Received: 7 November 2023 | Revised: 2 May 2024 | Accepted: 18 July 2024

DOI: 10.1002/eap.3035

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

Functional diversity of ground beetles improved aphid control but did not increase crop yields on European farms

Roman Bucher[1] | **Péter Batáry**[2,3] | **Julia Baudry**[4] | **Léa Beaumelle**[5] | **Andrea Čerevková**[6] | **Enrique G. de la Riva**[7] | **Tara Dirilgen**[8,9,10] | **Róbert Gallé**[2] | **Emmanuelle Kesse-Guyot**[4] | **Ewa Rembiałkowska**[11] | **Adrien Rusch**[12] | **Dara A. Stanley**[8,9] | **Werner Ulrich**[13] | **Klaus Birkhofer**[1]

[1]Department of Ecology, Brandenburg University of Technology Cottbus-Senftenberg, Cottbus, Germany

[2]'Lendület' Landscape and Conservation Ecology, Institute of Ecology and Botany, Centre for Ecological Research, Vácrátót, Hungary

[3]Faunistics and Wildlife Conservation, Department of Agriculture, Ecotrophology, and Landscape Development, Anhalt University of Applied Sciences, Bernburg, Germany

[4]Sorbonne Paris Nord University, Inserm U1153, INRAE U1125, CNAM, Nutritional Epidemiology Research Team (EREN), Epidemiology and Statistics Research Center – University of Paris (CRESS), Bobigny, France

[5]French National Centre for Scientific Research CNRS, UPS, Toulouse, France

[6]Institute of Parasitology SAS, Košice, Slovak Republic

[7]Area of Ecology, Department of Biodiversity and Environmental Management, Faculty of Biological and Environmental Sciences, University of León, León, Spain

[8]School of Agriculture and Food Science, University College Dublin, Dublin, Ireland

[9]Earth Institute, University College Dublin, Dublin, Ireland

[10]Department of Biology, Maynooth University, Maynooth, Kildare, Ireland

[11]Department of Functional and Organic Food, WULS, Warsaw, Poland

[12]INRAE, Bordeaux Sciences Agro, ISVV, SAVE, Villenave d'Ornon, France

[13]Department of Ecology and Biogeography, Nicolaus Copernicus University, Toruń, Poland

Correspondence
Roman Bucher
Email: roman.bucher@b-tu.de

Funding information
Environmental Protection Agency (EPA), Grant/Award Number: 2019-NC-MS-11; BiodivERsA3 ERA-Net COFUND Programme (2018-2019 BiodivERsA Joint Call) (FunProd); Hungarian National Research, Development and Innovation Office, Grant/Award Number: NKFIH KKP 133839; Agence Nationale de la Recherche (ANR); National Science Centre, Grant/Award Number: UMO-2019/32/Z/NZ8/00008; Deutsche

Abstract

Land-use intensification is often associated with a decline in functional diversity, potentially undermining the provision of ecosystem services. However, how changes in traits affect ecosystem processes remains poorly understood. Variation in trait values among species in a community may drive ecosystem processes. Alternatively, the mass ratio hypothesis proposes that trait values of the dominant species in a local community are related to ecosystem processes. Using data from 159 farms in six European countries, we quantified the impact of local and landscape-level land-use intensity on ground beetles as pest control agents. We then assessed the extent to which functional diversity and community-weighted mean trait values relate to pest control and cereal yield. In addition, we assessed how the responses to land use and the effects of

Forschungsgemeinschaft (DFG), Grant/Award Numbers: 662944, FIP 16/1; Slovak Academy of Sciences, Grant/Award Number: BiodivERsA3/2018/885/FunProd

Handling Editor: Emily A. Martin

different species on pest control and yield varied with their traits to compare the relative impact of the traits studied. Functional diversity of ground beetles improved aphid removal, but did not translate into higher crop yields. Pest control of aphids was enhanced by a higher proportion of smaller, mobile ground beetles with a preference for the vegetation layer. Smaller, predatory ground beetles in communities improved crop yield. The magnitude of responses to land-use intensification and the effects on pest control and yield were more strongly influenced by body size than other traits. Our study provides evidence that reduced management intensity can improve pest control by supporting small-sized, macropterous ground beetles. In contrast to the claims of ecological intensification, our joint analysis of the direct effects of land use on yield and indirect effects via functional diversity of ground beetles and pest control suggests that ecosystem services by ground beetles cannot compensate for the yield gap due to a reduction in land-use intensity.

KEYWORDS
ecological intensification, ecosystem services, landscape composition, land-use intensity, pest control, predation, traits

INTRODUCTION

Land-use intensification is a major driver of global change (Díaz et al., 2019; Sala et al., 2000). While land-use intensification has contributed to food security for growing demand, it is often paralleled with a dramatic decline in biodiversity, undermining the sustainable provision of multiple ecosystem services (Cardinale et al., 2012; Naeem et al., 1994). If ecosystem services such as pest control and pollination are impaired, it jeopardizes food production and human well-being (Dainese et al., 2019; Hooper et al., 2005). As an alternative, ecological intensification aims to reduce negative impacts on nature and to improve food production by supporting ecosystem service providers (e.g., by mixed cropping and diversified crop rotation, set-asides, or increasing the quality and quantity of semi-natural habitats; Bommarco et al., 2013; Kleijn et al., 2019). To halt the loss of ecosystem functionality due to conventional agricultural intensification, but simultaneously increase agricultural production in an environmental-friendly way, a better understanding of the links between land use, biodiversity, and ecosystem service provision is crucial (de la Riva et al., 2023; Martin et al., 2019; Ulrich et al., 2023).

Land-use intensification occurs at different spatial scales. At the local field scale, the application of fertilizers and pesticides as well as the frequency of mechanical management practices are increased. At the landscape scale, the average field size is increased, and semi-natural habitats such as field margins, hedges, and forests are replaced by arable land, leading to landscape homogenization. In addition, the effects of fertilizer and pesticide applications can expand into neighboring fields via surface waters, leaching into the ground, and airborne drift (Kleijn & Snoeijing, 1997). Land-use intensification at both scales reduces biodiversity and leads to a multitrophic homogenization of biological communities (Tscharntke et al., 2005). This is not a random process, with individuals of some species being more prone to extinction than others (e.g., Rader et al., 2014). Trait analysis can help explain and predict how different organisms respond to land-use intensification (i.e., response traits) and how changes in community composition affect ecosystem functioning (i.e., effect traits; Violle et al., 2007). These traits are phenotypic characteristics that can be measured on individual organisms (Diaz & Cabido, 2001; Wong et al., 2019) and are linked to individual fitness: a particular trait or combination of traits might be favorable for survival and reproduction in a certain environment but not in another (Shipley et al., 2016). Analyses based on traits are therefore very useful to understand natural community assembly, but also indicate how anthropogenic environmental changes affect community composition (Shipley et al., 2006). Trait-based analyses can provide a more mechanistic understanding of how organisms respond to land-use intensification revealing patterns across taxonomic and geographic boundaries.

