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► **To cite this version:**

El Aziz Djoudi, Ewen Amossé, Stéphanie Aviron, Klaus Birkhofer, Benjamin Libereau, et al.. Multi-trophic arthropod communities modulated by local farming system and landscape heterogeneity. *Landscape Ecology*, 2026, <10.1007/s10980-026-02298-y>. <hal-05489251>

HAL Id: hal-05489251

<https://hal.science/hal-05489251v1>

Submitted on 2 Feb 2026

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Multi-trophic arthropod communities modulated by local farming system and landscape heterogeneity

El Aziz Djoudi · Ewen Amossé · Stéphanie Aviron · Klaus Birkhofer · Benjamin Libereau · Manuel Plantegenest · Julien Pétilion

Received: 3 September 2025 / Accepted: 20 January 2026
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Abstract

Context Organic farming is increasingly used worldwide in recent decades, but the role of this farming system in shaping the trophic structure of arthropod communities remains poorly understood, especially at different spatial scales. Therefore, the contribution of landscape heterogeneity in shaping arthropod's trophic guilds remain understudied.

Objectives In this study, we assessed how the evenness, the abundance and the taxonomic richness of arthropod trophic groups were shaped by the local farming system, landscape heterogeneity (including

the percentage of semi-natural habitats and organic fields), and their interaction.

Methods Arthropod's trophic guilds (ground and vegetation-dwelling) were sampled in 20 spatial independent pairs of conventional (CF) and organic (OF) fields located in Brittany (Western France) by using pitfall traps and sweep nets replicated in time and space.

Results A total of 95,822 arthropods belonging to 197 taxonomic groups were sampled. Farming system has a strong overall positive effect on the community structure of both ground- and vegetation-dwelling arthropods. Landscape heterogeneity, alone and in interaction with farming systems, affected positively the diversity and abundance of most trophic groups for both ground- and vegetation-dwelling arthropods. Organic farming therefore affected the trophic composition of arthropod communities not only locally, but also at the landscape scale.

Conclusions Our study highlights the strong positive effect of farming system and the landscape heterogeneity on arthropod communities and more importantly the interconnection between different spatial scales in this process. Taking these aspects into account is therefore crucial in understanding arthropod community dynamics in agroecosystems.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-026-02298-y>.

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Keywords Trophic guilds · Winter wheat · Western France · Pitfall trap · Sweep net

Introduction

Land use change (conversion and intensification) is one of the major causes of biodiversity losses worldwide. Biodiversity is crucial for ecosystem stability, productivity and multifunctionality (Cardinale et al. 2012; Allan et al. 2015; Lefcheck et al. 2015). However, most of the studies are based on results of experiments testing the effects of certain levels of species richness on a single ecosystem function at the time (Naeem et al. 2012), whereas ecosystem functions are often shaped by several trophic groups and interconnected processes (e.g. Soliveres et al. 2016). Extrapolating results from experiments focusing on a single function to infer the role of biodiversity in complex ecosystems ignores the interactions that may occur between several ecosystem functions (Zavaleta et al. 2010) and ecosystem services (Birkhofer et al. 2015). It has been shown, also, that spatial scale is crucial in understanding ecosystem functioning and biodiversity locally is driven by the species pool on the landscape level (Tscharrntke et al. 2012). Therefore it is crucial to take into account and understand how local habitat conditions and landscape characteristics, simultaneously and in interaction, modulate the diversity and abundance of different trophic groups (Lefcheck et al. 2015). However the relationships between biodiversity, local habitat and landscape heterogeneity may substantially vary among taxa and trophic guilds (Sirami et al. 2019).

Trophic interactions are modulated by processes that generally extend beyond the local habitat scale, partly because species often use different habitats to fulfill their life cycle (Dunning et al. 1992; Tscharrntke et al. 2007; Smith et al. 2014). Both land-use change and intensification have a severe impact on biodiversity in agricultural landscapes and the functioning of agroecosystems at different spatial and temporal scales (Brose and Hillebrand 2016). Biodiversity loss is the direct and indirect result of habitat destruction, simplification and fragmentation (e.g. conversion of natural areas into arable fields see: Tscharrntke et al. 2012) but also the consequences of the farming practices that generally affect negatively the individuals, the communities and the environment (e. g. intensive ploughing, excessive use of pesticides, see: Köhler and Trieb-skorn 2013; Rundlöf et al. 2016). Organic farming has been promoted as an alternative to conventional

farming due to the widely recognized positive effects on local biodiversity in most (Bengtsson et al. 2005; Fuller et al. 2005; Gabriel et al. 2010), but not all taxonomic groups (Birkhofer et al. 2014).

