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Inconsistent responses of carabid beetles and spiders to land-use intensity and landscape complexity in north-western Europe

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ABSTRACT

Reconciling biodiversity conservation with agricultural production requires a better understanding of how key ecosystem service providing species respond to agricultural intensification. Carabid beetles and spiders represent two widespread guilds providing biocontrol services. Here we surveyed carabid beetles and spiders in 66 winter wheat fields in four northwestern European countries and analyzed how the activity density and diversity of carabid beetles and spiders were related to crop yield (proxy for land-use intensity), percentage cropland (proxy for landscape complexity) and soil organic carbon content, and whether these patterns differed between dominant and non-dominant species. <17 % of carabid or spider species were classified as dominant, which accounted for >90 % of individuals respectively. We found that carabids and spiders were generally related to different aspects of agricultural intensification. Carabid species richness was positively related with crop yield and evenness was negatively related to crop cover. The activity density of non-dominant carabids was positively related with soil organic carbon content. Meanwhile, spider species richness and non-dominant spider species richness and activity density were all negatively related to percentage cropland. Our results show that practices targeted to enhance one functionally important guild may not promote another key guild, which helps explain why conservation measures to enhance natural enemies generally do not ultimately enhance pest regulation. Dominant and non-dominant species of both guilds showed mostly similar responses suggesting that management practices to enhance service provisioning by a certain guild can also enhance the overall diversity of that particular guild.

1. Introduction

In Europe, farming and biodiversity conservation have always been tightly interlinked (Batáry et al., 2015). Over the course of thousands of years of traditional extensive farming practices, many species have adapted to human disturbance and have even come to depend on agricultural habitats (Sutcliffe et al., 2015). However, the intensification of agriculture with high inputs of anthropogenic chemicals and homogenization of agricultural landscapes has negatively impacted farmland biodiversity and currently threatens many species (Goulson et al., 2015; Gámez-Virués et al., 2015; Emmerson et al., 2016; Dainese et al., 2019). Recent attempts to make modern farming more sustainable, such as ecological intensification (Bommarco et al., 2013), rely on promoting the ecosystem services provided by communities of species that occur naturally on farmland. More diverse communities of service-providing organisms often provide higher levels of services as different species occupy different niches and complement each other (Letourneau et al., 2009; Ollerton, 2017; Dainese et al., 2019; Snyder, 2019). Furthermore,

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higher evenness of functional groups can also promote service provisioning because more even communities occupy each niche more completely (Crowder et al., 2010; Aldebron et al., 2020; Yuan et al., 2019, but see Dainese et al., 2019). Maintaining high biodiversity levels on farms could thus serve both biodiversity conservation and ecosystem service provisioning, thereby potentially making agricultural production more sustainable (Tscharntke et al., 2012).

However, Kleijn et al. (2011) argued that the species providing most of the services to farming are different species than the species that are threatened in their existence. Different management practices are therefore required when aiming at enhancing ecosystem service provisioning or conserving rare species. For example, crop pollination is mainly provided by a relatively small set of dominant bee species, while the contribution of threatened bee species is negligible (Kleijn et al., 2015; Winfree et al., 2015). These dominant crop pollinators are generally robust to land-use change, being able to persist even in intensively managed agricultural landscapes, and can relatively easily be promoted by generic, local-scale conservation measures (Kleijn et al., 2015). In contrast, non-dominant or rare bee species are often more susceptible to agricultural intensification and loss of semi-natural habitats (Fijen et al., 2019; Harrison et al., 2019), and the conservation of these species typically requires more targeted conservation measures and landscape-scale approaches (Pywell et al., 2012; Senapathi et al., 2015).

While in recent years our understanding of how dominant and non-dominant crop pollinating species respond to environmental change has greatly advanced, we know much less about this for natural enemies that provide pest control services, another key ecosystem service to crops (Bianchi et al., 2006; Losey and Vaughan, 2006). As far as we know, very limited studies have examined whether dominant and non-dominant natural enemies respond differently to environmental drivers. To date, most studies have focused on responses in richness and abundance of the entire species pool with only a small proportion of studies distinguishing between rare and common species or generalist and specialist species (Desender and Bosmans, 1998; Niemelä, 2001; Desender et al., 2010).

Predatory natural enemies generally come from a wider range of different arthropod orders and families (e.g. beetles, wasps, lacewings, hoverflies and spiders) and have more variation in life history traits than pollinators. This can partly explain the lack of a general framework for landscape and local scale drivers of natural enemy diversity or abundance (Karp et al., 2018; Martin et al., 2019; Mei et al., 2021). For example, while many natural enemies are positively related to landscape-scale cover of semi-natural habitat (Chaplin-Kramer et al., 2011), some species groups (e.g. coccinellid beetles and spiders) have been shown to be positively related to cover of cropland (Rand and Tscharntke, 2007). Even species within the same taxon but with different ecological traits can display different response patterns. For instance, Duan et al. (2019) found that ground-hunting spiders and predatory carabids were more sensitive to the decline of the area of suitable habitats than aerial dispersing spiders and small-sized omnivorous carabids. Furthermore, species groups could be differently affected by local land-use intensity as well, as illustrated by spiders and carabid beetles responding negatively to fertilizer application but staphylinid beetles responding positively (Gagic et al., 2017; Mei et al., 2021). Within species groups, local land-use intensity could also alter species evenness, as for example shown by Li et al. (2018) who found that higher total nitrogen input decreased the species richness of spiders while total abundance was unaffected, resulting in spider assemblages being more dominated by a small subset of species.

Effects of local land-use intensity and landscape composition can furthermore be moderated by local soil characteristics. Soils with high organic matter content can provide alternative food resources when prey levels in the crop are low, thereby supporting more stable populations of natural enemies (Birkhofer et al., 2008; Aguilera et al., 2021). High soil organic matter also helps to shape complex soil structure (Bulluck III et al., 2002), which potentially provides more spatial niches for natural enemies. By providing these additional resources, fields with high soil organic matter content can therefore mitigate the negative effects of on-field management and landscape simplification on natural enemies (Riggi and Bommarco, 2019; Redlich et al., 2021). However, to date little is known about how landscape complexity, land-use intensity and soil organic matter jointly shape natural enemy communities on agricultural fields, and whether responses differ for dominant and non-dominant species, hindering the design of more targeted conservation strategies.

