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Predator body sizes and habitat preferences predict predation rates in an agroecosystem

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Abstract

Top-down control of pest populations by their natural enemies is a crucial ecosystem service supporting agricultural production. The relationship between predator community composition and predation rates of pests remains poorly investigated. A deeper understanding of the processes shaping interaction strength in agroecosystems is needed if we are to accurately predict natural pest control services. Functional traits in a community can provide insights into processes shaping community assembly and ecosystem functioning. Functional diversity indices can be constructed from a single trait, such as body length, or from the integration of multiple traits, such as body length, hunting mode and habitat preference. However, their performance in predicting ecosystem functioning and services remains largely unexplored. We used empirical data replicated at landscape scales to examine which component of ground-dwelling predator community structure (activity-density, species richness, evenness, taxonomic distinctness and functional diversity) of spiders, carabids and staphylinids best predicted predation rates of aphids in spring cereals. Functional diversity explained a greater part of variation in predation rates than any other taxonomic or activity-density component. Among the indices for functional diversity, single-trait indices better predicted variation in aphid predation rates compared with multiple-trait indices. In particular, we found that the community-average value of body-size of ground-dwelling predators was negatively related to predation rates of aphids, whereas the proportion of spiders with a preference for arable land was positively related to predation rates. Additional analyses of body-size distributions of ground-dwelling predators suggested that intraguild predation was a key process shaping the relationship between predator community composition and the level of aphid pest control. Considering the functional trait composition of communities provides a more mechanistic understanding of the processes shaping the strength of trophic interactions in terrestrial ecosystems, thus improving predictive power. Body-size distribution and habitat preference appear to be particularly valuable in predicting the level of natural pest control by ground-dwelling predators in an agroecosystem.

Zusammenfassung

Die Schädlingsbekämpfung durch natürliche Feinde ist eine wichtige ökosystemare Dienstleistung und trägt positiv zur landwirtschaftlichen Produktion bei. Der Zusammenhang zwischen der Zusammensetzung von Räubergemeinschaften und der

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Frassleistung an Schädlingspopulationen ist jedoch wenig untersucht. Ein besseres Verständnis der Prozesse welche Interaktionen zwischen natürlichen Feinden und Schädlingen bestimmen, ist für Vorhersagen von Schädlingskontroll-Leistungen wichtig. Die funktionellen Eigenschaften in Tiergemeinschaften können dabei Einblicke in Prozesse liefern und verschiedene Indizes, welche auf einzelnen oder mehreren Eigenschaften basieren, wurden für die Analyse von Gemeinschaften entwickelt. Beziehungen zwischen diesen Indizes und ökosystemaren Funktionen und Dienstleistungen wurden bisher jedoch nicht ausreichend untersucht. In dieser Studie wurden auf der Landschaftsebene replizierte, empirische Daten verwendet um Beziehungen zwischen der Gemeinschaftsstruktur (Aktivitätsdichte, Artenzahl, Äquität, taxonomische Verschiedenheit und funktionelle Diversität) von Spinnen, Lauf- und Kurzflügelkäfern und Frassleistungen an Blattlauspopulationen zu untersuchen. Die funktionelle Diversität erklärte den höchsten Anteil der Variation der Frassleistung und Indizes welche auf einzelnen Eigenschaften basierten waren dafür besser geeignet als multivariate Indizes. Der für Abundanzen von Räuber-Arten gewichtete Körpergrößenindex stand in einer negativen Beziehung zur Frassleistung an Blattläusen. Gemeinschaften mit einem hohen Anteil von Spinnen, die Agrarhabitate präferieren, zeigten eine hohe Frassleistung an Blattläusen. Zusätzliche Analysen der Körpergrößenverteilung in Räubergemeinschaften deuten außerdem darauf hin, dass Intragilde-Prädation ein wichtiger Prozesse, für die Bestimmung der natürlichen Kontrolle von Blattlauspopulationen ist. Eine Berücksichtigung der funktionellen Eigenschaften in Räubergemeinschaften ermöglicht ein verbessertes, mechanistisches Verständnis der Prozesse welche trophische Interaktionen in terrestrischen Ökosystemen beeinflussen. Sowohl die Berücksichtigung von Körpergrößenverteilungen als auch von Habitat-Präferenzen sind von besonderer Bedeutung für die Vorhersage der Schädlingskontroll-Leistung durch laufaktive generalistische Prädatoren im Agrarland.

Keywords: Functional diversity; Ecosystem services; Body-size; Ecosystem functioning; Predator–prey interactions; Intraguild predation; Life-history traits; Biological control

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Introduction

Global biodiversity is increasingly threatened by environmental changes such as climate change or land use intensification (Tylianakis, Laliberté, Nielsen, & Bascompte, 2010; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). Rapid rates of biodiversity loss have been observed for several taxa around the globe (Pereira, Navarro, & Martins, 2012). Agricultural production depends on ecosystem services such as pollination, biological control, nutrient retention, and regulation of water flows (Bommarco, Kleijn, & Potts, 2013). Although these services are mediated by communities of beneficial organisms, it is not well understood how changes in communities will affect ecosystem functioning and services. Understanding the consequences of altered communities for ecosystem functioning and delivery of ecosystem services is an unresolved challenge for ecologists.