In this study we aimed to investigate the effects of farming system at the field scale (Organic Farming vs. Conventional Farming, further abbreviated as OF and CF respectively), landscape heterogeneity (i.e. landscape composition and configuration see Fahrig et al. 2011) as well as their interactions on multi-trophic arthropod communities in agroecosystems. In particular, we tested the following hypotheses: i) Farming systems (OF vs. CF) locally drive the structure of trophic guilds, for both ground and vegetation communities. We expected the evenness among trophic levels to be higher in OF mainly due to higher habitat quality for several trophic groups in OF compared to CF fields. We expected this effect of the farming system is more pronounced for trophic groups of ground-dwelling arthropods because they are more likely to be impacted by harmful farming practices in CF (e.g. the use of pesticides and other chemical inputs) and their lower dispersal capacities compared to vegetation dwelling communities. We also expect OF fields to have increased number of individuals and higher taxonomic richness of dominant trophic groups, mainly because of reduced intensity of harmful agricultural practices (compared to the use of pesticides and other chemical inputs in CF) but also the consequence of higher habitat quality at the field scale (e.g. more food resources and shelters see: Bengtsson et al. 2005; Hole et al. 2005). ii) Landscape heterogeneity shapes arthropod communities (e.g. increased effect of semi-natural habitats, see: Djoudi et al. 2018, 2019; Gallé et al. 2020; Deppe and Fischer 2023; Deppe et al. 2025). We expect a positive effect of the proportion of SNH and organic farming as well as the diversity and the size (Gallé et al. 2020) of the different landscape patches/elements on both the number of individuals and taxonomic richness of dominant trophic groups, because mainly they provide diverse food resources and/or complementary habitat (Diekötter et al. 2010; Rader et al. 2014). iii) Finally the effect of local habitat is modulated by the characteristics of the surrounding landscape. We expect that the landscape heterogeneity could buffer the negative effect of the local habitat, especially in CF fields and enhance the local number of individuals and taxonomic richness mainly in OF fields.

Material and methods

Study site

The study was conducted in Brittany, Western France (48° 06' 53'' N, 1° 40' 46'' O). The study area is characterized by agriculture dominated by mixed crop-livestock farming systems (mostly winter cereals, corn and grassland). Forty fields (twenty pairs of organic and conventional fields) cultivated with winter wheat (*Triticum aestivum*) were selected in an area of about 200,000 ha along a landscape gradient of the proportion of organic farming around the sampled fields (radius of 500 m; ranging from 0 to 40.4%). A Moran's I test indicated no spatial autocorrelation (Moran's I = -0.297, $P=0.221$) between the proportion of organic farming in the surrounding landscape and the selected sites.

All organically managed field were certified according to EU regulation Nr. 834/2007. Landscape sites/variables were digitized from aerial ortho-photographs (BD ORTHO IGN, 2015, <https://geoservices.ign.fr/bdortho>). Landscape metrics were computed to characterize the composition and configuration (the two metrics however were not tested for independence) of land cover types in the surrounding of each focal field. The landscape was characterized in a radius of 500 m around each focal field. This distance was selected because it is relevant to describe the response of arthropod communities to landscape elements (Schmidt and Tscharrntke 2005; Batáry et al.

2007). In total, twelve variables were computed, one local variable (field scale) and eleven landscape variables: proportion of SNH, proportion of each farming system, the mean patch size, land cover diversity (i.e. the number of different land cover and their relative proportion in the landscape) (Table 1) using the Chloé2012 software (Boussard and Baudry 2014).

Arthropod sampling and identification

Ground-dwelling arthropods

Ground-dwelling arthropods were sampled using pitfall traps (100 mm diameter) from April to July 2016. Traps were filled with brine solution (30% NaCl and 70% water). In each field, three pitfall traps were randomly placed. Pitfall traps were placed at least 10 m away from field margins to minimize potential edge effects. Traps were left open continuously and collected every two weeks, for a total of five sampling periods.

Vegetation-dwelling arthropods

Vegetation-dwelling arthropods were sampled using a sweep net along transects towards the center of the field, from April to July 2016. In each field arthropods sampling, along three transects, was performed every two weeks. The sweep net sampling was standardized by transect length (20 m) and the number of sweeps per transect (20 sweeps). Transect were

Table 1 Local and landscape variables with variable type (qualitative vs. quantitative), unit, min–max and mean (together with the standard error) values

Variable	Variable type	Unit/class	Min–Max	Mean (\pm SE)
Farming system (organic vs. conventional)	qualitative	OF; CF	-	-
Proportion of organic farming	quantitative	% of cover	27.83–80.18	54.2 \pm 1.88
Proportion of conventional farming	quantitative	% of cover	0–40.38	19.01 \pm 1.64
Proportion of orchards	quantitative	% of cover	0–16.21	1.11 \pm 0.43
Proportion of Woodland	quantitative	% of cover	0–18.62	4.61 \pm 0.76
Proportion of Grass strips	quantitative	% of cover	0–4.21	0.88 \pm 0.15
Proportion of Meadows	quantitative	% of cover	2.44–61.8	28.42 \pm 2.05
Hedgerow length	quantitative	% of cover	0.55–1.99	1.25 \pm 0.06
Proportion of winter crops	quantitative	% of cover	8.9–57.98	31.3 \pm 1.99
Proportion of spring crops	quantitative	% of cover	0–55.17	21.32 \pm 1.67
Mean patch size	quantitative	m ²	7550.8–21,223.9	12,692.71 \pm 499.68
Land cover diversity	quantitative	Shannon index	1.15–1.75	1.43 \pm 0.02

established at least 10 m away from field margins to minimize potential edge effects.