Two main hypotheses have emerged on how species traits might influence ecosystem functioning at the community level. The mass ratio hypothesis proposes that the trait value of dominant species in a community (i.e., community-weighted means; Garnier et al., 2004) is expected to be related to ecosystem processes (Grime et al., 1988; Kleijn et al., 2015). Alternatively, the niche complementarity hypothesis predicts that variation in trait values among species in a community (functional diversity sensu stricto) leads to more efficient use of resources among co-existing species, thereby enhancing ecosystem processes (Flynn et al., 2011; Tilman et al., 1996). While the mass ratio hypothesis is more targeted at traits that facilitate functioning (e.g., plant biomass production in the presence of plant species capable of nitrogen fixation), the complementarity hypothesis proposes higher ecosystem stability in space and time (i.e., different functional groups complement each other under different environmental disturbance regimes or take over if a particular group of organisms is lost; Loreau et al., 2001). Previous studies revealed inconsistent results regarding the relative importance of mass ratio and complementarity hypothesis, suggesting that complementarity effects drive most of the relationships between biodiversity and ecosystem functioning (Gagic et al., 2015; Greenop et al., 2018; Woodcock et al., 2019). In contrast, other studies report that ecosystem functioning is primarily driven by trait dominance (Garnier et al., 2016; Kleijn et al., 2015; Lavorel et al., 2011).

Trait-based approaches are well established in plant ecology, whereas relationships between functional diversity and ecosystem service provision are less well studied in arthropods (but see Ricotta & Moretti, 2011 for an example evaluating the mass ratio and complementary hypothesis in arthropod taxa). This is due to the high abundance and diversity as well as due to the difficulty to measure and standardize traits across taxonomic groups (Gallé & Batáry, 2019; Wong et al., 2019). In order to overcome the obstacle of trait measurement, it is often assumed that intraspecific trait variation is smaller than interspecific variation in trait values/levels (Shipley et al., 2016), and species identity is used to infer the level of a certain trait from literature sources (i.e., species traits). In generalist predators, the relationship between the structure of communities and pest control is particularly complex and less predictable compared to more specialized antagonists (Segoli et al., 2023; Straub et al., 2008). This is due to the large diet breadth of generalist predators (e.g., Birkhofer et al., 2008) but also because of negative interactions between predators such as intraguild predation or behavioral interference (e.g., Ostandie et al., 2021; Staudacher et al., 2018), which can dampen top-down control of pests (Finke & Denno, 2005; Scheu, 2001). In addition, it is often unclear to which extent functional diversity effects cascade to regulatory and provisioning ecosystem services such as pest control and crop yield as they are often studied in isolation (see Ulrich et al., 2023). Among arthropods, ground beetles (Coleoptera, Carabidae) are diverse and ubiquitous generalist predators in various agroecosystems and effects of land-use intensification on ground beetle diversity are well-studied due to their sensitivity to environmental change (e.g., Diekötter et al., 2010; Gallé et al., 2019; Gayer et al., 2019; Rusch et al., 2013). Ground beetles exhibit versatile trophic lifestyles, with many species being exclusively carnivorous while others feed on plant material or are omnivorous (e.g., scavengers). Although ground beetles spend most of their adult life on the ground, they prey on aphids that feed on crop plants or drop to the ground (Roubinet et al., 2017; Török et al., 2021). Thus, ground beetles are interesting and relevant model organisms to study how traits mediate the response to land-use intensity as well as to which extent traits influence the pest control potential of generalist arthropod predators.

In this study, we aimed to address these knowledge gaps by simultaneously quantifying direct and indirect relationships between land-use intensification, functional diversity of ground beetle communities, pest control services, and crop yields. We used information about local and landscape-level land-use intensity and crop yields of 159 farms from six European countries together with the functional diversity and community-weighted means of ground beetle traits and aphid removal to assess the respective relationships in structural equation models. In addition, we assessed to what extent impacts of local and landscape-level land-use intensity as well as influences on pest control and crop yield vary with the different traits of ground beetles. We expected that local land-use intensity (amount of N fertilizer application and frequency of herbicide and insecticide application) and land use in the surrounding landscape (the proportion of arable land) reduce the functional diversity of ground beetles due to the homogenization of biotic communities. In addition, we expected a lower community-weighted mean body size and a higher proportion of mobile beetles in fields and landscapes with increasing land-use intensity because smaller and mobile species are less vulnerable to frequent disturbances. Larger ground beetles can increase or decrease pest control depending on the relative role of size-related predation rates and higher intraguild predation of larger ground beetles on smaller ones. Furthermore, a higher proportion of exclusively predatory ground beetles and ground beetles that climb on plants are expected to enhance aphid control and consequently crop yield. These functional aspects of ground beetles could also directly enhance crop yield via the control of other pest organisms (i.e., independent of their impact on aphid predation). We were also interested in which specific traits mediate the community response to land-use intensity and which traits in the ground beetle community relate to pest control and crop yields. This multivariate approach allowed us to estimate the relative importance of specific traits in relation to land-use intensity, functional diversity, and ecosystem services.

MATERIALS AND METHODS

Study area and intensification variables

The underlying data are a subset of a broader European project (AGRIPOPES; Emmerson et al., 2016) selected based on the availability of reliable biological control data. The data used here were acquired in six European countries (France, Germany, Ireland, the Netherlands, Poland, and Sweden), allowing a large-scale assessment of the interrelationship between land-use intensification, functional diversity, biological control potential, and yield across European cereal-dominated agroecosystems. In each country, 21–30 farms separated by at least 1 km were selected so that the range of cereal productivity in each region (an area between 30 × 30 km and 50 × 50 km, see Appendix S1: Table S1) was as large as possible based on the average cereal yield in the 3 years before sampling. Thus, a farm was considered the administrative and ecological unit under study (i.e., decision-making level). Local land-use variables were obtained via questionnaires conducted by personal interviews with all farmers. Here, we focused on fertilization (the total amount of N applied) as well as on the frequency of insecticide and herbicide applications during the previous year. The three local land-use variables were later divided by the mean across all regions and summed in a land-use intensity index (according to Blüthgen et al., 2012). To measure landscape-level land-use intensification, the AGRIPOPES consortium quantified the percentage cover of non-irrigated, annually tilled arable crops (CORINE CLC5-Code 211) within a 1000 m radius centered on focal fields. This is a well-defined habitat category that can reliably be retrieved from raster satellite data (CORINE; Büttner, 2014) of the studied region. Similar to the standardization in the land-use intensity index, the cover of arable crops in the landscape and yield data was divided by the mean across all regions.