A number of studies have demonstrated a positive relationship between species richness and the rate, or the stability, of ecosystem functioning (Cardinale et al., 2012). However, not all species contribute equally to ecosystem functions and an increasing amount of evidence indicates that taking community composition in terms of relative abundance and functional traits into account can provide major insights on processes shaping emergent functions of assemblages (Cadotte, Carscadden, & Mirotchnick, 2011; Hillebrand, Bennett, & Cadotte, 2008). The increased interest for functional approaches has led to the development of several metrics to quantify the multidimensionality of functional diversity (Ricotta & Moretti 2011; Villéger, Mason, & Mouillot, 2008). Functional composition of a community is often analysed using either indices related to individual traits, or by composite indices combining information about multiple traits (Ricotta & Moretti 2011; Villéger et al., 2008). The latter are increasingly used in studies of community assembly (Villéger, Miranda, Hernández, & Mouillot, 2010; Flynn et al., 2009), whereas single-trait indices are largely used in studies that examine the effect of functional composition on a particular ecosystem function or service (Lavorel et al., 2011; Díaz et al., 2007). Moreover, the hypothesis that the evolutionary history of species within a community captures main differences in trait composition, such that phylogenies can be used as a proxy for functional diversity, has recently received attention (Cadotte et al., 2011; Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011). The potential for these indices to predict a particular ecosystem function or service remains, however, poorly studied (but see Flynn et al., 2011).

Top-down control of pest populations by their natural enemies is an important ecosystem service that supports agricultural production (Losey & Vaughan, 2006). A recent meta-analysis showed that positive relationships between predator species richness and prey suppression are likely to occur in agricultural ecosystems (Letourneau, Jedlicka, Bothwell, & Moreno, 2009). These positive relationships emerge from niche complementarity among predator species, such as predation occurring at different times in the season, or facilitation between species. However, negative or neutral relationships due to antagonistic interactions such as intraguild predation also appear in a non-negligible proportion of cases

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(Letourneau et al., 2009). Therefore, a deeper understanding of the processes shaping relationships between predator community composition and top-down control is needed if we are to accurately predict natural pest control services. Including functional traits to investigate mechanisms driving the effects of multiple predator species on top-down control is a promising, but underused, approach (Schmitz, 2009).

Body size is a critical life-history trait in determining the type and the strength of interactions among species within food webs (Schneider, Scheu, & Brose, 2012; Woodward et al., 2005). It is often used as a surrogate for interaction strengths, because many life-history traits such as dispersal ability, feeding behaviour, or metabolism are strongly related to body size (Brown, Gillooly, Allen, Savage, & West, 2004). Consequently, the ratio between predator and prey body-sizes is often considered as a good predictor of predator–prey dynamics. Other traits such as habitat preference and hunting mode can have important consequences for predator–prey interactions, and can potentially predict top-down control of herbivores (Schmitz, 2009).

Here we used empirical data to examine which component of predator community structure that best predicted predation rates. Among the several components of community structure, we tested activity-density, species richness, evenness, taxonomic distinctness, and several metrics of functional diversity as predictors for predation rates. Including functional traits into biodiversity–ecosystem functioning relationships has provided major insights into the processes shaping communities and processes (Díaz et al., 2007). Based on this we hypothesized that functional diversity metric(s) would better explain variation in predation rates compared with taxonomic or activity-density related predictors. Because the functional composition of communities has been described either with single indices related to individual traits, or with composite indices combining information among multiple traits, we also compared the efficiency of single versus multiple-traits indices to predict predation rates. We hypothesized that multiple-trait indices would better predict predation rates compared with single trait indices, as the former combine information about functional traits relevant for a particular ecosystem function.

Materials and methods

Predator sampling

Predator sampling was conducted in 2011 on 19 conventional spring barley fields distributed over the Province of Scania in southern Sweden (approx. 56°N, 13°30′E). Fields were selected along two orthogonal gradients: a gradient of proportion of ley (mixes of grass and clover cultivated for forage production) in the landscape and a gradient of landscape complexity to represent the variety of agricultural landscapes of this region. Further details about the study design and site selection can be found in Appendix A and in Rusch, Bommarco, Jonsson, Smith, and Ekbom (2013). We focused on ground-dwelling predators because parasitoids are known to be of very limited importance in the studied region and because our experiment took place after the peak of foliage-dwelling predators (Thies et al., 2011). Ground-dwelling predatory arthropods were sampled in a 20 m × 100 m area not treated with insecticides and located at the edge of the field. Three pitfall traps (diameter: 12 cm; depth: 12 cm) were placed along a transect located in the middle of the experimental area. The pitfall traps were put 10 m apart and were kept open seven days in a row between 20 June and 1 July after which densities of naturally occurring aphids (*Rhopalosiphum padi* L.) peaked in all fields. Collected samples were stored in 70% ethanol and ground beetles, spiders, and rove beetles were identified to species. See Appendix A: Table S1 for a list of species and number of individuals in each group.