All individuals were identified at different taxonomic level (from order to species) that allowed us to assign them to a trophic group by using available literature sources in the BETSI database (Pey et al. 2014).

Statistical analyses

To compare the evenness of the number of individuals across trophic groups between farming systems, Pearson's Chi-squared test (χ^2) was applied to look for dependencies between the distributions of the trophic groups, for both ground and vegetation-dwelling arthropod communities. Because of differences in scales (units) between the range of values exhibited by predictor variables was high, then predictor variables were mean-centered and standardized prior to analysis.

Variables selection

To reduce multicollinearity between variables, variable selection was first applied. A method of 'Clustering of variables' that arranges variables into homogeneous clusters, i.e. groups of variables strongly related to each other and thus providing the same information was performed (Chavent et al. 2011). This method allows analysing both quantitative and qualitative variables at the same time. A bootstrap approach was then used to assess the stability of the variable partitioning and to determine the optimal number of clusters (R package 'ClustOfVar' v.0.8: Chavent, 2013). At the end of this selection, six variables were kept (farming system and five landscape variables: % of Organic Farming, % of woody elements, % of meadows, Mean patch size (MPS), Land cover diversity (SHDI)) for subsequent analyses (Figure T1).

Influence of field farming system and landscape context on multi-trophic community structure

To test for a relationship between the selected local and landscape predictor variables and number of individuals and taxonomic richness of arthropods, General Linear Mixed-effect Models (GLMM)

(Zuur et al. 2009), model averaging (Burnham and Anderson 2002) and multi-model inference (Grueber et al. 2011) were used. In each model, a nested spatial random effect was added to account for the spatial dependence between observations: site (landscape around each pair of organic/conventional fields) and field within sites. Full models on the number of individuals and taxonomic richness of both ground- and vegetation-dwelling arthropods included the following predictor variables: farming system as fixed effect, proportions of organic farming, woodlands and meadows, SHDI (land cover diversity) MPS (mean patch size) as well as the interactions between farming system and all landscape variables.

Full models were first fitted using the 'glmer' function in the R package 'lme4' (v.1.1–12; Bates et al. 2015). To assess the appropriate distribution, statistics on residuals were first calculated with Poisson distribution. When over-dispersion was observed (assessed by comparing the sum of squared Pearson residuals to the residual degrees of freedom: O'Hara and Kotze 2010), a negative binomial distribution was used. Each model was fitted using the appropriate distribution type and link function. Poisson distribution was selected for the taxonomic richness of ground- and vegetation-dwelling arthropods. Negative binomial distribution was selected for their number of individuals.

Model selection procedure started with the standardization of all predictor variables (Grueber et al. 2011) using the 'standardize' function of the R package 'arm' (v. 19–3; Gelman and Su 2015). The 'dredge' function of the R package 'MuMin' (v. 1.16.4; Barton 2016) was then used to fit all possible combinations of models, and their associated Akaike's Information Criteria corrected for small sample sizes were calculated (AICc; Hurvich and Tsai 1989). A list of the best fitted models with $\Delta AICc < 2$ was generated with the 'get.models' function of the R package 'MuMin', and was used for model averaging with the 'model.avg' function in the 'MuMin' package. The final averaged models provided model-averaged coefficients for each retained predictor variable and variable importance (i.e., the sum of the model weights within the set of models that included this variable). Finally, 95% confidence intervals (CI) were calculated for the model-averaged parameter estimates with the 'confint' function in the 'MuMin'

package. All analyses were conducted using R software (R Core Team 2016).

Results

A total of 95,822 individuals belonging to 197 taxonomic groups (183 in OF and 154 in CF; see taxonomic list in Table T1) were sampled. In OF fields, 35,263 arthropods belonging to 144 taxonomic groups were captured with pitfall traps and 21,271 individuals belonging to 112 taxonomic groups were captured with sweep nets. In CF fields, 31,040 individuals belonging to 128 taxonomic groups were caught with pitfall traps and 8,248 individuals belonging to 81 taxonomic groups were caught with sweep nets (see Table T1). For both ground and vegetation dwelling communities, the total number of individuals was always higher in OF except for Saprothagous guild on the ground-dwelling communities which was higher in CF (see Table T2).