Here we used data on natural enemy communities in 66 paired winter wheat fields in four northwestern European countries (Germany, the Netherlands, Sweden and United Kingdom) to investigate the response of natural enemy communities to landscape complexity, local land-use intensity and soil organic matter content, and specifically examined whether and how responses differ between dominant and non-dominant species. We focused on carabid beetles and spiders as they represent the two groups of natural enemies in arable fields in northwestern European and are widely used as bioindicators (Lang et al., 1999; Borchard et al., 2014). We used pitfall traps to collect carabids and spiders in field pairs that covered a gradient in land-use intensity and landscape complexity, with fields within pairs having contrasting soil organic carbon content. We asked 1) how activity density, species richness and evenness of total carabid beetles and spiders are related to local land-use intensity and landscape complexity; 2) whether these relationships are affected by different soil organic carbon content, and 3) whether the response patterns differ between dominant and non-dominant species.

2. Methods

2.1. Experimental design

In 2014, we selected eight pairs of winter wheat fields in the Netherlands, Sweden and United Kingdom and nine pairs in Germany, resulting in 33 pairs in total. The sites were a subset of the data used by Gagic et al. (2017) for which we were able to obtain species level data of carabid beetles and spiders. All of the fields were conventionally managed. The paired fields were selected to have contrasting levels of soil organic carbon, resulting from differences in management history such as use of organic or mineral fertilizers as well as different crop rotation or tillage practices, the fields within a pair were selected to have similar landscape complexity and soil condition (e.g. pH and soil texture) as far as possible. Except in the Netherlands, field sites were closer to their paired field than to fields in other pairs (Table S1). Due to high soil variability in the Netherlands, to ensure pairs had matching soil type and local landscape context, it was not always possible to pair fields geographically, thus all fields were located in a single study region. We took soil samples to validate that soil organic carbon (SOC) content levels differed within field pairs. In each field, we randomly collected five soil samples at a distance of 5–8 m from the crop edge before the first fertilizer application by farmers which were then pooled and mixed. Mean SOC content in Germany was 1.63 % (SD ± 1.03) for high sites and 1.20 % (SD ± 0.49) for low sites; the Netherlands, averaged 2.00 % (SD ± 0.23) in high sites and 1.39 % (SD ± 0.30) in low sites; in Sweden, high sites had 4.44 % (SD ± 1.11) SOC and low sites 2.90 % (SD ± 0.42); in the United Kingdom, high sites had 1.48 % (SD ± 0.57) and low sites 1.05 % (SD ± 0.30). Because the differences between paired high and low SOC content sites turned out to be relatively small, for this study we decided to include SOC content as a continuous variable rather than a factorial one.

The field pairs were selected across a gradient in landscape complexity, estimated as the percentage of cropland within a 1-km radius around each study field. The percentage of cropland is often used to quantify landscape complexity and is generally negatively correlated with it (Rusch et al., 2016; Martin et al., 2019).

In each field, we selected a study plot that was at least 12 × 14 m in size, with the longer side bordering a field boundary, and at least 10 m away from the nearest field corner. Within each pair, the field boundary characteristics were selected to be similar (e.g. to avoid that one field had a field boundary with a high plant richness while the other field had a field boundary with low plant richness). One of the objectives of the original study was to experimentally examine the impacts of fertilizer and pesticide applications (Gagic et al., 2017). For this purpose, each plot was subdivided into four subplots to which four treatments were randomly assigned: all combinations of presence or absence of the experimental application of insecticides and fertilizers. Insecticides were pyrethroid (broad spectrum) and applied once by using backpack sprayers in May in Germany, the Netherlands and Sweden and in June in the United Kingdom. Fertilizers were ammonium nitrate based and were applied three times in Germany and the UK, twice in Sweden and once in the Netherlands. Insecticides and fertilizers were applied by project members and were consistent with the typical type, amount and frequency within each country and in accordance with local recommended rates (Table S1). Farmers were allowed to use herbicides and fungicides in the treatment plots.

We used wheat yield as an indicator of local land-use intensity as this represents the end result of all short- and long-term management practices (Dietrich et al., 2012; Gabriel et al., 2013; Winqvist et al., 2014). Wheat was manually harvested in four randomly located subplots of 0.25 m^2 each. The harvested grains were air dried to approximately 14 % moisture content and then weighted, expressed as grain dry weight per hectare (t/ha).

2.2. Surveying ground-dwelling arthropods

Pitfall traps (polypropylene beakers 155 mm high and 95 mm across) were used to survey ground-dwelling arthropods during the wheat flowering season (late May to early June). We placed one pitfall trap in the center of each treatment subplot at least 10 m from the field edge and filled it with 200 mL of a mixed solution of 2/3 water and 1/3 glycol and a drop of detergent to lower surface tension. A square aluminum plate was placed approximately 10 cm above each pitfall trap to prevent flooding by rain. Pitfall traps were opened for 10 days. All of the collected arthropods were stored in 70 % ethanol solution for later identification. For the purpose of our study, the two most abundant species groups, carabid beetles (Carabidae) and adult spiders (Araneae), were selected as our bioindicators and they were counted and identified to species level using standard keys (Hackston, 2020; Nentwig et al., 2021). We determined the diet preference of each carabid beetle species based on Larochelle (1990) and the hunting strategy of all observed spider species based on Cardoso et al. (2011) following Gallé et al. (2019). Furthermore, because the arthropod communities will inevitably differ in composition between countries, we classified the carabids or spiders as *nationally* dominant and non-dominant species based on whether species made up respectively more or less than 5 % of the total number of individuals caught of each species group in a country following Kleijn et al. (2015).

2.3. Statistical analyses

All analyses were performed using R version 4.2.0 (R Core Team, 2022). Since the focus of our study was on across-field effects of land-use intensity, not on the subplot-scale effects of the different experimental management treatments (which had already been examined by Gagic et al., 2017), we pooled the collected carabid beetles and spiders over the different treatments and we averaged the wheat yield across all four treatments per field to use it as indicator of local land-use intensity. Because each field had been subjected to the same combination of treatments and earlier analyses showed that the effects of these treatments on carabid beetle and spider activity density were generally not influenced by the environmental variables (Appendix 3 of Gagic et al., 2017), we are confident that pooling the samples didn't affect the relationships of the environmental variables across fields.