Ground beetle sampling

A set of one to three winter wheat fields per farm was selected to sample ground beetles and estimate biological control potential. Winter barley was used instead if no winter wheat fields were available (less than 20% of all studied fields). Sampling took place during spring and summer 2007 and was synchronized using the phenological stages of winter wheat in each region. Ground beetles were sampled using two pitfall traps per field. Pitfall traps were covered with a plastic lid to protect the traps from precipitation and were filled with 150 mL of ethylene glycol. The traps were located at 10 m distance from the edge toward the center of the field and were active during two periods of 7 days each. The first sampling period started 1 week after the appearance of spikes of winter wheat and the second sampling period coincided with the milk-ripening stage of winter wheat. Ground beetles caught in pitfall traps were stored in 70% ethanol, and beetles of one randomly selected trap per field were identified to species level (see Appendix S1: Table S2 for information about the number of individuals and species found in each region).

Biological control potential

During the emergence of the first inflorescence of winter wheat, the biological control potential was estimated by a 2-day trial, which was repeated once within 8 days. In the morning of the first day, three living pea aphids (*Acyrthosiphon pisum*) of the third or fourth instar were glued to plastic labels. At 12.00, three labels were placed on the ground at the sampling point of the pitfall traps. At 18.00 the following day, the labels were removed and the number of remaining aphids was counted (see Östman et al., 2001). In some regions, aphid removal measurements were unreliable or interrupted (e.g., by heavy rain), and only data of one of the two rounds were used. If biological control potentials are compared across regions, the proportion of removed aphids is used as a response or explanatory variable.

Ground beetle traits

We collected information about available traits of ground beetles that are relevant for the relationship to the studied environmental gradient and ecosystem function. The choice and coding of traits further depended on the availability and quality of trait information for the sampled species in the literature (see Table 1). The five traits selected were; body size, trophic position, mobility, stratum, and phenology. Body size is probably the most frequently used response and effect trait, known to be affected by land-use intensity (Birkhofer, Meub, et al., 2015; Birkhofer, Smith, et al., 2015) and related to the predation rate of aphids (Rusch et al., 2015). We included

TABLE 1 Summary of all traits included to calculate functional diversity as well as in the multivariate 4th corner models and the respective main literature sources.

Trait	Variable quality	Trait value/levels	Source
Body size	Numerical[a]	**[mm]**	Benisch (2023), Lompe (2023)
	Binary	1–12 mm	
	Binary	12–24 mm	
	Binary	>24 mm	
Trophic position	Binary	**Predator**	Lindroth (1985/1986), Turin (2000)
	Binary	Herbivore	
Mobility	Binary	**Macropterous**	Lindroth (1985/1986), Turin (2000)
	Binary	Brachypterous	
Stratum	Binary	Endogeic	Luka et al. (2009)
	Binary	Epigeic	
	Binary	**Vegetation**	
Phenology	Binary	**Spring breeding**	Lindroth (1985/1986), Turin (2000)
	Binary	Autumn breeding	

Note: Trait values/levels in bold were used to calculate community-weighted means. Categorical traits allow species to be assigned to more than one category (e.g., omnivorous to be predator and herbivore).

[a]Numerical body size was used to calculate community-weighted mean body size, whereas the three size categories were used in the multivariate 4th corner models and to calculate functional diversity to achieve comparable variable qualities across traits.

ground beetle body size as a numerical variable to calculate community-weighted means (see below) but also as binary coded trait with three size categories (see Table 1) to achieve a comparable trait quality with regard to the other traits for the calculation of functional diversity as well as for the comparison of the explanatory importance among the different traits. Binary coded traits with several trait levels (so-called fuzzy coded traits) further allow species to be assigned to several trait levels (e.g., omnivorous beetles were assigned to herbivorous and carnivorous categories). We collected body size information for all species sampled, whereas, for the other traits, we lacked information for nine rare species. These species had to be excluded from the calculation of community-weighted means and functional diversity. The phenology of ground beetles (spring vs. autumn breeders) may also provide information about which species respond to land use or affect aphid control, which is temporarily more confined to springtime (e.g., Hanson et al., 2016). Ground beetle wing morphology is a further morphological characteristic related to land-use intensity (brachypterous vs. macropterous). The trophic position (herbivorous vs. carnivorous) might indicate the impact of ground beetle communities on pest control and yield (i.e., only carnivorous beetles contribute to pest control). Finally, the preference for strata (in the soil vs. on the ground vs. in the vegetation) can be related to complementarity in predation or if ground beetles can reach pest organisms on crop plants. While some traits are considered to be response and effect traits (e.g., body size and phenology), others are expected to mainly respond to land-use change (e.g., wing morphology) or mainly affect pest control (e.g., trophic position and stratum preference). Because the separation into response and effect traits is often ambiguous, we simultaneously quantified responses and effects for all traits in the respective structural equation models.

Functional index calculation

For the calculation of functional metrics of the ground beetle communities, we proceeded in two steps corresponding to the mass ratio and the niche complementarity hypotheses. First, we calculated community-weighted means of selected trait values/levels (see Table 1) using the R-package FD (Laliberté et al., 2022). Among the chosen traits, community-weighted mean body size was negatively correlated ($p < 0.001$) with the proportion of spring breeding, macropterous, and predatory ground beetles in the community but uncorrelated to the proportion of ground beetles with a preference for living on plants. Second, we calculated Gower distances between the species based on all five traits. For this, we standardized the binary coded traits so that trait values across trait categories (e.g., soil/ground/vegetation) summed up to one for each trait (stratum in this example). We used the gawdis function in R to group and weight trait categories to equalize the influence of each trait on species similarity regardless of the number of categories per trait (de Bello et al., 2021). Based on this similarity matrix, we calculated Rao Quadratic Entropy as a measure of functional diversity sensu stricto. Rao Quadratic Entropy is the average of the dissimilarity between each pair of species in a local community, weighted by the abundances of both species (script in de Bello et al., 2010). Rao Quadratic Entropy should be independent of species richness at higher numbers of species (approximately more than 10 species per site; Carmona et al., 2017). However, in our relatively species-poor arable fields (see Appendix S1: Table S2) functional diversity increased with species richness ($t = 9.049$, df = 157, $p < 0.001$).

Structural equation models

We evaluated the direct impacts of local and landscape-level land-use intensity on functional diversity and community-weighted means in separate piecewise structural equation models (model no. 1: LME; R-Package nlme, Pinheiro, 2009). We further quantified influences of either functional diversity or community-weighted means on pest control (model no. 2: GLMM following binomial error distribution including an observation level random effect to account for overdispersion; R-Package lme4, Bates et al., 2009). Finally, we quantified to which extent local land use, functional diversity or community-weighted means, and pest control contributed to yields (model no. 3: LME). The community-weighted mean stratum (i.e., the proportion of ground beetles living on plants) showed a quasi-Poisson distribution. Impacts of local and landscape-level land-use intensity on community-weighted mean stratum were therefore modeled with a GLMM following Poisson-error distribution, including an observation level random effect to account for overdispersion. All other relationships with community-weighted means were evaluated with LME's. All models included country identity as a random effect. Since piecewise structural equation models produce no valid global covariance matrix, *p*-values across the set of Shipley's tests of directed separation were combined in Fisher's *C* statistics as an alternative goodness-of-fit (Shipley, 2000). Marginal and conditional R^2-values and Fisher's *C* as well as standardized coefficients (with the exception of the GLMM) were calculated with the piecewiseSEM R-package (Lefcheck et al., 2023). Marginal R^2-values consider only the variance of fixed effects, while the conditional R^2-values additionally take random effects (i.e., country identity) into account. Thus, the two R^2-values indicate to which extent relationships can be attributed to the included variables or due to differences in respective variables between the countries. In non-Gaussian response models (log) odds ratios are not comparable across models, and they cannot be exactly standardized since coefficients are reported on the link (linear) scale, while variance can only be computed from the raw data on the non-linear scale. In these cases, the SD used for the standardization of coefficients is computed as the square root of the variance of the predictions (on the linear scale) plus the correlation between the observed and predicted values of dependent variables (see Grace et al., 2018).