The functional evenness, as the distribution of the number of individuals across trophic groups, significantly differed between the two farming systems, for both ground-dwelling ($\chi^2=3132.9$, $P<0.001$) and vegetation-dwelling arthropods ($\chi^2=701.63$, $P<0.001$) (Fig. 1). The farming system also had a significant effect on both the number of individuals

and taxonomic richness of most ground-dwelling trophic groups (Table 2). The number of individuals and taxonomic richness of ground-dwelling arthropods were significantly higher in OF than in CF fields for all trophic groups, except for the taxonomic richness of saprophagous arthropods (Fig. 2). The number of individuals and taxonomic richness of ground-dwelling predators were positively influenced by the surrounding proportions of woodlands (Table 2, Fig. 3A, C) and meadows (Table 2, Fig. 3B, D). The number of ground-dwelling predators was significantly influenced by the interaction between farming system and landscape diversity (SHDI; the effect being non-significant in OF fields and negative in CF fields) and mean patch size (MPS; the effect being positive in OF fields and non-significant in CF fields: Table 2).

Farming system significantly affected the number of individuals and the taxonomic richness of all vegetation-dwelling trophic groups, always being higher in OF fields compared to CF fields (Table 3, Fig. 4). The number of omnivorous arthropods was significantly and negatively influenced by the proportion of organic farming in the landscape (Table 3; Fig. 5). The number of phytophagous arthropods was significantly influenced by the interaction between farming system and proportion of

Fig. 1 Number of individuals and their density distribution, taxonomic richness (respectively A-C: ground dwelling trophic groups, B-D: vegetation dwelling trophic groups) depending on the farming system

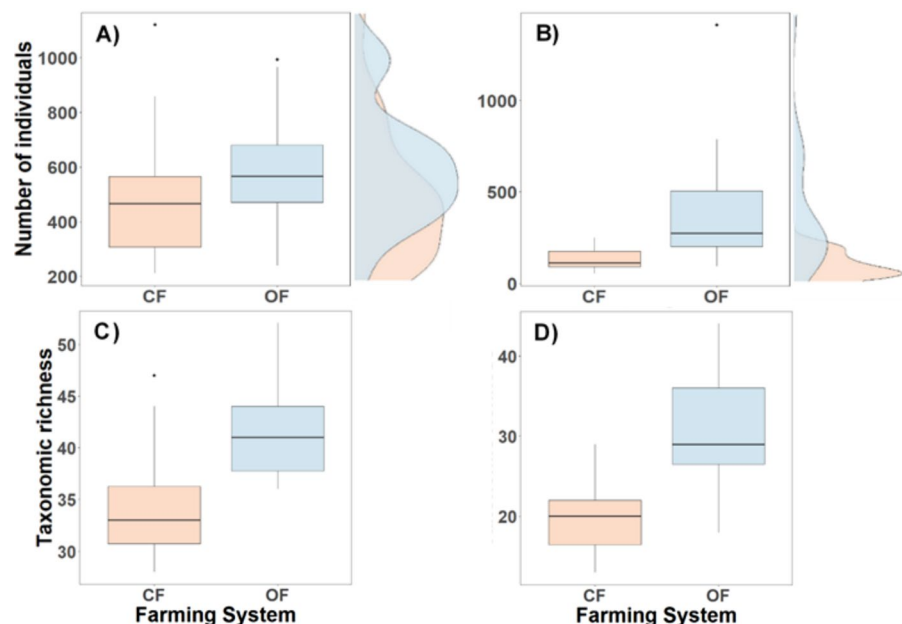


Table 2 Model-averaged coefficients estimates from the averaged best-fitting models predicting the number of ground-dwelling arthropods and the taxonomic richness in relation to farming system and landscape heterogeneity with 95% confidence interval (CI). Asterisks (*: $0.05 < p \leq 0.01$, **: $0.01 < p \leq 0.001$ and ***: $p < 0.001$)