Our response variables included activity density, species richness and evenness of all carabid beetles and spiders, and activity density and species richness of dominant and non-dominant carabids and spiders respectively. We calculated E_{var} index based on the observed number of individuals to describe the community evenness, this index is independent from species richness thus measured the true evenness of each site and suitable for meta-analysis (Smith and Wilson, 1996). E_{var} ranges from 0 (maximally uneven) to 1 (perfectly even). Evenness was only calculated for sites with >5 individuals, as evenness values for sites with fewer individuals are not very reliable and have strong influence on response patterns. Our explanatory variables included wheat yield as an indicator of land-use intensity, percentage cropland as an indicator of landscape complexity and SOC content. We used an information theoretic approach, with which we can assess the relative importance of explanatory variables based on a candidate set of best models. For landscape-scale studies that examine multiple hypotheses simultaneously, this is generally preferred over inferring significant relationships with explanatory variables from a single best model (Grueber et al., 2011) and the information theoretic approach is now becoming rapidly accepted as a more robust approach for many kinds of complex ecological studies (e.g., Knapp et al., 2022; Bishop et al., 2023). First, generalized linear mixed models (GLMM, package glmmTMB; Magnusson et al., 2017) with the appropriate error distribution and link function for each response variable were constructed (Table 1). To be able to generalize observed patterns within countries, we mean-centered SOC, wheat yield and proportion of cropland within each country (van de Pol and Wright, 2009). The within-country centered explanatory variables were subsequently scaled (centered data divided by two standard deviations) across the entire dataset as this would allow us to use the effect sizes of predictors to compare their relative importance (using R package 'standardize'; Eager, 2021). For each response variable, we constructed a global model containing the three standardized explanatory variables and all their two-way interactions as fixed factors and field pair nested in country as random factors. To check for multicollinearity of explanatory variables, we calculated variance inflation factors (VIF; Draper and Smith, 1998) of all full models. The highest VIF was 1.05, which is well below the threshold of 3 (Zuur et al., 2007). Next, for each response variable we constructed an all-subsets model set consisting of all possible combinations of the fixed factors and their two-way interactions, using the function "dredge" from the R package MuMIn (Bartoń, 2020). We first ranked the models in the model set based on their Akaike Information Criterion values corrected for small sample size (AICc) and calculated full-model averaged parameter estimates and parameter weights (or variable importance; i.e. the probability that a given explanatory variable appears in the most appropriate model) based on all models with Δ AICc < 2 (Burnham et al., 2011). The best supported relationships (based on variable importance and the confidence interval of the effect size not overlapping zero) were visualized using R package "visreg" (Breheny and Burchett, 2020).

3. Results

Overall, we collected 3284 carabid beetles belonging to 63 species and 2730 adult spiders belonging to 71 species and 15 families. Carabid beetle activity density was highest in Sweden (2106 individuals belonging to 36 species), followed by Germany (485 individuals and 29 species), United Kingdom (456 and 20) and the Netherlands (237 and 18) (Table 2). Adult spider activity density was highest in Germany (1237 individuals and 50 species), followed by Sweden (1066 and 39), the Netherlands (288 and 14) and the United Kingdom (139 and 19) (Table 3).

Across all countries, 9 carabid beetle species and 12 spider species were classified as nationally dominant, and these species accounted for respectively 90.3 % and 91.0 % of all collected carabid and spider specimens. The majority of the nationally dominant species occurred in

Table 1

Results for generalized linear mixed models examining the effects of soil organic carbon content (SOC), proportion of cropland within 1-km radius (Lcrop), crop yield (Yield) and their interactions on diversity of carabids and spiders. Model averaged parameter estimates (β) and 95 % confidence intervals (95 % CI) are given for each explanatory variable included in the candidate set of best models (ΔAICc <2, Table S2), predictors with confidence intervals not overlapping zero are indicated in bold. Relative importance (ω, sum of model weights including that predictor) of each predictor is given. Distribution and link function of GLMMs: G, Gaussian distribution with identity link function; P, Poisson distribution with log link function; NB, negative binomial distribution with log link function; zero-inflated, models with zero inflation.

Guild	Group	Diversity index	Distribution and link function	Predictor	β	95 % CI	ω
Carabids	Total	Activity density	NB	(Intercept)	3.448	2.626 to 4.270	–
				SOC	0.203	−0.468 to 0.874	0.43
				Lcrop	0.193	−0.302 to 0.688	0.53
				Yield	0.016	−0.157 to 0.189	0.10
				SOC × Lcrop	−0.282	−1.508 to 0.944	0.21
		Species richness	P	(Intercept)	1.767	1.285 to 2.250	–
				SOC	0.125	−0.130 to 0.379	0.65
				Lcrop	−0.021	−0.143 to 0.101	0.21
				Yield	**0.228**	**0.030 to 0.426**	**1**
		Evenness	G	(Intercept)	0.527	0.471 to 0.584	–
				SOC	0.071	−0.060 to 0.202	1
				Lcrop	**−0.097**	**−0.175 to − 0.018**	**1**
				SOC × Lcrop	0.129	−0.140 to 0.398	0.61
	Dominant	Activity density	NB	(Intercept)	3.145	2.278 to 4.011	–
				SOC	0.173	−0.487 to 0.834	0.29
				Lcrop	0.312	−0.327 to 0.951	0.66
				SOC × Lcrop	−0.456	−2.066 to 1.154	0.29
		Species richness	G	(Intercept)	3.080	1.919 to 4.241	–
				Yield	0.372	−0.368 to 1.112	0.63
	Non-dominant	Activity density	NB	(Intercept)	1.797	1.097 to 2.498	–
				SOC	**0.675**	**0.122 to 1.228**	**1**
				Lcrop	−0.020	−0.234 to 0.194	0.35
				SOC × Lcrop	−0.337	−1.407 to 0.733	0.35
		Species richness	P	(Intercept)	1.079	0.528 to 1.629	–
				SOC	0.261	−0.146 to 0.668	0.76
				Lcrop	−0.041	−0.251 to 0.168	0.25
				Yield	0.131	−0.196 to 0.459	0.53
Spiders	Total	Activity density	NB	(Intercept)	3.403	2.597 to 4.209	–
				Lcrop	−0.134	−0.488 to 0.220	0.52
				Yield	−0.117	−0.423 to 0.189	0.55
				Lcrop × Yield	−0.279	−1.105 to 0.547	0.36
		Species richness	G	(Intercept)	7.812	4.111 to 11.513	–
				Lcrop	**−2.638**	**−4.048 to -1.227**	**1**
				Yield	−0.236	−1.0.301 to 0.829	0.51
				Lcrop × Yield	−0.940	−4.110 to 2.231	0.32
		Evenness	G	(Intercept)	0.578	0.470 to 0.686	–
				SOC	0.038	−0.065 to 0.141	0.51
				Yield	−0.0002	−0.033 to 0.032	0.18
				SOC × Yield	0.031	−0.113 to 0.175	0.18
	Dominant	Activity density	NB	(Intercept)	3.204	2.477 to 3.932	–
				Lcrop	−0.049	−0.299 to 0.200	0.27
				Yield	−0.134	−0.488 to 0.219	0.56
				Lcrop × Yield	−0.242	−1.101 to 0.616	0.27
		Species richness	G (zero-inflated)	(Intercept)	3.881	2.962 to 4.799	–
				Lcrop	−0.285	−0.900 to 0.331	0.61
				Yield	−0.284	−0.875 to 0.307	0.63
				Lcrop × Yield	−0.140	−0.903 to 0.623	0.17
	Non-dominant	Activity density	NB	(Intercept)	1.548	0.373 to 2.723	–
				SOC	−0.061	−0.366 to 0.244	0.22
				Lcrop	**−0.594**	**−0.982 to 0.206**	**1**
				Yield	−0.045	−0.296 to 0.206	0.58
				Lcrop × Yield	−0.531	−1.605 to 0.542	0.58
		Species richness	P	(Intercept)	1.041	0.140 to 1.942	–
				Lcrop	**−0.433**	**−0.676 to -0.190**	**1**