Predation rates

Aphid predation rates were quantified using an exclusion experiment. In each field during the barley milk ripening stage (between 18 and 27 July 2011), four replicates of pairs of natural enemies treatments were established along the transect located in the middle of the experimental strip. The pairs included: (i) an open treatment where all natural enemies had access to the prey and (ii) a cage treatment where all ground-dwelling and flying natural enemies were excluded (mesh size: 0.5 cm; diameter: 0.3 m, height: 1 m.). In the open treatment there was no cage around the infested plants, and crop plants around each treatment plot were removed in a radius of approximately 40 cm to limit aphid dispersal. For each pair, the two treatment plots were randomly allocated along the transect and separated by 2 m. Pairs were separated by 5 m. Twenty-four late instar bird cherry-oat aphids (*R. padi)* distributed on eight barley plants in pots were introduced in each replicate of each treatment. The number of remaining aphids was counted after 5 days. For each field, suppression of aphids due to natural enemies was quantified as the average proportion of aphids observed in the open treatment in relation to aphid numbers in the cage treatment (see Rusch et al., 2013). The exclusion experiment took place in the same strip used for sampling predators.

Taxonomic distinctness

We used the average taxonomic distinctness (Δ^+) as a proxy for phylogenetic diversity. Δ^+ is the average path length between any two randomly chosen species in a Linnaean classification tree (Clarke & Warwick, 2001). The Linnaean tree for spiders was based on species, genus, family, and Orbicularia vs. non-Orbicularia classifications (Jocqué & Dippenaar-Schoeman, 2007). For carabids and rove beetles the tree was based on species, genus, tribe, and subfamily classifications. All taxonomic information was derived from the Fauna Europaea database (Audisio & Vigna, 2013).

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Functional traits

For each taxonomic group, we collected information on several life-history traits from the literature (See Appendix A: Table S2). These traits were selected because they provide relevant information about the predation functioning of the taxonomic groups. We particularly selected traits related to body size, habitat preference, hunting strategy and diet which are key traits for understanding trophic interactions and predation rates (Woodcock et al., 2014; Schmitz, 2009; Bell et al., 2008). Ground beetles were characterized by body length, wing morphology, breeding season, and diet (see Appendix A: Table S3). For spiders, information was collected on body length, hunting mode, habitat preferences, and preference for strata (See Appendix A: Table S4). Rove beetles were classified according to diet of adults and body length (See Appendix A: Table S5). Body length and diet indicate prey types, prey size range, and feeding rates and provide information on dispersal ability as well; breeding period, habitat preference, and hunting strategy give information about period of colonization or activity rates of predators in the field, spatio-temporal co-occurrence with prey availability in the field during the season and foraging mode; wing morphology provides information about dispersal abilities. We only considered traits that were poorly correlated as high collinearity between traits or redundancy are known to overweight these traits when calculating functional diversity indices (Weiher, 2010).

Two single-trait indices were calculated for each trait: the community-weighted mean (CWM) which is the abundance-weighted mean trait value in the community, and the functional divergence (FDvar) representing the variance in trait values weighted by the abundance of each species in the community (Leps, Bello, Lavorel, & Berman, 2006; Mason, MacGillivray, Steel, & Wilson, 2003). Categorical traits were treated as independent binary variables allowing us to calculate CWM values for each category (Leps et al., 2006). These two single-trait indices are complementary and provide information about the dominant trait values and the distribution of traits values within a community. CWM and FDvar of body size were calculated for the entire predator community and separately for carabids, spiders and staphylinids. See Appendix A for details about CWM and FDvar calculation are.

We also used trait information to calculate four multiple-trait indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis) (Villéger et al., 2008; Laliberté & Legendre, 2010). Multiple-trait indices for rove beetles were not calculated because of the limited number of traits available for this group.

Single and multiple trait indices were calculated using the FD package in R (R Development Core Team, 2012; Laliberté & Shipley, 2011). It implements a distance-based approach that is able to handle continuous, ordinal, nominal, multi-choice nominal, and binary variables.

Data analyses

A sequential procedure was used to determine which component of community structure most accurately predicted predation rates of aphids. First, for each group of predators separately, we examined how single components of community structure explained patterns in the level of predation. We examined the relationship between mean predation rates and activity-density, taxonomic (species richness, evenness (Pielou), and taxonomic distinctness), or functional components (single and multiple trait indices) using linear models. Then, for combinations of predator groups, i.e., combinations of two or three predator groups, we explored which single taxonomic (species richness and evenness) or functional (CWM and FDvar for body size) variable that best explained predation rates. Since several life-history traits were taxon-specific, we only included here activity-density, species richness, evenness, CWM, and FDvar for body size as they were the only components that were possible to calculate for the entire predator community. Finally, we analysed how combined information on several aspects of community structure explain the level of predation rate. Therefore, all models resulting from the combination of variables that significantly explained a part of variation in the level of predation rates in previous steps were compared based on AICc and adjusted R^2. A validation procedure was applied for each model to check that underlying statistical assumptions were valid in all cases. All statistical analyses were performed using R, version 2.15 (R Development Core Team, 2012).

Results

We found no effect of activity-density, species richness, evenness, or taxonomic distinctness of spiders, carabids, or staphylinids on predation rates of aphids (Table 1). Among single-trait indices for spiders, CWM and FDvar of habitat preference for arable land were significantly and positively related to the level of predation (Table 2 and Fig. 1; Appendix A: Table S6). None of the other single-traits (CWM and FDvar) or multiple traits indices for spiders were significantly associated to the level of predation rates (Table 2 and Appendix A: Table S6). Similarly, none of the single-trait or multiple-trait indices for carabids and staphylinids were significantly related to predation rates of aphids (data not shown).

