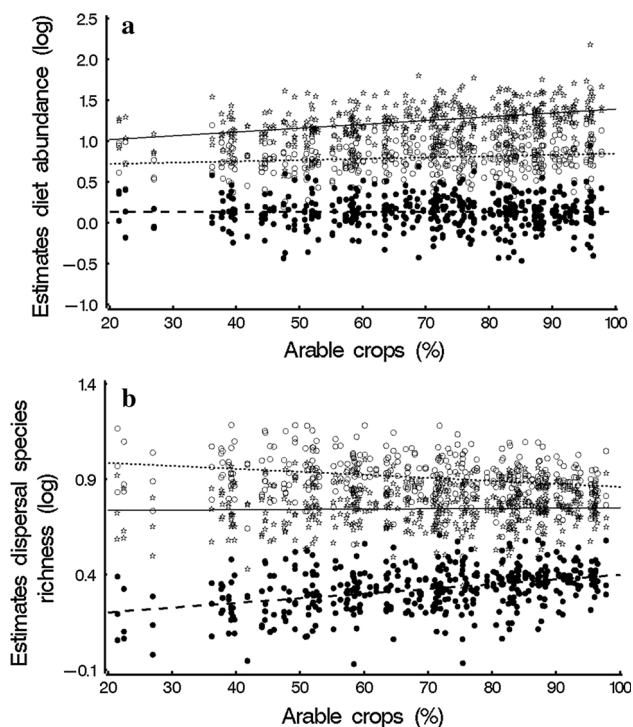timates and residuals) and yield (from ca 1,000 to 7,000 kg/ha). *Black dots* and *broken line* = phytophagous beetles, *open dots* and *stippled line* = carnivorous beetles, *stars* and *solid line* = omnivorous beetles. **c** The relationship between abundance of ground beetles (Carabidae) in different dispersal groups (model estimates and residuals) and yield (from ca 1,000 to 7,000 kg/

ha). *Black dots* and *broken line* = wingless beetles (brachypterous), *open dots* and *stippled line* = winged beetles (macropterous), *stars* and *solid line* = wing dimorphic beetles. The abundance of wingless beetles did not show a significant overall relationship given the random structure of the statistical model (i.e. accounting for region; see text). **d** The relationship between the abundance of ground beetles (Carabidae) in different size groups (model estimates and residuals) in relation and yield (from ca 1,000 to 7,000 kg/ha). *Black dots* and *broken line* = small beetles (<6 mm), *open dots* and *stippled line* = medium sized beetles (6–10 mm), *stars* and *solid line* = large beetles (>10 mm)

been shown to have positive effects on a number of taxa (e.g. Bengtsson et al. 2005; Hole et al. 2005). Therefore organic farming appears not to compensate for changes in trait composition caused by agricultural intensification. A recent study considering the traits composition in butterfly communities came to the same conclusion (Jonason et al. 2012).

High yields are often correlated with high input of inorganic fertilizers and pesticides, and have been shown to affect both biodiversity and ecosystem services negatively (Geiger et al. 2010). In our study, increased yields did not affect the total species richness of ground beetles, but it did affect the species' trait composition in the ground beetle community. Phytophages and omnivores decreased in species richness whereas carnivores remained unaffected, thereby resulting in carnivorous species becoming more dominant with local intensification. Higher yields are related to reduced weed cover (Geiger et al. 2010), which can be disadvantageous to phytophagous and omnivorous

insects (Kromp 1989). The fact that carnivore species were not negatively affected by increasing yields might contribute to enhanced biological control of agricultural pests.

Increased crop yield corresponded to an overall decline in the abundance of ground beetles, and this was largely attributed to a decline of larger species since small and medium sized beetles were not affected. This finding supports several previous studies where large species have been found to be less tolerant to local intensification such as pesticide use and soil management (Blake et al. 1994; Ribera et al. 2001; Kotze and O'Hara 2003; Barbaro and van Halder 2009). This is mainly due to larger beetles having a lower reproductive output and longer development time, and thereby being more sensitive to disturbances. Smaller beetles on the other hand have been shown to be unaffected (Aviron et al. 2005), or even positively influenced (Blake et al. 1994) by agricultural intensification.