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)	CI
<i>Saprophagous number of individuals</i>						
Far_syst	-0.315	0.098	0.099	3.186	0.001 **	0.194
SHDI	-0.192	0.168	0.169	1.141	0.254	0.352
Far_syst:SHDI	0.143	0.215	0.216	0.665	0.506	0.224
MPS	-0.036	0.096	0.097	0.375	0.708	0.425
Meadows	0.064	0.110	0.111	0.575	0.565	0.143
Far_syst:Meadows	-0.030	0.116	0.117	0.255	0.799	0.748
<i>Phytophagous number of individuals</i>						
Far_syst	0.873	0.122	0.123	7.072	<0.001***	0.242
Woodland	-0.426	0.249	0.252	1.692	0.090	0.493
Far_syst:Woodland	0.528	0.313	0.315	1.674	0.094	0.457
OF_landscape	-0.065	0.135	0.136	0.480	0.631	0.480
MPS	0.019	0.082	0.082	0.229	0.819	0.240
Far_syst:MPS	0.066	0.189	0.190	0.349	0.727	0.109
SHDI	-0.069	0.168	0.169	0.410	0.682	0.657
<i>Predator number of individuals</i>						
Far_syst	0.129	0.068	0.069	1.878	0.064	0.134
Meadows	0.290	0.090	0.091	3.189	0.001 **	0.178
MPS	0.215	0.109	0.110	1.949	0.051	0.216
SHDI	-0.205	0.126	0.128	1.606	0.108	0.251
Woodland	0.237	0.112	0.113	2.092	0.034 *	0.222
Far_syst:MPS	0.714	0.174	0.176	4.061	<0.001***	0.345
Far_syst:SHDI	0.803	0.191	0.193	4.164	<0.001***	0.378
Far_syst:Woodland	-0.064	0.140	0.141	0.453	0.650	0.520
Far_syst:Meadows	0.045	0.116	0.117	0.386	0.699	0.200
<i>Omnivore number of individuals</i>						
Far_syst	0.468	0.099	0.100	4.690	<0.001***	0.196
MPS	0.141	0.106	0.107	1.324	0.185	0.209
Far_syst:MPS	0.672	0.216	0.218	3.076	0.002**	0.428
Meadows	0.021	0.064	0.064	0.330	0.742	0.142
OF_landscape	0.012	0.053	0.053	0.229	0.819	0.159
<i>Phytophagous taxonomic richness</i>						
Far_syst	0.808	0.093	0.094	8.571	<0.001***	0.185
Meadows	-0.018	0.056	0.056	0.325	0.745	0.252
MPS	0.014	0.050	0.051	0.269	0.788	0.132
Woodland	0.007	0.041	0.041	0.168	0.867	0.149
<i>Predator taxonomic richness</i>						
Far_syst	0.136	0.050	0.051	2.684	0.007 **	0.099
Meadows	0.130	0.052	0.053	2.463	0.013 *	0.103
Woodland	0.186	0.051	0.051	3.618	<0.001***	0.101
MPS	0.008	0.027	0.027	0.292	0.771	0.064
Far_syst:Meadows	0.011	0.049	0.049	0.231	0.817	0.145
SHDI	-0.006	0.026	0.026	0.231	0.818	0.134
<i>Omnivore taxonomic richness</i>						

Table 2 (continued)

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)	CI
Far_syst	0.199	0.064	0.065	3.061	0.002 **	0.128
SHDI	0.020	0.047	0.047	0.421	0.674	0.059
Woodland	0.009	0.032	0.032	0.272	0.785	0.073
MPS	-0.005	0.026	0.026	0.193	0.847	0.166
OF_landscape	-0.005	0.027	0.027	0.193	0.847	0.172
Meadows	0.004	0.024	0.024	0.152	0.879	0.100

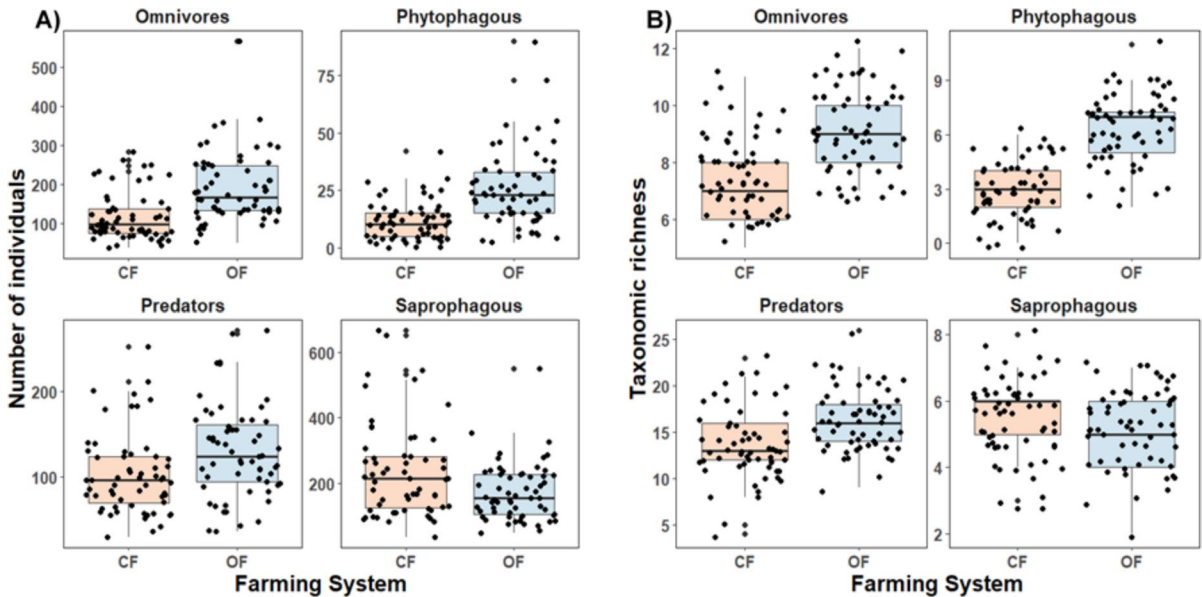


Fig. 2 Comparison between **A** number of individuals and **B** taxonomic richness of ground-dwelling arthropods per trophic group depending on the farming system (significant effect in Table 2)

woodland, with the effect being positive in OF, but not in CF fields (Table 3, Fig. 6).