When spiders, carabids, and staphylinids were considered together, we found no effect of activity-density, species richness, or evenness on predation rates of aphids (Table 1). We compared models with CWM for body size for all potential combinations among spiders, carabids, and staphylinids and found that the CWM for body size of carabids and spiders considered together explained the largest amount of variation in mean predation rates of aphids ($R^2 = 0.35$, $P = 0.01$) (Table 3 and Fig. 2). CWM for body size of all predators

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Table 1. Results of single variables models using activity-density, species richness, evenness or taxonomic distinctness of spiders, carabids and staphylinids to explain predation rates of aphids in barley fields.

Explanatory variables	Estimate	*t*-Value	*P*-value	R^2	R^2 adj	AICc
Activity-density						
All predators	0.00	−0.40	0.68	0.00	0.00	−4.11
Spiders	0.00	0.91	0.37	0.04	0.01	−4.84
Carabids	0.00	−1.14	0.27	0.07	0.01	−5.33
Staphylinids	0.00	−0.41	0.68	0.00	0.00	−4.11
Species richness						
All predators	0.00	−0.81	0.42	0.03	0.00	−4.65
Spiders	0.01	−0.36	0.72	0.00	0.00	−4.07
Carabids	0.00	−0.97	0.34	0.05	0.00	−4.96
Staphylinids	0.00	−0.49	0.62	0.01	0.00	−4.19
Evenness						
All predators	0.18	0.57	0.57	0.01	0.00	−4.65
Spiders	0.10	0.24	0.80	0.00	0.00	−3.99
Carabids	0.23	0.98	0.34	0.05	0.00	−3.67
Staphylinids	0.19	0.75	0.46	0.03	0.00	−4.55
Taxonomic distinctness						
Spiders	0.00	−0.07	0.93	0.00	0.00	−4.11
Carabids	0.00	−0.88	0.38	0.04	0.00	−6.38
Staphylinids	0.00	1.15	0.26	0.07	0.01	−7.01

Table 2. Results of single variable models using community weighted mean trait values of individual traits and multiple-trait indices for spiders to predict the level of predation rates of aphids in barley fields.

Explanatory variables	Estimate	*t* Value	*P*	R^2	R^2 adj	AICc
Body size						
CWM body size	−0.07	−1.85	0.08	0.16	0.11	−9.88
Hunting mode						
CWM Ambusher	−1.46	−1.73	0.10	0.15	0.10	−9.48
CWM Foliage runner	0.71	1.08	0.29	0.06	0.00	−7.65
CWM Ground runner	−0.31	−1.68	0.11	0.14	0.09	−9.30
CWM Space-web weaver	−2.09	−0.84	0.41	0.04	0.00	−7.16
Preferred habitat						
CWM Forest	0.07	0.12	0.90	0.00	0.00	−6.39
CWM Moor	−1.01	−1.96	0.07	0.18	0.13	−10.25
CWM Meadow	0.02	0.07	0.94	0.00	0.00	−6.38
CWM Arable land	**0.55**	**2.34**	**0.03**	**0.24**	**0.20**	**−9.26**
CWM Ruderal	0.69	1.26	0.22	0.08	0.03	−8.08
CWM Shrub	−0.39	−0.61	0.54	0.02	0.00	−6.80
Preferred strata						
CWM under stones/soil crevices	−1.40	−1.54	0.14	0.12	0.07	−8.88
CWM herb layer	2.17	1.01	0.32	0.05	0.00	−7.49
CWM shrub layer	0.08	0.26	0.79	0.00	0.00	−6.46
CWM tree trunk	0.32	1.29	0.21	0.08	0.03	−8.16
CWM tree canopy	−0.09	−0.35	0.72	0.00	0.00	−6.52
Multi-traits indices						
Fric	−0.33	−1.64	0.11	0.13	0.08	−9.19
FEve	−0.22	−0.29	0.77	0.00	0.00	−6.47
FDiv	−0.76	−1.11	0.27	0.06	0.00	−7.73
FDis	−0.85	−1.08	0.29	0.06	0.00	−7.64

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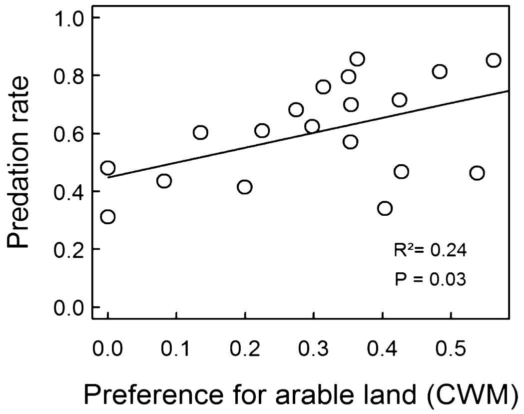

Fig. 1. Relationship between predation rates of aphids and the community weighted mean trait value of habitat preference for arable land of spiders.