Fourth-corner model

In a second step, we were interested in the extent to which local and landscape level land-use intensity effects on ground beetle communities are mediated via the different traits, as well as to which extent the various traits contribute to aphid removal and yield. For this, we calculated a fourth-corner model, which evaluates multivariate relationships between ground beetle communities, any environmental variable (land use, yields, etc.), the trait matrix, and the interaction between environmental variables and the trait matrix (i.e., the fourth corner; Dray & Legendre, 2008). In order for the models to converge, we had to run the fourth corner analysis for each country separately because ground beetle species composition differed quite substantially between the countries (see Appendix S1: Figure S1). Data and R-code used for all analyses are available in Dryad (Bucher et al., 2024).

RESULTS

Structural equation model for functional diversity

Local land-use intensity and the percentage of arable land in the surrounding landscape were not significantly related to the functional diversity of ground beetle communities (land use: $t = 0.349$, df = 151, $p = 0.728$; percentage of arable land: $t = 0.437$, df = 151, $p = 0.663$). The comparison of marginal versus conditional R^2-values indicated that variation in the functional diversity of ground beetles was mainly explained by differences between the countries ($R^2_m = 0.01$, $R^2_c = 0.46$). Local land-use intensity strongly increased crop yield (Figure 1; $t = 10.620$, df = 150, $p < 0.001$). The functional diversity of ground beetles was positively correlated with pest control ($t = 3.488$, df = 159, $p < 0.001$), but not directly ($t = -0.819$, df = 150, $p = 0.414$) or indirectly (via pest control of aphids; $t = 0.171$, df = 150, $p = 0.011$) with

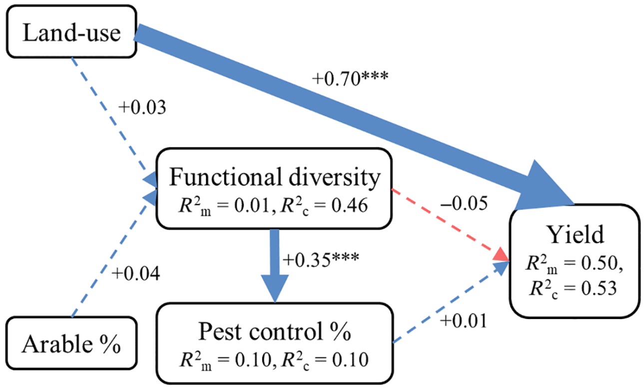

FIGURE 1 Proposed causal relationships between local land-use intensity, the percentage of arable land in the landscape, the functional diversity of ground beetles and crop yield as well as relationships between functional diversity, pest control (measured as the percentage of removed aphids), and crop yield. Marginal R^2-values (R^2_m) indicate the variation explained by fixed effects, conditional R^2-values (R^2_c) indicate the variation explained by fixed and random effects (country identity). Blue arrows indicate positive, red arrows negative correlations and the strength of arrows corresponds to standardized path coefficients (--- = ns, ***$p < 0.001$).

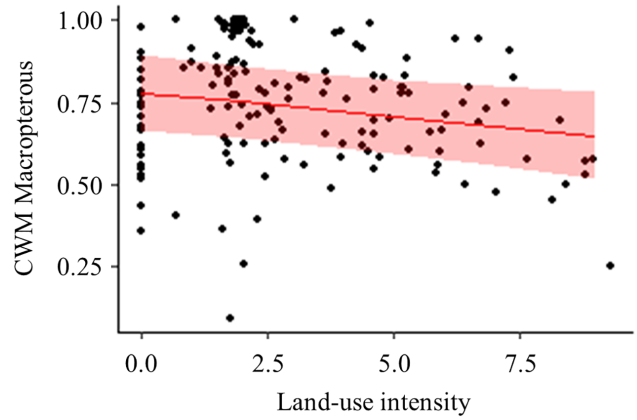

FIGURE 2 The negative relationship between local land-use intensity and the proportion of macropterous (high mobility) ground beetles in communities ($p < 0.05$). CWM, community-weighted mean.

crop yield. Overall, the observed data did not contradict our a priori causal structure linking land-use intensity, pest control, and crop yield with the functional diversity of ground beetles (Fisher's $C = 5.77$, df = 6, $p = 0.45$).

Structural equation models for different traits

Among the structural equation models for the different traits, the proportion of macropterous ground beetles declined with increasing land-use intensity but not with a higher percentage of arable land in the surrounding landscape (Figure 2; land use: $t = -2.326$, df = 151, $p = 0.021$; percentage of arable land: $t = -1.422$, df = 151, $p = 0.157$). The community-weighted mean of all other traits was neither related to local land-use intensity nor to the percentage of arable land within the 1000 m radius (land use: $t < \pm 1.305$, df = 151, $p > 0.128$; percentage of arable land: $t < \pm 0.840$, df = 151, $p > 0.402$). Similar to the structural equation model for functional diversity, local land-use intensity strongly increased crop yield in all structural equation models for the community-weighted means of the different traits ($t > 10.045$, df = 150, $p < 0.001$).

A higher proportion of macropterous ground beetles in communities was positively associated with pest control (Figure 3b; $t = 3.107$, df = 159, $p < 0.01$). In contrast, larger ground beetles in communities reduced pest control (Figure 3c; $t = -3.021$, df = 159, $p < 0.01$). We found a tendency for increased pest control in communities with a higher proportion of ground beetles living in the vegetation (Figure 3d; $t = 1.818$, df = 159, $p = 0.069$). The percentage of predatory ground beetles in the community or the proportion of spring breeding ground beetles in communities had no influence on pest control ($t < 1.537$, df = 159, $p > 0.124$). For structural equation models with all community-weighted mean trait values, pest control measured as the percentage of removed aphids was not related to crop yield ($t = -0.090$, df = 150, $p = 0.928$).

Larger ground beetles in local communities reduced crop yield (Figure 4a; $t = -2.333$, df = 150, $p = 0.021$), whereas the percentage of predatory ground beetles in the community significantly increased crop yield (Figure 4b; $t = 2.810$, df = 150, $p < 0.01$). The proportion of macropterous ground beetles, ground beetles with a preference for the vegetation stratum, or the proportion of spring breeding ground beetles in communities were not related to crop yield ($t < 0.224$, df = 150, $p < 0.823$).