all countries (Tables 2 and 3). *Pterostichus melanarius*, which was the second most frequently observed carabid species across four countries, was classified as a dominant species in all four countries and accounted for 20.8 % of all observed carabid individuals. *Anchomenus dorsalis* and *Poecilus cupreus* were dominant species in three countries and accounted for 14.9 % and 13.8 % of all individuals respectively. Six out of nine dominant carabid species were carnivorous and the other three species were omnivorous; none of the dominant carabids were herbivorous. Of the twelve spider species that were dominant in at least one country, none was dominant in all four countries. However, *Erigone atra* and *Pardosa palustris* were dominant species in three countries, with relative activity density of 6.9 % and 5.9 %, respectively. Nine dominant species of spiders were active hunters and the remaining three were web builders.

Total carabid species richness in wheat fields was best explained by crop yield (variable importance $\omega = 1.00$), with species richness increasing with crop yield (model-averaged coefficient $\beta = 0.228$; Table 1; Fig. 1a). There was little support for relationships between total carabid beetle activity density and any of the explanatory variables (the candidate set of models that were within Δ AICc < 2 of the best models included the intercept-only model which indicates that none of the explanatory variables makes a meaningful contribution to explaining the response variable; Table S2), but total carabid beetle evenness was negatively related to the percentage cropland in a 1 km radius ($\beta =$

Table 2
Species list of carabid beetles in Germany (GE), the Netherlands (NL), Sweden (SE) and the United Kingdom (UK). Diet preference of each species is presented. Species that were classified as dominant in at least one country (>5 % of total abundance in each country) are shown in bold.

Species no.	Species	Diet preference	GE	NL	SE	UK	Sum
1	***Trechus secalis***	carnivore	0	0	**745**	1	746
2	***Pterostichus melanarius***	omnivore	**87**	**50**	**434**	**112**	683
3	***Anchomenus dorsalis***	carnivore	**147**	3	**203**	**136**	489
4	***Poecilus cupreus***	carnivore	**52**	**129**	**270**	1	452
5	***Bembidion lampros***	carnivore	11	10	**137**	18	176
6	***Trechus quadristriatus***	carnivore	**71**	0	45	**41**	157
7	***Nebria brevicollis***	omnivore	0	0	2	**94**	96
8	***Pseudophonus rufipes***	omnivore	**32**	0	42	19	93
9	***Agonum muelleri***	carnivore	0	**12**	30	0	42
10	*Clivina fossor*	omnivore	0	7	35	0	42
11	*Demetrias atricapillus*	omnivore	0	0	30	10	40
12	*Amara similata*	omnivore	1	0	25	0	26
13	*Calathus fuscipes*	carnivore	13	0	4	5	22
14	*Bembidion obtusum*	omnivore	4	1	16	0	21
15	*Loricera pilicornis*	carnivore	16	1	1	2	20
16	*Harpalus affinis*	herbivore	5	8	6	0	19
17	*Carabus granulatus*	carnivore	1	1	14	0	16
18	*Amara plebeja*	omnivore	0	0	14	0	14
19	*Zabrus tenebrioides*	carnivore	12	0	0	0	12
20	*Microlestes minutulus*	carnivore	8	0	0	0	8
21	*Stomis pumicatus*	omnivore	3	0	5	0	8
22	*Patrobus atrorufus*	herbivore	0	4	4	0	8
23	*Carabus nemoralis*	carnivore	0	0	8	0	8
24	*Pterostichus niger*	carnivore	0	0	8	0	8
25	*Brachinus crepitans*	omnivore	7	0	0	0	7
26	*Notiophilus aquaticus*	carnivore	0	0	6	0	6
27	*Pterostichus strenuus*	carnivore	0	0	5	0	5
28	*Amara ovata*	omnivore	1	1	0	2	4
29	*Nebria salina*	omnivore	0	0	0	4	4
30	*Badister bullatus*	carnivore	1	0	0	2	3
31	*Bembidion femoratum*	omnivore	0	3	0	0	3
32	*Pterostichus vernalis*	carnivore	0	3	0	0	3
33	*Amara lunicollis*	omnivore	0	0	3	0	3
34	*Amara aulica*	omnivore	2	0	0	0	2
35	*Calathus ambiguus*	carnivore	2	0	0	0	2
36	*Notiophilus biguttatus*	carnivore	1	0	0	1	2
37	*Poecilus versicolor*	carnivore	0	1	1	0	2
38	*Amara familiaris*	omnivore	0	0	2	0	2
39	*Bembidion aeneum*	omnivore	0	0	2	0	2
40	*Notiophilus aesthuans*	carnivore	0	0	2	0	2
41	*Calathus micropterus*	carnivore	0	0	0	2	2
42	*Laemostenus terricola*	omnivore	0	0	0	2	2
43	*Leistus fulvibarbis*	omnivore	0	0	0	2	2
44	*Asaphidion flavipes*	carnivore	1	0	0	0	1
45	*Brachinus explodens*	carnivore	1	0	0	0	1
46	*Diachromus germanus*	herbivore	1	0	0	0	1
47	*Harpalus rubripes*	herbivore	1	0	0	0	1
48	*Harpalus tardus*	omnivore	1	0	0	0	1
49	*Molops piceus*	carnivore	1	0	0	0	1
50	*Ophonus azureus*	carnivore	1	0	0	0	1
51	*Poecilus lepidus*	carnivore	1	0	0	0	1
52	*Bembidion monticola*	omnivore	0	1	0	0	1
53	*Bembidion quadrimaculatum*	carnivore	0	1	0	0	1
54	*Harpalus latus*	omnivore	0	1	0	0	1
55	*Amara communis*	omnivore	0	0	1	0	1
56	*Bembidion guttula*	herbivore	0	0	1	0	1
57	*Harpalus quadripunctatus*	herbivore	0	0	1	0	1
58	*Harpalus smaragdinus*	herbivore	0	0	1	0	1
59	*Ophonus rufibarbis*	herbivore	0	0	1	0	1
60	*Pterostichus oblongopunctatus*	omnivore	0	0	1	0	1
61	*Synuchus vivalis*	carnivore	0	0	1	0	1
62	*Amara equestris*	herbivore	0	0	0	1	1
63	*Pterostichus madidus*	carnivore	0	0	0	1	1
	Total		485	237	2106	456	3284