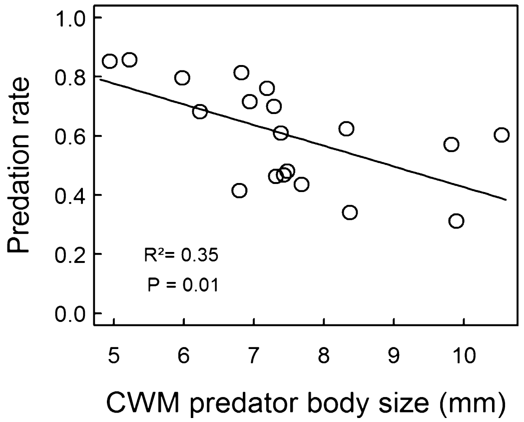

Fig. 2. Relationship between predation rates of aphids and the community weighted mean trait value for body size of spiders and carabids.

together was negatively related to mean predation rates of aphids ($R^2 = 0.29$, $P = 0.01$, Table 3), but was a less accurate predictor than CWM for body size of carabids and spiders together. The CWM for carabids and spiders together was also negatively related to predation rates of aphids. None of the other models using CWM for body size for combinations of predator groups explained a significant part of the variation in the level of predation rates (Table 3). None of the models using FDvar for body size estimated for all potential combinations of predator groups explained the level of predation rates (see Appendix A: Table S7).

When comparing all possible models resulting from the combinations of single variables, we found that two competing models explained a part of variation in mean predation rates of aphids ($\Delta i < 2$; Table 4). The first model included only CWM for body size of carabids and spiders, and the second model included both CWM for body size of carabids and spiders as well as CWM of habitat preference of spiders for arable land. CWM for body size was negatively related to predation rates of aphids and was the best predictor of predation rates as indicated by AICc values and adjusted-R^2 values (Table 4).

Discussion

Our study confirms the first prediction that functional metrics explain a greater part of the variation in predation rates than taxonomic or activity-density variables. However, contrary to what we expected, single trait indices better predicted predation rates than multiple trait indices. In particular, we found that CWM related to body-size of predators and habitat preference of spiders best predicted predation rates.

The ratio between predator and prey body sizes is known to be a key factor in determining interaction strength and food web stability (Brose et al., 2008; Emmerson & Raffaelli, 2004). It has been shown that interaction strength scales with the body-size ratio of predators and prey suggesting that an increase in average top predator size in a food web should lead to higher *per capita* predation rates and reduced prey biomass (Emmerson & Raffaelli, 2004). Allometric theory predicts a hump-shaped relationship between predation rates and predator–prey body-mass ratios with maximum predation rates at optimal body-mass ratios and decreasing feeding rates towards smaller and larger predator–prey body mass ratios (Brose, 2010). Therefore, the efficiency with which a predator exploits a prey of a certain size is related to the predator's own size (usually one to two orders of magnitude larger than the prey's size) due to allometric dependencies

Table 3. Results of single variable models using community weighted mean trait values for body size of predators to predict the level of predation rates of aphids in barley fields. Each model used a CWM value for body size resulting from each possible combination among predator groups.

Explanatory variables	Estimate	*P* value	R^2	R^2 adj	AICc
CWM Body size Spiders	−0.07	0.08	0.16	0.11	−9.88
CWM Body size Carabids	−0.01	0.48	0.02	0.00	−6.93
CWM Body size Staphylinids	−0.01	0.73	0.00	0.00	−6.51
CWM Body size Sp + C	−0.07	0.01	0.35	0.32	−14.81
CWM Body size Sp + St	−0.09	0.06	0.18	0.14	−10.33
CWM Body size C + St	−0.03	0.13	0.12	0.07	−8.89
CWM Body size Sp + C + St	−0.06	0.01	0.29	0.25	−13.07

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Table 4. Model selection table between all potential models resulting from the combination of community variables that significantly predicted predation rates. The best-fitted model corresponds to the model with the lowest AICc score. LL: log-likelihood, AICc: Akaike information criterion for small samples, $\Delta i = \mathrm{AICc}_i - \mathrm{AICc}_{\min}$, and w_i: Akaike weights. $\Delta i < 2$ indicate that two competing models are selected to explain a mean predation rates of aphids (model 1 et model 2). Model 1 includes CWM for body size of carabids and spiders as predictor and model 2 includes CWM for body size of carabids and spiders as well as CWM for habitat preference of spiders for arable land.

Model	Int.	CWM body size	CWM arable land	CWM body size: CWM arable land	R^2	Adj-R^2	df	LL	AICc	Δi	w_i
1	1.15	−0.07	–	–	0.35	0.32	3	11.2	−14.8	0.00	0.55
2	0.92	−0.05	0.27	–	0.41	0.33	4	12.02	−13.2	1.62	0.24
3	0.45	–	0.51	–	0.23	0.19	3	9.58	−11.6	3.25	0.10
4	0.68	−0.01	1.24	−0.12	0.44	0.33	5	12.55	−10.5	4.32	0.06
5	0.61	–	–	–	0.00	0.00	2	6.99	−9.2	5.58	0.03

of handling time, attack rate, and interference competition (Schneider et al., 2012; Brose, 2010).