Overall, the observed data did not contradict our a priori causal structure linking land-use intensity, pest control, and crop yield with the community-weighted mean values of the different traits (Body size: Figure 5a, Fisher's $C = 5.749$, df = 6, $p = 0.452$; Predatory: Figure 5b, Fisher's $C = 4.745$, df = 6, $p = 0.577$; Macropterous: Figure 5c, Fisher's $C = 6.634$, df = 6, $p = 0.356$; Vegetation: Figure 5d, Fisher's $C = 6.016$, df = 6, $p = 0.421$). We found no significant relationships between the proportion of spring breeding ground beetles in communities and the other variables.

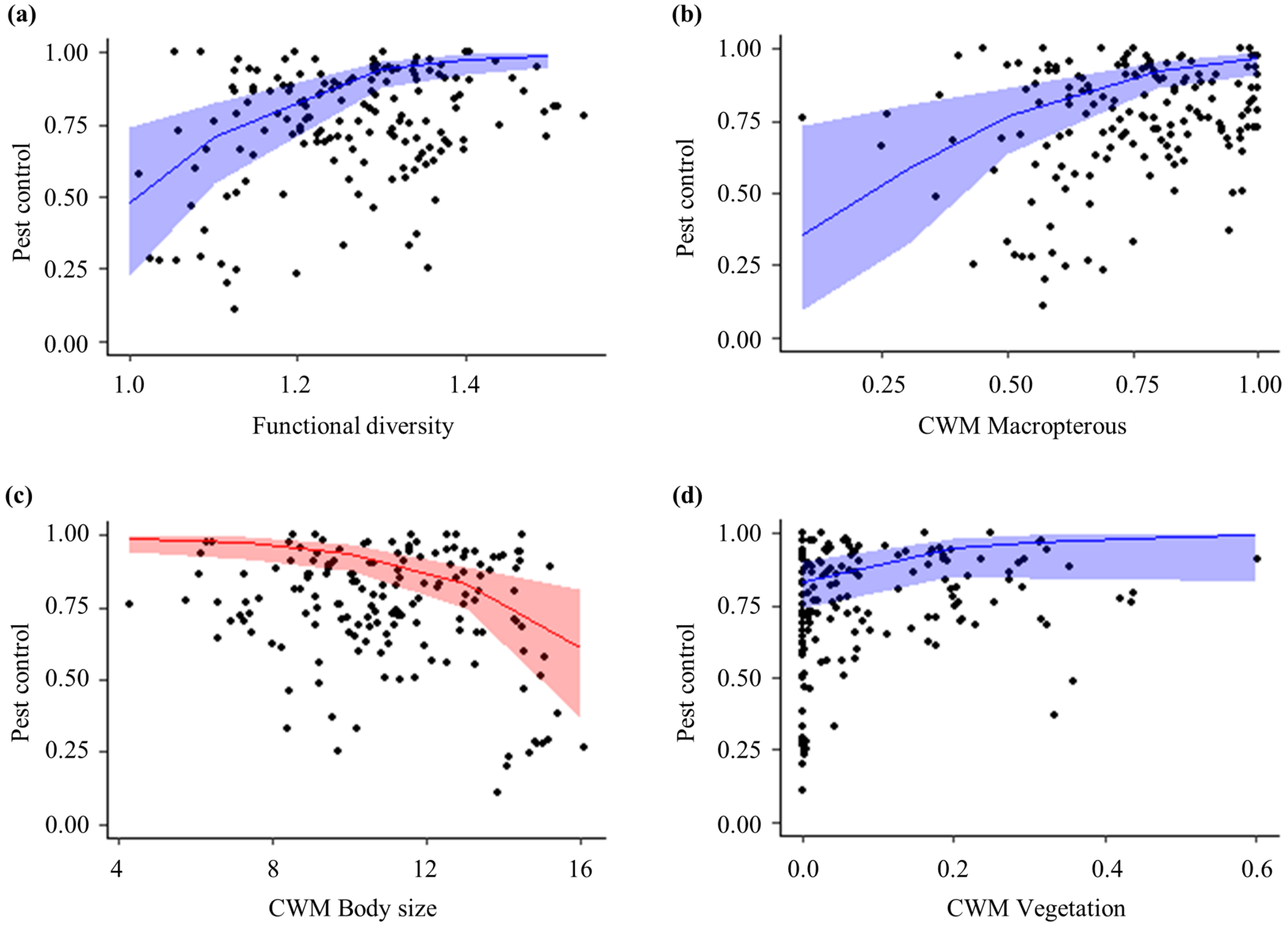

FIGURE 3 (a) The positive relationship between the functional diversity of ground beetles and pest control (measured as the percentage of removed aphids) ($p < 0.001$). (b) The positive relationship between the percentage of macropterous ground beetles and pest control ($p < 0.01$). (c) The negative correlation between the community-weighted mean (CWM) body size of ground beetles with pest control ($p < 0.01$). (d) The tendency of increased pest control of ground beetle communities with a higher proportion of beetles with a preference to live in the vegetation ($p < 0.1$).

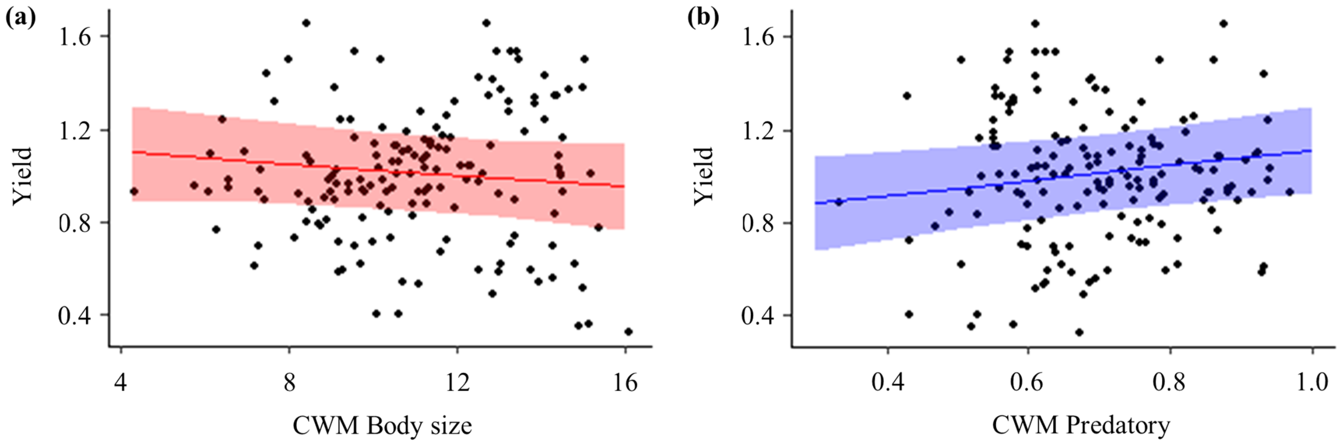

FIGURE 4 (a) The negative correlation between the community-weighted mean (CWM) body size of ground beetles and standardized crop yield ($p < 0.05$). (b) The positive relationship between the proportion of predatory ground beetles in communities and standardize crop yield ($p < 0.01$).