Discussion

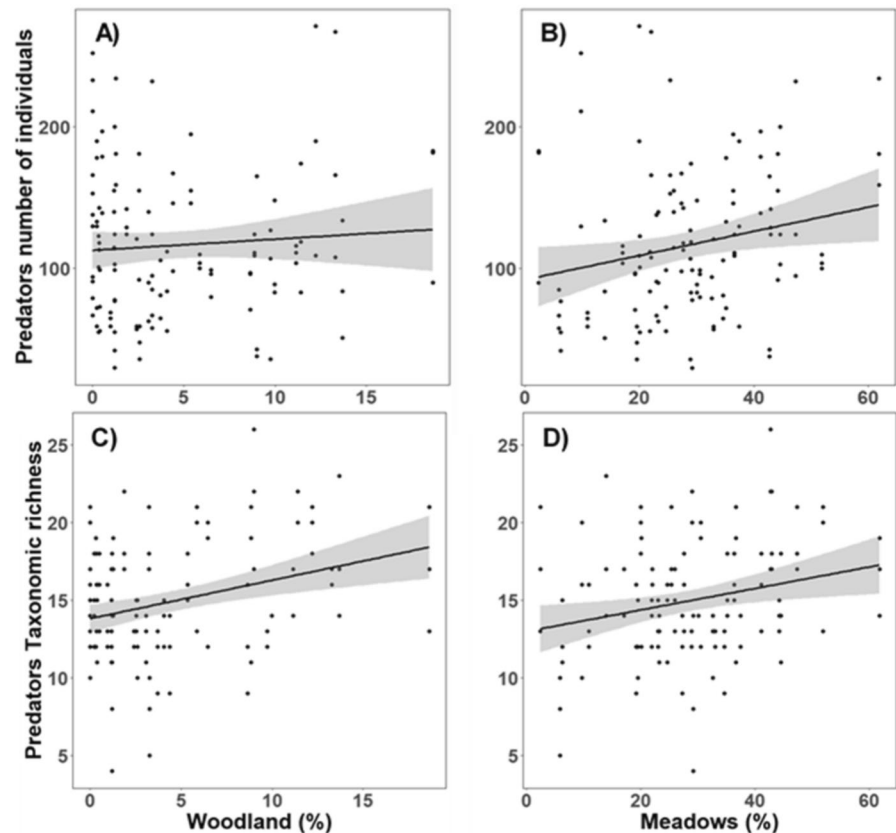
Organic farming, as compared to conventional farming, had a strong effect on the trophic structure (including evenness) of ground- and vegetation-dwelling arthropods. Evenness across trophic groups was significantly higher in organically managed fields and this difference was most pronounced for ground-dwelling arthropods. Ground-dwelling communities were dominated by saprophagous taxa in CF fields, whereas vegetation-dwelling communities were dominated by phytophagous taxa in OF fields,

which supports our first hypothesis. The number of individuals and taxonomic richness of arthropods was significantly higher in OF fields for all trophic groups, for both ground and vegetation dwelling arthropods, except for saprophagous arthropods that were more abundant in CF fields. Finally, landscape heterogeneity (and the proportion of woodlands in particular) in interaction with farming system affected the diversity and abundance of trophic groups in both ground and vegetation-dwelling arthropods, supporting our second hypothesis.

Farming system

Our results are partly in line with previous meta-analysis/reviews (Bengtsson et al. 2005; Hole et al.

Fig. 3 Number of individuals and taxonomic richness of ground-dwelling predators depending on the percentage of woodland (A, C) and Meadows (B, D) in the landscape. (significant effect in Table 2)



2005; Tschardt et al. 2005a, b; Tuck et al. 2014; Rundlöf et al. 2016) that highlighted positive effects of organic farming on the structure of arthropod communities. However, in our study we found positive effects of organic farming on trophic groups that were previously not assumed to benefit from organic farming (e.g. soil- or ground-dwelling saprophagous arthropods, see Bengtsson et al. 2005, Rundlöf et al. 2016 or herbivores, see Rundlöf et al. 2016) but the abundance of soil- or ground-dwelling saprophagous arthropods did not generally respond to organic farming in previous small scale (e.g. microhabitat) long-term trials (soil mesofauna: Birkhofer et al. 2008a; Meyer et al. 2021) or field trials (soil macrofauna: Diekötter et al. 2010).

The differences between farming systems that explains the observed positive effects of organic farming on trophic groups are related to the practices associated with the two farming systems. Synthetic pesticides applied in CF fields are well recognized for their harmful effects on biodiversity (Köhler and Triebkorn 2013; Klaus Birkhofer et al. 2016) with

direct (by contact) or indirect (through the ingestion of contaminated prey or a reduction of prey availability) negative effects on arthropods (Geiger et al. 2010; Köhler and Triebkorn 2013). Herbicide application in conventional farming for example results in a generally lower diversity of plants in and around arable fields (Feber and Firbank 1997; Roschewitz 2005; Rundlöf and Smith 2006), rendering these habitats less attractive for herbivorous animals in general (Birkhofer et al. 2014). At the local scale, greater plant diversity supports a higher number of arthropod predators (e.g. Landis et al. 2000; Letourneau et al. 2009; Bennett and Gratton 2013) through providing more food resources and higher structural complexity (resource- and structure-mediated effects: Diehl et al. 2012). The lack of herbicide applications in OF, results in denser vegetation and higher weed diversity (Tuck et al. 2014; Henckel et al. 2015) and these conditions likely provide a beneficial microclimate (e.g. temperature, moisture) for many arthropod species. Other practices such as the application of organic fertilizers are beneficial to arthropods (Garratt et al.