We found a negative relationship between predation rates of aphids and the community averaged body size of carabids and spiders. Possible, non-exclusive reasons, to explain such a pattern would be a switch in prey preference, negative behavioural interactions, and intraguild predation with increasing average body size of predators. If predator communities increase in average body-size, because of higher abundance of larger species, then the larger predator species within a community are expected to exploit smaller predators or larger alternative prey instead of the prey that does not change in body-size. Thus, motifs within the food web may change from exploitative competition among predators to intraguild predation (Schneider et al., 2012), reducing interaction strengths with the basal prey. Another possibility is that motifs within the food web may change from exploitative competition to independent trophic chains if larger predators preferred alternative phytophagous preys. These findings fit well with our results, where high levels of predation were found in fields where carabid and spider body size distributions overlapped considerably (Fig. 3). In contrast, low levels of predation were found in fields with distributions of carabid body sizes that were distinctively different from the distribution of spider body sizes, suggesting a higher potential for intraguild predation (Fig. 3). The result that predation rates of aphids linearly decreased with the increase in average body size of predators suggests that negative interspecific interactions are common in communities of ground-dwelling predators in agroecosystems. Several recent studies have confirmed high levels of intraguild predation among ground-dwelling predators in arable fields especially between carabids and spiders (Davey et al., 2013; Prasad & Snyder, 2006). For instance, Davey et al. (2013) revealed that the relatively large ground beetle *Pterostichus melanarius* (Coleoptera: Carabidae) consumed a high amount of relatively small linyphiid spiders. Even if it is recognized that pitfall data are biased and tend to overestimate abundances of larger species, we are confident about the relationship found in our study (see also Hancock & Legg, 2012). We used the same protocol in all sampled fields and therefore the inherent bias of the method is the same in all communities. A change in the mean trait value of body length for a community can therefore be interpreted as an effective change in the community and not as a methodological artefact.

In our functional analysis, we found that the average proportion of spider species with a preference for arable fields was significantly and positively related to the level of aphid predation rates. Our results thereby confirmed that several of these species (e.g., *Pardosa agrestis*, *Tenuiphantes tenuis*, *Pachygnatha degeeri*) are among the major predators of aphids in agroecosystems (Kuusk, Cassel-Lundhagen, Kvarnheden, & Ekbom, 2008; Harwood, Sunderland, & Symondson, 2005) even if not all agrobiont spiders may primarily feed on aphids (Birkhofer, Entling, & Lubin 2013).

Considering the functional trait composition of communities provides a more mechanistic understanding of the processes shaping the predation of pest species in agroecosystems compared to other components of community structure. These findings are in accordance with the results of several recent studies on various ecosystem processes (Flynn et al., 2011; Mouillot, Villéger, Scherer-Lorenzen, & Mason, 2011; Cadotte, Cavender-Bares, Tilman, & Oakley, 2009). Bell et al. (2008) found that the inclusion of functional traits related to the way in which predators fed on aphids did not improve the prediction of predation rate in comparison to a taxonomic approach. This difference might result from the fact that Bell et al. mainly used behavioural traits and information about the feeding ecology and did not include information on body size or habitat requirements. We found that single-trait indices, or a small subset of single-trait indices, more closely described predation rates on herbivores than composite indices of functional diversity. These results are in line with a recent study comparing the performance of single versus mutli-trait indices in linking environmental variation and functional composition to ecosystem services (Butterfield & Suding, 2013). When ecosystem processes are mechanistically linked to a single trait, multiple-trait indices might be poorly suited to describe a specific ecosystem service emerging from an assemblage, and may instead veil existing relationships. However, multiple-trait indices may still describe general trends in synergies and/or trade-offs of several ecosystem functions or services (Mouillot et al., 2011). Finally, even if we took great care in selecting traits

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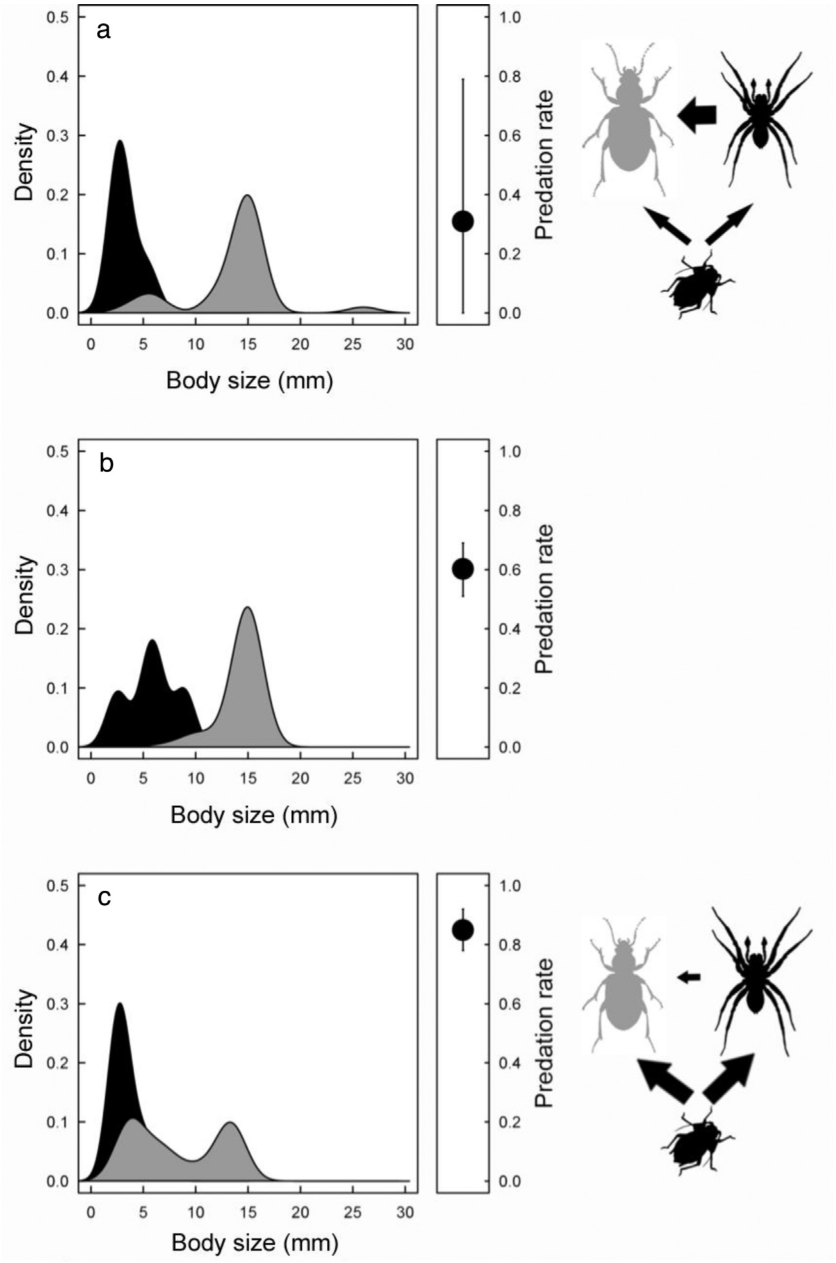