Fourth corner models

Relationships between local land-use intensity, the percentage of arable land in the surrounding landscape, pest control, or crop yield and respective trait levels differed between countries (see Appendix S1: Table S3). Body size was generally more strongly affected by local land-use intensity and by the percentage of arable land than the other traits, as indicated by the higher mean magnitude of coefficients for body size (Table 2). The body size of ground beetles also contributed more to the interaction of ground beetle communities with pest control as well as

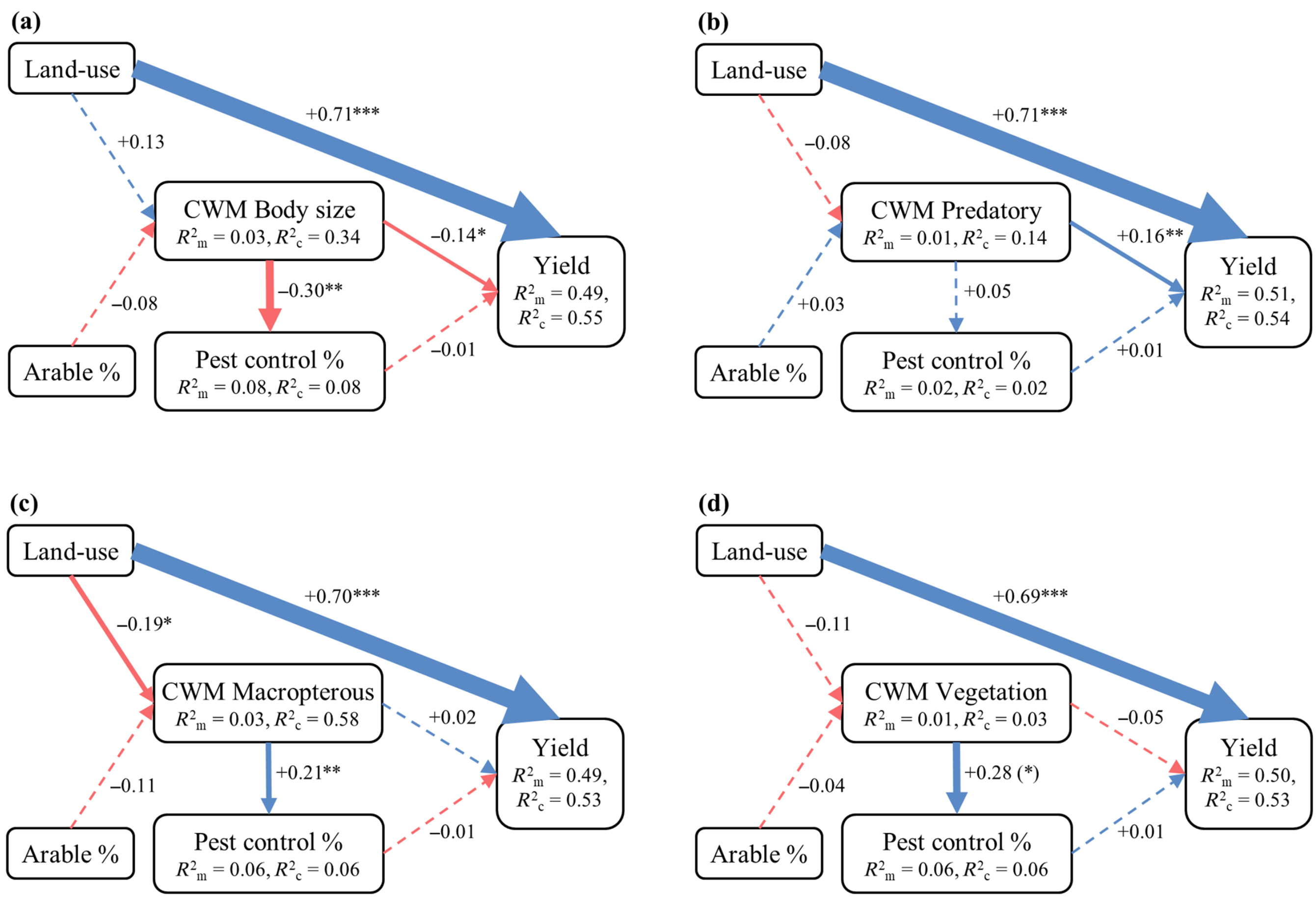

FIGURE 5 Structural equation models with local land-use intensity, the percentage of arable land in the landscape, the community-weighted mean (CWM) of (a) body size, (b) proportion of predatory ground beetles, (c) proportion of macropterous (high mobility), and (d) the proportion of ground beetles with a preference for the vegetation stratum. Marginal R^2-values (R^2_m) indicate the variation explained by fixed effects, conditional R^2-values (R^2_c) indicate the variation explained by fixed and random effects (country identity). Blue arrows indicate positive, red arrows negative correlations and the strength of arrows corresponds to standardized path coefficients (--- = ns, (*) $p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

TABLE 2 Summary of the mean magnitude of interaction coefficients (coef. ± SE) of each trait with local land-use intensity, the percentage of arable land in the landscape, pest control, and crop yield across the six regions.

Trait	Coef. land-use	Coef. arable %	Coef. pest control	Coef. yield
Body size	1.812 ± 0.892	2.717 ± 2.135	3.821 ± 2.544	1.702 ± 0.614
Trophic position	0.067 ± 0.018	0.106 ± 0.042	0.117 ± 0.026	0.081 ± 0.033
Mobility	0.143 ± 0.079	0.049 ± 0.014	0.118 ± 0.039	0.055 ± 0.014
Stratum	0.181 ± 0.106	0.170 ± 0.107	0.165 ± 0.079	0.145 ± 0.077
Phenology	0.065 ± 0.021	0.117 ± 0.013	0.053 ± 0.012	0.098 ± 0.033

Note: The consistently higher coefficients for body size for all target variables compared to the other traits (see Appendix S1: Table S3 for country-wise interaction coefficients).

crop yield compared to all other traits (Table 2). The relationship between the three body size classes of ground beetles and aphid removal (i.e., negative association with ground beetles larger than 24 mm) mirrors the relationship between community-weighted body size and pest control (Figure 3c**)** but indicates high variation between the study regions.