−0.097; Fig. 1b). Additionally, carabid beetle evenness tended to increase with increasing SOC content ($\beta = 0.071$; $\omega = 1.00$), but the 95 % confidence interval of the model averaged coefficient overlapped zero (Table 1). There was strong support for a positive relationship between SOC content and the activity density of non-dominant carabid species ($\beta = 0.675$; Fig. 1c).

Species richness of all spiders and non-dominant spider species richness and activity density were all strongly negatively related to the proportion of cropland within a 1 km radius (Table 1; Fig. 1d,e,f). There was little support for any of the explanatory variables being related to the activity density of all spiders (the 95 % confidence intervals of all model averaged coefficients overlapped zero and the candidate model set that were within Δ AICc < 2 of the best model included the intercept-only model; Table S2). This mainly reflected the lack of response of the

Table 3
Species list of spiders in Germany (GE), the Netherlands (NL), Sweden (SE) and the United Kingdom (UK). Family and hunting strategy of each species are presented. Species that were classified as dominant in at least one country (>5 % of total abundance in each country) are shown in bold.

Species No.	Species	Family	Hunting strategy	GE	NL	SE	UK	Sum
1	***Oedothorax apicatus***	Linyphiidae	active hunter	**602**	2	**178**	5	787
2	***Pardosa prativaga***	Lycosidae	active hunter	12	**40**	**257**	4	313
3	***Pachygnatha degeeri***	Tetragnathidae	web builder	48	4	**185**	**31**	268
4	***Erigone atra***	Linyphiidae	active hunter	**70**	**19**	**94**	5	188
5	***Agyneta rurestris***	Linyphiidae	web builder	**146**	0	21	1	168
6	***Pardosa palustris***	Lycosidae	active hunter	17	**35**	**88**	**22**	162
7	***Trochosa ruricola***	Lycosidae	active hunter	53	**58**	23	**11**	145
8	***Pardosa agrestis***	Lycosidae	active hunter	44	**84**	5	6	139
9	***Bathyphantes gracilis***	Linyphiidae	web builder	14	0	**62**	**20**	96
10	***Erigone dentipalpis***	Linyphiidae	active hunter	**88**	0	6	0	94
11	***Pardosa amentata***	Lycosidae	active hunter	6	**38**	38	0	82
12	*Tenuiphantes tenuis*	Linyphiidae	web builder	32	0	14	2	48
13	***Pardosa pullata***	Lycosidae	active hunter	1	2	17	**22**	42
14	*Porrhomma microphthalmum*	Linyphiidae	web builder	7	0	17	0	24
15	*Drassyllus lutetianus*	Gnaphosidae	active hunter	10	0	7	1	18
16	*Diplostyla concolor*	Linyphiidae	web builder	11	0	3	0	14
17	*Pardosa lugubris*	Lycosidae	active hunter	12	0	0	0	12
18	*Mermessus trilobatus*	Linyphiidae	active hunter	10	0	0	2	12
19	*Robertus arundineti*	Theridiidae	web builder	0	0	10	0	10
20	*Micrargus subaequalis*	Linyphiidae	active hunter	4	0	4	0	8
21	*Porrhomma convexum*	Linyphiidae	web builder	0	0	7	0	7
22	*Micaria pulicaria*	Gnaphosidae	active hunter	2	0	2	2	6
23	*Xysticus ulmi*	Thomisidae	active hunter	0	1	3	1	5
24	*Argenna subnigra*	Dictynidae	active hunter	4	0	0	0	4
25	*Drassyllus pusillus*	Gnaphosidae	active hunter	3	0	1	0	4
26	*Araeoncus humilis*	Linyphiidae	active hunter	2	0	2	0	4
27	*Pisaura mirabilis*	Pisauridae	web builder	1	2	1	0	4
28	*Clubiona reclusa*	Clubionidae	active hunter	0	0	4	0	4
29	*Xysticus kochi*	Thomisidae	active hunter	3	0	0	0	3
30	*Zodarion italicum*	Zodariidae	specialist	3	0	0	0	3
31	*Pachygnatha clercki*	Tetragnathidae	web builder	2	0	1	0	3
32	*Pardosa paludicola*	Lycosidae	active hunter	0	0	3	0	3
33	*Haplodrassus minor*	Gnaphosidae	active hunter	2	0	0	0	2
34	*Walckenaeria atrotibialis*	Linyphiidae	active hunter	2	0	0	0	2
35	*Aulonia albimana*	Lycosidae	active hunter	2	0	0	0	2
36	*Pardosa riparia*	Lycosidae	active hunter	2	0	0	0	2
37	*Xerolycosa miniata*	Lycosidae	active hunter	2	0	0	0	2
38	*Neottiura bimaculata*	Theridiidae	web builder	2	0	0	0	2
39	*Zodarion rubidum*	Zodariidae	specialist	2	0	0	0	2
40	*Phrurolithus festivus*	Phrurolithidae	active hunter	1	0	1	0	2
41	*Oedothorax fuscus*	Linyphiidae	active hunter	1	0	0	1	2
42	*Alopecosa accentuata*	Lycosidae	active hunter	1	0	0	1	2
43	*Oedothorax retusus*	Linyphiidae	Active hunter	0	0	2	0	2
44	*Histopona torpida*	Agelenidae	web builder	1	0	0	0	1
45	*Drassodes pubescens*	Gnaphosidae	active hunter	1	0	0	0	1
46	*Drassyllus praeficus*	Gnaphosidae	active hunter	1	0	0	0	1
47	*Haplodrassus signifer*	Gnaphosidae	active hunter	1	0	0	0	1
48	*Trachyzelotes pedestris*	Gnaphosidae	active hunter	1	0	0	0	1
49	*Hahnia nava*	Hahniidae	web builder	1	0	0	0	1
50	*Bathyphantes parvulus*	Linyphiidae	web builder	1	0	0	0	1
51	*Pocadicnemis juncea*	Linyphiidae	active hunter	1	0	0	0	1
52	*Porrhomma errans*	Linyphiidae	web builder	1	0	0	0	1
53	*Phrurolithus minimus*	Phrurolithidae	active hunter	1	0	0	0	1
54	*Sibianor tantulus*	Salticidae	active hunter	1	0	0	0	1
55	*Asagena phalerata*	Theridiidae	web builder	1	0	0	0	1
56	*Ozyptila claveata*	Thomisidae	active hunter	1	0	0	0	1
57	*Eratigena picta*	Agelenidae	web builder	0	1	0	0	1
58	*zygiella x-notata*	Araneidae	web builder	0	1	0	0	1
59	*Prinerigone vagans*	Linyphiidae	active hunter	0	1	0	0	1
60	*Ceratinella scabrosa*	Linyphiidae	active hunter	0	0	1	0	1
61	*Diplocephalus latifrons*	Linyphiidae	active hunter	0	0	1	0	1
62	*Dismodicus bifrons*	Linyphiidae	active hunter	0	0	1	0	1
63	*Porrhomma pygmaeum*	Linyphiidae	web builder	0	0	1	0	1
64	*Satilatlas britteni*	Linyphiidae	web builder	0	0	1	0	1
65	*Savignia frontata*	Linyphiidae	active hunter	0	0	1	0	1
66	*Stemonyphantes lineatus*	Linyphiidae	web builder	0	0	1	0	1
67	*Walckenaeria nudipalpis*	Linyphiidae	active hunter	0	0	1	0	1
68	*Segestria senoculata*	Segestriidae	web builder	0	0	1	0	1
69	*Achaearanea riparia*	Theridiidae	web builder	0	0	1	0	1
70	*Porrhomma cambridgei*	Linyphiidae	web builder	0	0	0	1	1
71	*Piratula uliginosa*	Lycosidae	active hunter	0	0	0	1	1
	Total			1237	288	1066	139	2730