Table 3 Model-averaged coefficients estimates from the averaged best-fitting models predicting the number of vegetation-dwelling arthropods and taxonomic richness in relation to farming system and landscape heterogeneity with 95% confidence interval (CI). Asterisks (*: $0.05 < p \leq 0.01$, **: $0.01 < p \leq 0.001$ and ***: $p < 0.001$)

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)	CI
<i>Phytophagous number of individuals</i>						
Far_syst	1.150	0.137	0.139	8.304	<0.001***	0.272
SHDI	-0.141	0.248	0.251	0.563	0.573	0.492
Woodland	0.554	0.268	0.271	2.046	0.040 *	0.530
Far_syst:SHDI	-1.027	0.364	0.368	2.793	0.005 **	0.721
Far_syst:Woodland	1.227	0.362	0.366	3.354	0.001 ***	0.717
OF_landscape	-0.036	0.111	0.112	0.322	0.748	0.488
Meadows	-0.035	0.109	0.110	0.318	0.750	0.483
<i>Predator number of individuals</i>						
Far_syst	0.327	0.142	0.143	2.280	0.022 *	0.281
Woodland	0.076	0.155	0.156	0.489	0.625	0.188
OF_landscape	-0.026	0.091	0.092	0.283	0.777	0.457
Meadows	-0.011	0.068	0.068	0.160	0.873	0.393
<i>Omnivore number of individuals</i>						
Far_syst	0.680	0.124	0.125	5.435	1e-07 ***	0.245
OF_landscape	-0.360	0.151	0.153	2.356	0.018 *	0.300
Woodland	0.009	0.084	0.085	0.106	0.915	0.292
Far_syst:Woodland	0.121	0.234	0.234	0.515	0.607	0.147
SHDI	0.028	0.091	0.091	0.308	0.758	0.212
<i>Phytophagous taxonomic richness</i>						
Far_syst	0.638	0.069	0.070	9.163	<0.001 ***	0.136
OF_landscape	-0.134	0.094	0.095	1.414	0.157	0.186
SHDI	-0.052	0.086	0.087	0.598	0.550	0.246
Far_syst:SHDI	-0.048	0.110	0.110	0.440	0.660	0.427
MPS	-0.024	0.063	0.063	0.380	0.704	0.250
Woodland	-0.008	0.036	0.037	0.212	0.832	0.256
<i>Predator taxonomic richness</i>						
Far_syst	0.153	0.069	0.070	2.190	0.028 *	0.137
Woodland	0.085	0.079	0.079	1.075	0.282	0.097
Far_syst:Woodland	-0.018	0.070	0.070	0.250	0.803	0.335
<i>Omnivore taxonomic richness</i>						
Far_syst	0.276	0.092	0.092	2.984	0.002 **	0.181
Woodland	0.030	0.067	0.067	0.442	0.659	0.096
OF_landscape	-0.014	0.051	0.051	0.279	0.780	0.251
SHDI	0.007	0.039	0.039	0.191	0.849	0.134

2011) by improving soil quality and the availability of additional prey (Schmidt et al. 2005), but are not exclusive to OF or CF. The long-term application of synthetic fertilizers only permitted under CF may however even affect arthropods negatively (Birkhofer et al. 2008a, 2008b). The observed higher abundance of saprophagous arthropods in CF in our study can best be explained by the higher application rates

of organic fertilizer under CF as compared to fields under OF in our study region.

Landscape heterogeneity

Some trophic groups of ground- and vegetation-dwelling arthropods were also affected by landscape heterogeneity, but mainly depending on the local