DISCUSSION

Besides the prominent positive land-use intensity-crop yield relationship, the proportion of macropterous beetles was the only functional aspect of ground beetle communities that were related to land-use intensity. Functional diversity, the proportion of macropterous ground beetles, and the proportion of ground beetles with a preference for the vegetation stratum were positively associated with pest control while a larger community-weighted mean body size reduced pest control. The community-weighted mean body size was negatively related to crop yield, whereas a higher proportion of predatory ground beetles resulted in higher crop yields. Our trait-specific analyses for the different regions revealed a heterogeneous pattern with specific response/effect-trait relationships being positive in one region but negative in another. Across all regions, the magnitude of the response of different taxa as well as their effect on pest control and yield, was more strongly influenced by body size than by other traits. Our results contrast with the general hypothesis that higher functional diversity of natural enemies improves pest control and thereby contributes to increased crop yield. While pest control was improved in communities with smaller, mobile ground beetles that climb up the vegetation, crop yield was higher in fields with a higher proportion of smaller, predatory ground beetles. Furthermore, these relationships were mainly driven by differences between the study regions instead of land-use intensity gradients within the region.

Impact of land-use intensity on the functional diversity of ground beetles

In contrast to our expectation, we did not detect an overall decline in the functional diversity of ground beetles with increasing land-use intensity. This is surprising, since our fields covered an extensive land-use intensification gradient ranging from organically managed farms (no synthetic fertilizer and no pesticides) up to heavily managed farms with a mean fertilizer input of 529 kg/ha (see Appendix S1: Table S1 for more information about the land-use intensity for the different countries). Previous studies demonstrated a decline in arthropod diversity with increasing local management intensity and also in landscapes with a higher proportion of arable land (Habel et al., 2019; Seibold et al., 2019). However, many of these studies originate from grasslands with relatively higher species richness. While plant species richness strongly decreases with land-use intensity in our crop fields (mainly driven by fertilizer application), the species richness of ground beetles was unaffected (Geiger et al., 2010). Species richness in our fields was already strongly reduced, with only a few disturbance-tolerant ground beetle species remaining (Winqvist et al., 2014). Alternatively, the relatively low sampling effort at the field scale resulting from the trade-off with the high number of farm scale replicates might have contributed to low species numbers. We suppose that current land-use intensity or a higher proportion of arable land in the landscape is no longer reducing the functional diversity of ground beetles because ground beetle species richness is already strongly diminished and source populations of species with rare trait combinations are lacking. Although our study design was targeted to maximize the regional land-use intensity gradient, the observed relationships with functional diversity were mainly due to regional differences rather than management differences between farms within regions (see marginal vs. conditional R^2 values in the structural equation models). The different European regions differed in management intensity with higher land-use intensity in Ireland (particularly N fertilizer and insecticide application) compared to the remaining regions (see Appendix S1: Table S1; Emmerson et al., 2016). In addition, weed control differed between countries with the highest herbicide application frequency in Germany while agricultural weeds were mostly mechanically controlled in the Netherlands and Poland (Emmerson et al., 2016). Both aspects and many more unquantified parameters (e.g., biogeographical differences between communities, or differences in climate and soil types) likely contributed to the region-specific trait responses and effects.

The proportion of macropterous ground beetles was the only community-weighted mean trait value that was related to land-use intensity. Macropterous ground beetles are more mobile than brachypterous beetles with reduced wings. The dispersal ability of organisms is a key response trait to land-use intensification or to other disturbances. More disturbed sites are often characterized by more highly mobile arthropods that can escape disturbance regimes or quickly re-colonize fields after disturbances (Entling et al., 2011). However, the direction of the relationship is difficult to interpret in such observational studies: for example, the proportion of macropterous ground beetles can be smaller in more intensively used fields because these mobile individuals were able to avoid disturbances during the sampling period. Alternatively, some macropterous ground beetles might prefer more natural habitats (e.g., they feed on seeds of weeds largely lacking in conventional fields; Griffiths et al., 2007).

We were surprised that we did not find a general decline in the community-weighted body size with increasing land-use intensity across our regions. Previous studies reported a decline in ground beetle body size (i.e., lower abundance of large species) with increased land-use intensity (Birkhofer et al., 2017; Simons et al., 2016; Winqvist et al., 2014). Although body size turned out to be the most important response trait, the direction of the land-use effects differed between the regions likely due to differences in management practices, land-use history, or other environmental factors.

Influence of functional diversity on pest control and yield

The diversity in trait levels was positively related to pest control potential. According to our predictions, complementarity in traits might lead to a more efficient use of resources. For example, the variation in body size and different trophic levels likely widen the spectrum of food sources. Differences in predator phenology likely contribute to the temporal continuity of top-down control. In addition, complementarity in predator traits can reduce predator–predator encounters, for instance, due to differences in the use of space (i.e., preference for different strata) and thus reduce intraguild interference. Despite the positive relationship between functional diversity and pest control, functional diversity did not increase crop yield. Both aphids and ground beetles might play only a minor role as pests and biological control agents in winter wheat. Indeed, the severity of aphids as pests is further mediated by the transmission of diseases (Dedryver et al., 2010). However, aphid predation by ground-living polyphagous predators has been shown to increase yield in spring barley (Östman et al., 2003). Our study also indicates that the functional diversity of ground beetles did not directly contribute to crop yield (e.g., via the control of other pest organisms) and was negligible in light of the stark positive influence of land-use intensity on crop yield.

The relationship between the community-weighted mean body size of generalist predators and pest control is difficult to predict (Segoli et al., 2023). Across the studied regions, a higher proportion of larger ground beetles (body size >24 mm) was negatively associated with the number of removed aphids. This contradicts assumptions at the individual level where larger beetles consume more prey and are thus expected to have a higher pest control potential (Bertleff et al., 2021; Brose et al., 2008). At the community level, however, interactions become more complex with the possibility of switching to other prey sources including conspecifics or other predators (i.e., cannibalism, intraguild interference, or predation; Polis et al., 1989; Staudacher et al., 2018). There is both theoretical and empirical evidence that in such size-structured food webs, larger predators tend to feed on other predators and thus dampen predator top-down control of prey (Schneider et al., 2012). Our findings confirm former studies detecting a decline in aphid predation with a higher proportion of larger ground beetles (Rusch et al., 2015). Our trait-specific analysis points in the same direction, with smaller body size classes (<24 mm), tending to be positively associated with pest control, while the largest body size trait category (>24 mm) indicated a negative relationship with pest control. However, the variation between the study regions was relatively large (see marginal vs. conditional R^2 in Figures 1 and 5a–d). Aphids are small prey, and larger ground beetles likely prefer larger prey or other predators for food (e.g., spiders; Rusch et al., 2015). However, it is difficult to obtain a good quantification of aphid predation in the field because predator-aphid interactions are complex (e.g., predators in the vegetation induce dropping behavior and increase aphid predation on the ground; Losey & Denno, 1998). Ideally, different methods of aphid quantification should be applied to achieve a more realistic estimation of pest control. Negative relationships between the community-weighted mean body size and yield but positive relationships between the proportion of predatory ground beetles and yield also point to the mechanism that mainly smaller predatory ground beetles contribute to pest control and yield. In comparison, larger ground beetles are often scavengers or herbivores and dampen the pest control potential of ground beetles. Although methods were identical across the regions, pitfall traps have been shown to overestimate densities of large-bodied ground beetles and data collected in this way should, therefore, be taken cautiously (Arneberg & Andersen, 2003). Further studies at the community level deploying methods that quantify true densities (e.g., quadrat sampling data), including different prey and predator taxa, are needed to test whether this is a general pattern or merely a study organism and method-specific result.