Fig. 2 a The relationship between abundance of ground beetles (Carabidae) in different diet groups (model estimates and residuals) and landscape complexity (percentage of arable crops in a buffer zone with 1,000 m radius). *Black dots* and *broken line* = phytophagous beetles, *open dots* and *stippled line* = carnivorous beetles, *stars* and *solid line* = omnivorous beetles. b The relationship between species richness of ground beetles (Carabidae) in different dispersal groups (model estimates and residuals) and landscape complexity (percentage of arable crops in a buffer zone with 1,000 m radius). *Black dots* and *broken line* = wingless beetles (brachypterous), *open dots* and *stippled line* = winged beetles (macropterous), *stars* and *solid line* = wing dimorphic beetles

Changes in body size composition of the ground beetle community may affect interactions with other organisms and functioning in the agroecosystem. The body size of ground beetles can affect their value as food for birds (Blake et al. 1994), and interactions with other arthropod predators via intra-guild interactions and niche overlap (Woodward and Hildrew 2002). Ground beetle food preferences (Honek et al. 2007), feeding and other physiological rates (Peters 1983) can also be altered and consequently their performance as biological control agents could be affected (de Bello et al. 2010).

Enhanced dispersal ability allows a species to track resources and avoid unfavourable condition both at the local and landscape scale (den Boer 1990). At the local scale, Southwood (1977) suggested that species in highly disturbed sites have an elevated risk of local extinction, needing good dispersal capacities to persist in the landscape. Species with low mobility will, on the other hand, suffer most from local detrimental conditions (Tscharntke

et al. 2005a). On farmland, disturbances related to farming practice such as pesticide use or mechanical weed control are important for structuring communities (Stoate et al. 2001). Contrary to previous findings, we found that increased crop yield decreased the abundance of winged and dimorphic beetles, whereas the abundance of wingless beetles was unaffected, making them increasingly more dominant. The simple explanation for this may be that more mobile beetles disperse into more favourable sites, and the concentration of wingless beetle individuals is due to their inability to spread to less disturbed areas. Another explanation may be that wingless beetles spillover from adjacent non-crop habitats (Rand et al. 2006), exploring resources left behind by winged and wing-dimorphic species as they decline in abundance. If these beetles are reacting to the landscape at larger spatial scales, they may cope with small-scale disturbances in the field (Tscharntke et al. 2005a, b).

Habitat fragmentation is believed to affect species with different traits differently (Ewers and Didham 2006). In our study we found few examples of traits being affected by landscape simplification, which indicate that ground beetles are less affected by the landscape configuration than by local management. The overall increase in ground beetle abundance in homogeneous landscapes found in this study can be explained by the fact that arable fields constitute the main habitat for many of the ground beetle species in our study (Thiele 1977), and that they are positively affected by an increase in habitat area in the landscape.

The higher abundance of ground beetles in simplified landscapes with a high proportion of arable land was mainly driven by an increase in omnivores, whereas the abundance of carnivores and phytophages were unaffected by landscape complexity. Omnivores are expected to be less sensitive to landscape changes than both carnivores and phytophages (Holt et al. 1999), since they may utilize a greater number of resources. This is supported by studies showing that omnivores do (relatively) well in changed landscapes and in disturbed habitats (Purtauf et al. 2005b). Omnivores such as *Pterostichus melanarius* have previously been shown to be associated with cropped habitats (Aviron et al. 2005), and they may therefore benefit from an increase in habitat area. This change in community composition of phytophages, carnivores and omnivores along the landscape complexity gradient may affect the biological control potential of these natural enemies on arable pests (Hunter 2009).

We found more wingless beetle species in simple landscapes than in complex landscapes. This contradicts theory (Ewers and Didham 2006), but if arable fields are the main habitat for many ground beetles in the agricultural landscape (Thiele 1977), then they may perceive heterogeneous arable landscapes as being more fragmented than

homogeneous ones. Our findings partly support other findings where winged ground beetles in forests tended to be more fragmentation sensitive than their less mobile counter-parts (Barbaro and van Halder 2009). The fact that the species richness of winged and dimorphic species were unaffected by landscape simplification may also indicate that beetles with different dispersal mode exploit resources in the landscape at different spatial scales (Aviron et al. 2005).

Concluding remarks

Our study suggests that considering species' traits helps us understand the mechanisms behind responses to agricultural intensification at both the local and landscape scale. Furthermore, ecosystem functioning may also be affected when species with different ecological traits respond differently to local management and landscape changes. Agri-environment schemes or management actions designed to enhance or preserve species richness may not necessarily enhance species or traits important for ecosystem services or functions. The link between observed shifts in community trait composition due to agricultural intensification and landscape change, and potential changes in ecosystem functioning resulting from these shifts, deserve more attention.

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