Fig. 3. Distribution of spider (in black) and carabid (in grey) body sizes found in three barley fields representing three levels of aphid predation (expressed as proportion of population predated) (A–C). Barley fields were selected to represent the minimum, the median, and the maximum predation rates. Since predators most efficiently exploit prey usually one to two orders of magnitude smaller than their own size (Brose, 2010), intraguild predation is more likely to appear in (A) than in (C). This offers a potential explanation for the negative relationship between CWM body size of predators and predation rates of aphids. Arrows represent trophic interactions. Size of the arrows is proportional to interaction strength.

that provide relevant information about the function of predation, we cannot exclude the possibility that the low explanatory power of multiple-traits indices might come from combining traits that do not properly describe the functioning of the community in terms of predation.

Contrary to our findings, several studies have demonstrated that phylogenetic diversity or taxonomic distinctness are valuable predictors of ecosystem functioning (Cadotte et al., 2011; Flynn et al., 2011). While these indices may be useful surrogates of functional diversity, the results of our study do not confirm that taxonomic distinctness (a taxonomically-based proxy of phylogenetic diversity) captures aspects of functional diversity related to prey suppression. Instead, our results are in line with results of recent studies showing that phylogenetic diversity did not predict competition or production in different communities

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compared to the predictive power of trait diversity (Best, Caulk, & Stachowicz, 2013; Cahill, Kembel, Lamb, & Keddy, 2008). Similarly to multiple-trait indices, phylogenetic diversity may be a better predictor for ecosystem functions or services that depend on a broad suite of traits, whereas predation of aphids seems to depend on a limited number of key traits.

Because our aim was to examine the relationships between predator community structure and top-down control of herbivores, we only considered variables related to these two components. However, several environmental variables such as climate, local management, or landscape context can affect predation rates of aphids directly or indirectly (Diehl, Sereda, Wolters, & Birkhofer 2013). Moreover, we only considered trophic interactions between the ground-dwelling predator communities and populations of a single prey species. Therefore, even if field surveys indicated that *R. padi* was the main prey in the field, our approach fails to account for trophic interactions with alternative prey that might also affect aphid predation rates. Future research should examine how predator communities and interaction strengths respond to changes in environmental conditions and prey community composition.

From an applied perspective, our study emphasizes that considering the functional composition of ground-dwelling predators, and especially the body-size distribution of natural enemies, can have important implications for the delivery of natural pest control services in agroecosystems. Analyzing changes in body-size distribution within predator communities is useful for examining the effects of management options on natural pest control. Further research about how agri-environmental measures affect trait distribution, especially body-size distribution, of predator assemblages might provide a basis to design agricultural landscapes where conservation biological control is optimized and negative interactions between natural enemies are minimized.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2015.02.003.

References

Audisio, P., & Vigna Taglianti, A. (2013). Fauna Europaea: Coleoptera, Carabidae. In *Fauna Europaea version 2.6*. ⟨http://www.faunaeur.org⟩

Bell, J. R., Mead, A., Skirvin, D. J., Sunderland, K. D., Fenlon, J. S., Symondson, W. O. C., et al. (2008). Do functional traits improve prediction of predation rates for a disparate group of aphid predators? *Bulletin of Entomological Research*, *98*, 587.

Best, R. J., Caulk, N. C., & Stachowicz, J. J. (2013). Trait vs. phylogenetic diversity as predictors of competition and community composition in herbivorous marine amphipods. *Ecology Letters*, *16*, 72–80.

Birkhofer, K., Entling, M., & Lubin, Y. (2013). Agroecology: Trait composition, spatial relationships, trophic interactions. In D. Penney (Ed.), *Spider research in the 21st century: Trends & perspectives* , ISBN 9780957453012. Manchester: Siri Scientific Press.