The positive relationship between the proportion of macropterous ground beetles in communities and pest control was also unexpected. This is most likely due to the strong negative correlation with the community-weighted mean body size and unrelated to the mobility of ground beetles. The proportion of ground beetles with a preference to climb up the vegetation was not correlated with the community-weighted mean body size and tended to improve pest control. This functional group of ground beetles typically gets in contact with aphids and feeds on them.

Response/effect-trait framework and consequences for ecological intensification

If traits that respond to land-use change are identical to traits that affect pest control and yield, we should be able to predict and manipulate land-use effects to improve ecosystem services (Lavorel & Garnier, 2002). Our results indicate that the body size of ground beetles is indeed a key trait (largest positive and negative effects across the different regions) regarding impacts of local and landscape-level land use on ground beetle communities, as well as influencing pest control and crop yield. Although body size is easy to measure and universally applicable to a wide range of organisms, the mechanisms of relationships with community-weighted body size are tricky to interpret because body size is often correlated with other traits such as physiological rates, dispersal ability, and trophic position (Gallé & Batáry, 2019). The simultaneous analysis of community-weighted means of various traits can help better understand which functional characteristics of communities are particularly favorable for ecosystem services. Nonetheless, lacking consistent land-use relationships with most community-weighted means across study regions makes it difficult to give management recommendations. Here, a reduction in land-use intensity did improve pest control of aphids by promoting macropterous ground beetles in local communities (see Figure 5c).

Similar to most of the analyzed traits, functional diversity was unrelated to local and landscape-level land-use intensity, and observed differences were due to differences between the regions. Differences in functional diversity between the different countries (i.e., lower in France and The Netherlands than in Sweden and Poland, see Appendix S1: Table S2) due to national land-use histories cannot easily be manipulated by short-term management changes. As the functional diversity of ground beetles was not directly influenced by land-use intensity across regions, the ability to improve functional diversity and ecosystem services of ground beetles by reducing local land-use intensity or the proportion of arable land in the landscape is questionable. This highlights the importance of alternative conservation or restoration measures to enhance functional diversity, such as existing or newly created semi-natural landscape elements (e.g., single-standing trees, hedges, or flowering strips). The diversification of crops and livestock would be another measure to potentially increase functional diversity (diversified farming systems, Kremen et al., 2012). Furthermore, organic farms or semi-natural habitats should be better connected at the landscape scale to enhance the mobility of organisms and establish larger populations (Tscharntke et al., 2012).

Conclusion

In our pan-European study, we found a positive relationship between the functional diversity of ground beetles and pest control as well as positive and negative relationships of community-weighted mean trait values with pest control and crop yield, respectively. Although the functional diversity of ground beetles increased the pest control potential, it did not significantly contribute to crop yield, which was strongly determined by local land-use intensity. The body size of ground beetles was the key trait mediating communities' response to land-use changes and effects on pest control and yield. However, a lack of relationships with land-use intensity, inconsistent relationships across the regions, and correlations among traits complicate simple management recommendations. Our results also question whether local ecological intensification can support pest control if biotic communities are already strongly diminished. Nonetheless, reducing land-use intensity can improve aphid control by favoring more mobile ground beetles. How land-use practices interact with intraguild interference (e.g., via the complexity of vegetation structure) in size-structured predator communities could be a promising research field to improve our ability to foster pest control of generalist predators. In addition, trait-based approaches in arthropods can still improve by measuring traits on the individuals found at the sites instead of inferring species traits from the literature. So far, larval stages of ground beetles (and of other holometabolic groups of insects) are largely ignored in functional land use and ecosystem functioning studies despite the fact that the larval life stage makes up the major portion of the total lifespan. This contribution focuses on the direct and indirect relationships of functional ground beetle diversity with pest control of aphids. To achieve a more holistic picture of the link between land use and ecosystem services, the interplay of multiple taxonomic groups and ecosystem functions needs to be included.

ACKNOWLEDGMENTS

We thank J. Bengtsson for the permission to reanalyze the AGRIPOPES data and to make the data sub-set used in this publication openly available. We are grateful to B. Utecht for compiling trait information on ground beetles. We thank B. Woodcock and an anonymous reviewer for insightful comments on an earlier version of the manuscript. This research was funded through the 2018–2019 BiodivERsA joint call for research proposals, under the BiodivERsA3 ERA-Net COFUND programme, and with the funding organizations Agence Nationale de la Recherche (ANR), Deutsche Forschungsgemeinschaft (DFG, reference number 662944), Environmental Protection Agency (EPA), 2019-NC-MS-11, National Science Centre (NCN, UMO-2019/32/Z/NZ8/00008) and Slovak Academy of Sciences (SAS, BiodivERsA3/2018/885/FunProd). Péter Batáry and Róbert Gallé were supported by the Hungarian National Research, Development and Innovation Office (NKFIH KKP 133839), and Péter Batáry by the Deutsche Forschungsgemeinschaft (DFG FIP 16/1). The project was hosted at sDiv, the synthesis center of iDiv, the German Centre for Integrative Biodiversity Research, and benefited from the services of sDiv, through the grant received from BiodivERsA. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Bucher et al., 2024) are available in Dryad at https://doi.org/10.5061/dryad.pc866t1zs.

ORCID

Roman Bucher https://orcid.org/0000-0002-3001-2876
Péter Batáry https://orcid.org/0000-0002-1017-6996
Julia Baudry https://orcid.org/0000-0002-7919-6039
Léa Beaumelle https://orcid.org/0000-0002-7836-8767
Andrea Čerevková https://orcid.org/0000-0002-9615-9870
Enrique G. de la Riva https://orcid.org/0000-0002-3393-8375
Tara Dirilgen https://orcid.org/0000-0001-9687-9651
Róbert Gallé https://orcid.org/0000-0002-5516-8623
Emmanuelle Kesse-Guyot https://orcid.org/0000-0002-9715-3534
Ewa Rembiałkowska https://orcid.org/0000-0002-4109-5486
Adrien Rusch https://orcid.org/0000-0002-3921-9750
Dara A. Stanley https://orcid.org/0000-0001-8948-8409
Werner Ulrich https://orcid.org/0000-0002-8715-6619
Klaus Birkhofer https://orcid.org/0000-0002-9301-2443

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Bucher, Roman, Péter Batáry, Julia Baudry, Léa Beaumelle, Andrea Čerevková, Enrique G. de la Riva, Tara Dirilgen, et al. 2024. "Functional Diversity of Ground Beetles Improved Aphid Control but Did Not Increase Crop Yields on European Farms." *Ecological Applications* e3035. https://doi.org/10.1002/eap.3035