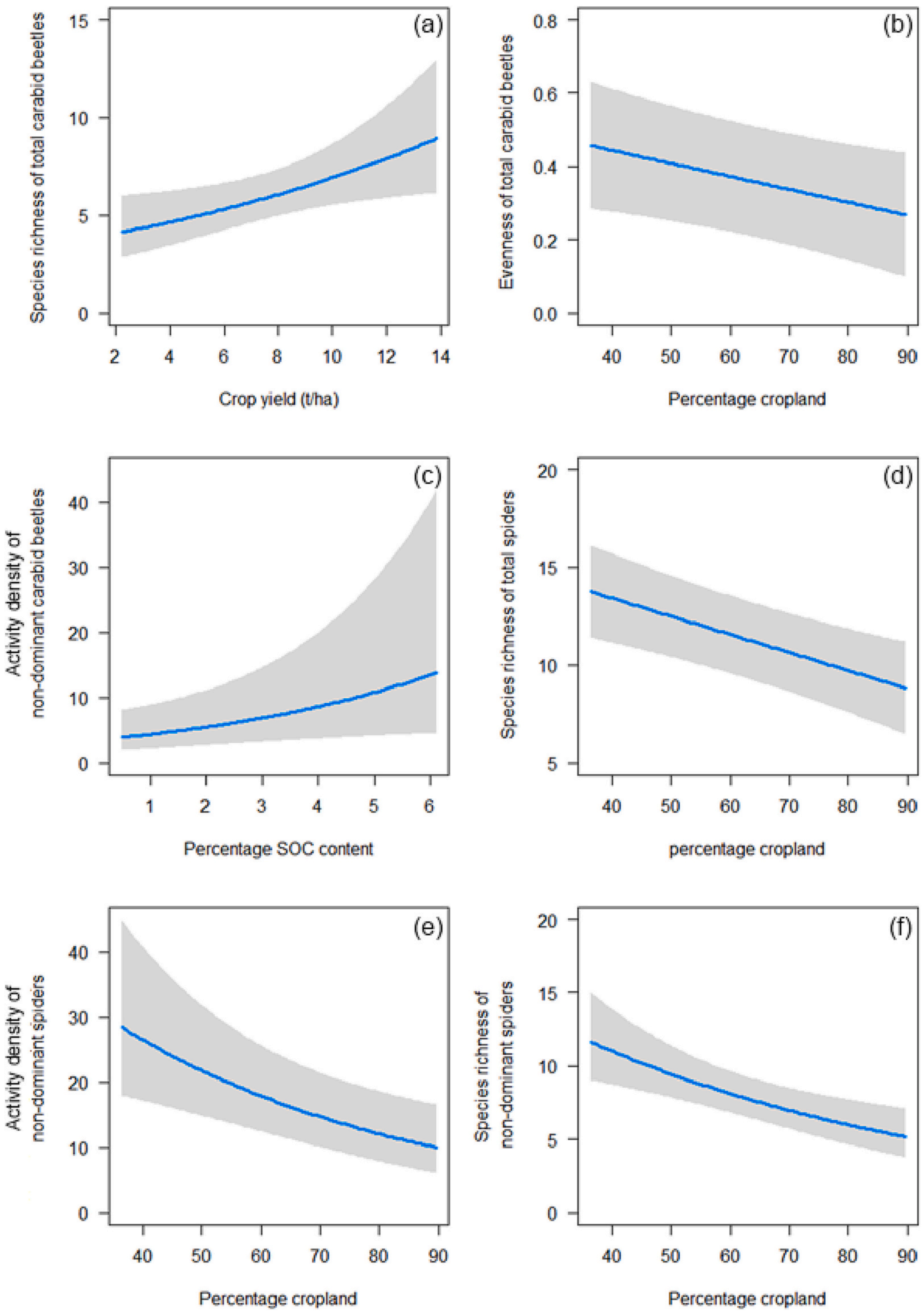

Fig. 1. A visualization of the relationships between different groups of carabid beetle and spider diversity and explanatory variables for which there was most support (high variable importance and confidence intervals of effect sizes not including zero). Panels show conditional partial regression plots of the relationships at the original scale of (a) species richness of carabid beetles and crop yield, (b) evenness of carabid beetles and percentage cropland in a 1 km radius, (c) activity density of non-dominant carabid beetles and SOC content and (d) spider species richness, (e) activity density of non-dominant spiders, (f) species richness of non-dominant spiders with percentage cropland in a 1 km radius. Fitted lines indicate the estimate effects and shaded areas indicate 95 % confidence intervals.

activity density of dominant spiders, which made up majority of all collected spiders, to any of the explanatory variables. Spider community evenness was not strongly related with any of the explanatory variables.

4. Discussion

Increasing land-use intensity and homogenization of agricultural landscapes have been found to be two important drivers of overall natural enemy loss (Hendrickx et al., 2007; Barnes et al., 2014; Dainese et al., 2019). However, our results indicate that the situation may be more complex. Across four European countries, we found partly contrasting relationships with our proxies for land-use intensity and landscape complexity for the two most abundantly occurring groups of natural enemies: carabid beetles and spiders. We found strong support for a positive relationship between carabid beetle species richness and crop yield while carabid evenness was negatively related to percentage cropland in the landscape and tended to be positively related to soil organic carbon content. The activity density of non-dominant carabid beetles was furthermore positively related with soil organic carbon content. In contrast, spider species richness and non-dominant spider species richness and activity density were all negatively related to percentage cropland while there was no support for relationships with crop yield or soil organic carbon content. This indicates that measures that support spiders may not have the same effect on carabid beetles and vice versa. Our communities of carabid beetles and spiders were dominated by a few common species with <17 % of the species accounting for >90 % of the individuals.

In line with many previous studies, we found spiders were negatively related with landscape simplicity (Clough et al., 2005; Schmidt and Tscharntke, 2005; Drapela et al., 2008; Batáry et al., 2012). Carabid beetles were not related with landscape simplicity. Winqvist et al. (2011) and Caballero-López et al. (2012) found carabid beetle activity density even to be positively related with landscape simplicity. This suggests that carabid beetles (especially dominant species) are less dependent on semi-natural habitats than spiders, although we found support for a negative relationship between landscape simplicity and carabid community evenness (Fig. 1b). A possible reason for the more consistent relationships with spiders than carabid beetles could be differences in diet preferences between the two guilds. Carabid beetle assemblages in cropland generally consist of carnivores, omnivores and herbivores while all spiders are strictly carnivorous (Duan et al., 2019; Gallé et al., 2019), this was also the case in our study (Table 2). This means that carabid beetles can utilize a wider range of food resources than spiders, making it easier for them to persist in cropland. Furthermore, many species of carabid beetles are known to lay eggs and spend their entire larval stages in arable soils (Lövei and Sunderland, 1996), suggesting they can complete their entire life cycle in cropland (Hanson et al., 2017; Boetzl et al., 2019). In contrast, the majority of spiders lay their eggs in sacs and hide the sacs in sheltered, undisturbed places or carry sacs with them while moving (Austin, 1985; Griswold, 1993). This makes arable fields relatively inhospitable places for spiders outside the crop growing season. At the start of each growing season, all spiders but not all carabid beetles therefore need to recolonize crop fields from the surrounding non-crop habitats (Öberg and Ekbom, 2006). Also, the multi-layered vegetation composed of trees, shrubs and grasses that can often be found in non-crop habitats provides a more complex vertical structure than crops, thus providing more spatial niches to simultaneously accommodate ground-dwelling and web-building spiders (Ditner et al., 2013; Garratt et al., 2017; Mestre et al., 2018). The negative relationships between proportion of cropland and evenness of carabids, species richness and activity density of non-dominant spiders seems to suggest that restoration of non-crop habitats in agricultural landscapes is especially beneficial for non-dominant species which generally include the species of conservation concern (Pywell et al., 2012).

The positive relationship between carabid beetle species richness and crop yield (Table 1, Fig. 1a), our proxy for land-use intensity, was somewhat unexpected as most previous studies have found negative relationships between land-use intensity indicators and activity density or species richness of carabids (Emmerson et al., 2016; Li et al., 2018; Wang et al., 2022). In another European cross-continental study Winqvist et al. (2014) found neutral to negative relationships between wheat yield and carabid beetle species richness and activity density. We cannot entirely rule out the possibility that the positive relationship between yield and carabid beetles in our study was driven by the carabids having a positive effect on crop yield, through natural pest control, although Gagic et al. (2017) found little support for this using partly the same data. A lack of consistent relationships between spider activity density and diversity and indicators of land-use intensity has been found before. Li et al. (2018) and Wang et al. (2022) found either negative or positive relationships between spider activity density and nitrogen depending on the composition of the landscape.