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*, 230–238.

Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, *24*, 28–34.

Brose, U., Ehnes, R. B., Rall, B. C., Vucic-Pestic, O., Berlow, E. L., Scheu, S., et al. (2008). Foraging theory predicts predator–prey energy fluxes. *Journal of Animal Ecology*, *77*, 1072–1078.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789.

Butterfield, B. J., & Suding, K. N. (2013). Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology*, *101*, 9–17.

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*, 1079–1087.

Cadotte, M. W., Cavender-Bares, J., Tilman, D., & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, *4*, e5695.

Cahill, J. F., Jr., Kembel, S. W., Lamb, E. G., & Keddy, P. A. (2008). Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology, Evolution and Systematics*, *10*, 41–50.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, Patrick, et al. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*, 59–67.

Clarke, K. R., & Warwick, R. M. (2001). A further biodiversity index applicable to species lists: Variation in taxonomic distinctness. *Marine Ecology-Progress Series*, *216*, 265–278.

Davey, J. S., Vaughan, I. P., Andrew King, R., Bell, J. R., Bohan, D. A., Bruford, Michael W., et al. (2013). Intraguild predation in winter wheat: Prey choice by a common epigeal carabid consuming spiders. *Journal of Applied Ecology*, *50*, 271–279.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Matthew Robson, T. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, *104*, 20684–20689.

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Diehl, E., Sereda, E., Wolters, V., & Birkhofer, K. (2013). Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: A meta-analysis. *Journal of Applied Ecology*, *50*, 262–270.

Emmerson, M. C., & Raffaelli, D. (2004). Predator–prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, *73*, 399–409.

Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., et al. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, *12*, 22–33.

Flynn, D. F. B., Mirotchnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology*, *92*, 1573–1581.

Hancock, M. H., & Legg, C. J. (2012). Pitfall trapping bias and arthropod body mass. *Insect Conservation and Diversity*, *5*(4), 312–318. http://dx.doi.org/10.1111/j.1752-4598.2011.00162.x

Harwood, J. D., Sunderland, K. D., & Symondson, W. O. C. (2005). Monoclonal antibodies reveal the potential of the tetragnathid spider *Pachygnatha degeeri* (Araneae: Tetragnathidae) as an aphid predator. *Bulletin of Entomological Research*, *95*, 161–167.

Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology*, *89*, 1510–1520.

Jocqué, R., & Dippenaar-Schoeman, A. S. (2007). *Spider families of the world* (2nd ed., pp. 336 pp). Tervuren: Koninklijk Museum voor Midden-Afrika.

Kuusk, A.-K., Cassel-Lundhagen, A., Kvarnheden, A., & Ekbom, B. (2008). Tracking aphid predation by lycosid spiders in spring-sown cereals using PCR-based gut-content analysis. *Basic and Applied Ecology*, *9*, 718–725.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.

Laliberté, E., & Shipley, B. (2011). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. In *R package version 1.0-11*.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, Jacky, et al. (2011). Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology*, *99*, 135–147.

Leps, J., Bello, F. D., Lavorel, S., & Berman, S. (2006). Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. *Preslia*, *78*, 481–501.

Letourneau, D. K., Jedlicka, J. A., Bothwell, S. G., & Moreno, C. R. (2009). Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 573–592.

Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, *56*, 311–323.

Mason, N. W. H., MacGillivray, K., Steel, J. B., & Wilson, J. B. (2003). An index of functional diversity. *Journal of Vegetation Science*, *14*, 571–578.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M., & Mason, N. W. H. (2011). Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, *6*, e17476.

Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global biodiversity change: The bad, the good, and the unknown. *Annual Review of Environment and Resources*, *37*, 25–50.

Prasad, R. P., & Snyder, W. E. (2006). Polyphagy complicates conservation biological control that targets generalist predators. *Journal of Applied Ecology*, *43*, 343–352.

R Core Team. (2012). *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria*. http://www.R-project.org/

Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia*, *167*, 181–188.

Rusch, A., Bommarco, R., Jonsson, M., Smith, H. G., & Ekbom, B. (2013). Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. *Journal of Applied Ecology*, *50*, 345–354.

Schmitz, O. J. (2009). Effects of predator functional diversity on grassland ecosystem function. *Ecology*, *90*, 2339–2345.

Schneider, F. D., Scheu, S., & Brose, U. (2012). Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters*, *15*, 436–443.

Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L. W., et al. (2011). The relationship between agricultural intensification and biological control: Experimental tests across Europe. *Ecological Applications*, *21*, 2187–2196.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – Ecosystem service management. *Ecology letters*, *8*, 857–874.

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, *143*, 2270–2279.

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*, 2290–2301.

Villéger, S., Miranda, J. R., Hernández, D. F., & Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, *20*, 1512–1522. http://dx.doi.org/10.1890/09-1310.1

Weiher, E. (2010). A primer of trait diversity. In A. E. Magurran, & B. J. McGill (Eds.), *Biological diversity: Frontiers in measurement and assessment*. Oxford, UK: Oxford University Press.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., et al. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, *20*, 402–409. http://dx.doi.org/10.1016/j.tree.2005.04.005

Woodcock, B. A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A. J., Heard, M. S., et al. (2014). National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. *Journal of Applied Ecology*, *51*, 142–151.

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