Our study found a positive relationship between soil organic carbon content and activity density of non-dominant carabid beetles (Table 1, Fig. 1c) and a positive trend between SOC content and carabid evenness (Table 1). These relationships may be linked as higher SOC content promoted increases in the activity density of non-dominant carabids may have driven an increase in the overall carabid beetle community evenness. We expected that higher soil organic carbon content could mitigate the negative effects of increasing land-use intensity and landscape simplification as it can provide additional food resources to what (pests on) crop plants have to offer (Scheu, 2001; Birkhofer et al., 2008). Interactions between the effects of SOC and landscape complexity or land-use intensity were retained in a number of the candidate sets of best models for both carabids and spiders, which suggests that SOC may influence the effect of landscape complexity and land-use intensity. However, support for these interactions was generally low and interaction effects were generally negative. This indicates that differences between fields with contrasting SOC content became smaller with increasing simplification of the landscape or local land-use intensity, which is opposite to our expectation. We found little to no support that SOC content was related to the composition of spider communities which may have to do with SOC providing more valuable resources to the partly herbivorous and omnivorous carabid beetle communities than the strictly carnivorous spider communities. Our study provides modest support that higher SOC content can enhance the activity density and possibly evenness of one important natural enemy group without negatively impacting another important natural enemy group. The relationships between natural enemies and SOC content is comparatively understudied. Because enhancing SOC has other benefits, such as reducing nitrogen leaching and maintaining food production (Tester, 1990; Lal, 2006; Diacono and Montemurro, 2015; Wei et al., 2016), it seems worthwhile to investigate the role of SOC in enhancing natural enemy communities and the services they provide in more detail.

In real-world landscapes, natural communities are generally composed of a few highly abundant species (dominant species) and many rare ones (McGill et al., 2007) and the findings of our study are largely in line with this. Only 9 out of 63 carabid beetle species and 12 out of 71 spider species were identified as nationally dominant species, but they accounted for 90.3 % and 91.0 % of all collected individuals respectively. Many of the dominant species were dominant in more than one country, which implies that across significant parts of a continent the pest control services are provided by a small number of species. Compared to dominant species, non-dominant species are generally believed to be more vulnerable for agricultural intensification (Purvis et al., 2000; Davies et al., 2004), but we found little support for this. Dominant and non-dominant carabids were related to crop yield and SOC content in similar ways. The only exception was landscape simplicity which showed contrasting relationships between dominant and non-dominant carabid beetle species. However, statistical support for these relationships was poor. Dominant and non-dominant spiders were similarly related to landscape complexity and yield, but relationships with landscape complexity were more pronounced for non-dominant than for dominant species (Table 1; Fig. 1e,f). The more pronounced effects of landscape complexity on non-dominant spiders may derive from the somewhat different predation strategies of this group compared to the dominant spiders. The ratio of individuals belonging to active hunting spiders or web building spiders was 3.7:1 while in the non-dominant group it was about 1:1 (Table 3). The permanent availability of the more complex vertical structure of semi-natural habitats compared to crops could therefore be more important for non-dominant than for dominant spiders. In our study, more than half of the dominant spider species were from the family of Lycosidae (Table 3), many species in this family are generally abundant on farmland and robust to on-field management practices and landscape change (Clough et al., 2005; Öberg and Ekbom, 2006; Öberg et al., 2007). An interesting exception was the most dominant web-building spider, i.e. *Pachygnatha degeeri*, the third most often observed spider species across all countries (Table 3). Harwood et al. (2005) found that this species relies heavily on aphids, which may explain why wheat crops are suitable habitats for them.

5. Conclusion

Simultaneously conserving agricultural biodiversity and maintaining crop yield requires us to understand how multiple guilds of natural enemies respond to environmental factors at different spatial scales. Focusing on carabid beetles and spiders, two extremely abundant and widely distributed species groups in agricultural landscapes, we found that they generally respond in contrasting ways to two key indicators of agricultural intensification. Our results provide a better understanding of why measures to enhance natural enemies often do not result in better pest regulation or enhanced crop yield (Chaplin-Kramer et al., 2011; Martin et al., 2013; Tscharntke et al., 2016). The positive relationship between carabid beetles and yield highlights the resilience of some species groups to intensification in agricultural landscapes (although clearly there are boundaries to the level of change communities can absorb without loss of function and service provision; see Deguines et al., 2014; Meehan and Gratton, 2015). This highlights the importance for conservation strategies of distinguishing between species that are well-adapted to anthropogenic landscapes and may actually benefit from modifications to maximize provision of benefits to humans and species that are negatively affected by such changes (Kleijn et al., 2011). A wealth of studies and multiple meta-analyses have focused on how land-use intensity and landscape complexity affect natural enemy diversity and abundance (Chaplin-Kramer et al., 2011; Shackelford et al., 2013; Winqvist et al., 2014; Dainese et al., 2019), but very few studies have examined relationships with soil organic carbon content, which in our study was positively related to components of carabid beetle communities, especially non-dominant species. For arable cropping systems, measures to enhance SOC content deserve more attention as it could potentially represent a management practice that can address multiple benefits to farmers as well as society. In line with the findings for SOC content, our results indicate that restoration of semi-natural habitats will most likely have the strongest positive effects on non-dominant species which generally include the species of conservation concern. Finally, our results suggest that the natural enemy communities providing important pest regulation services are dominated by a small subset of widely distributed species but that non-dominant species do not respond in markedly different ways to the examined potential drivers of biodiversity change than the observed dominant species. Management practices to strengthen populations of endangered farmland species may therefore also enhance service provision by the species group at large, which could be used as an additional argument for conservation. Open issues that remain are what proportion of all species of carabid beetles and spiders utilize farmland habitats and how non-farmland species respond to land-use change related to agricultural intensification.

CRediT authorship contribution statement

Z.M., J.S. and D.K. conceived this study; all authors contributed in the data compilation; Z.M. identified specimen of NL and UK. Z.M. and J.S. analyzed the data; Z.M., J.S. and D.K. wrote the first draft of the manuscript. All authors contributed substantially to revisions of the manuscript and gave final approval for its publication.

Declaration of competing interest

The authors declare no conflicts of interest.

Data availability

Data underlying this publication are available at https://doi.org/10.5061/dryad.6m905qg4x.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110128.

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