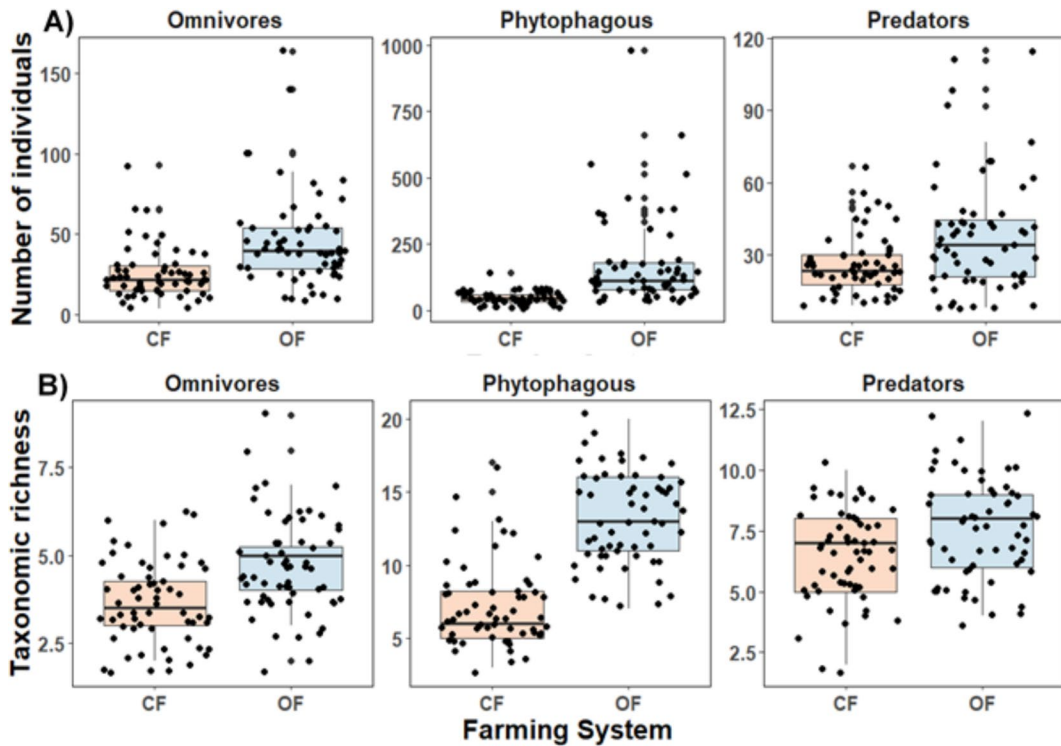


Fig. 4 Comparison between **A** number of individuals and **B** taxonomic richness of Vegetation-dwelling arthropods per trophic group depending on the farming system (significant effect in Table 3)

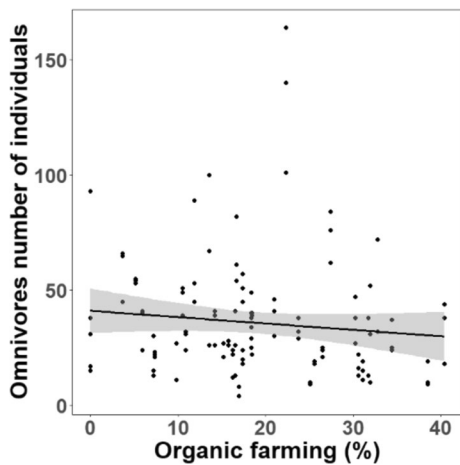


Fig. 5 Number of individuals of vegetation-dwelling Omnivores depending on the percentage of organic farming in the landscape (significant effect in Table 3)

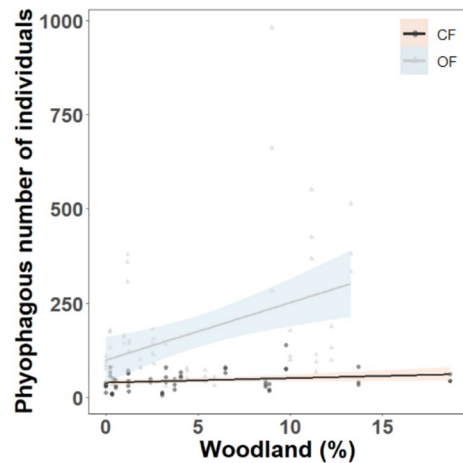


Fig. 6 Number of individuals of vegetation-dwelling phytophagous depending on the percentage of woodland and farming systems (significant effect in Table 3)

farming system. Our results therefore support the hypothesis that the size of the landscape-wide species pool may moderate local biodiversity (Tscharrntke

et al. 2012). Complex landscapes composed of different habitats usually support more diverse communities compared to more homogeneous landscapes

(Tscharntke et al. 2005a, b; Chaplin-Kramer et al. 2011; Martin et al. 2016). Heterogeneous landscapes support higher diversity by providing complementary habitats and better supply of trophic resources (Fahrig et al. 2011). These benefits, however, vary across spatial scale and depend on the mobility and degree of trophic specialization in species (Tamme et al. 2010; Bar-Massada and Wood 2014; Hicks et al. 2015; Stein and Kreft 2015). Dispersal and foraging occurs at large spatial scales and across multiple habitats in many arthropod predator species (Letourneau et al. 2009; Ekroos et al. 2015). The abundance and taxonomic richness of ground-dwelling predators were positively influenced by the proportion of SNH in the landscape (i.e. woodland and meadows). These positive effects may be explained by the fact that many taxa can benefit from the complementarity of resources between semi-natural and crop habitats (i.e. complementation, see Djoudi et al. 2019 for an example on carabids). Indeed Woodlands are habitats that can provide shelter, alternative food resources and overwintering sites for arthropod predators (Tscharntke et al. 2005a, b; Bianchi et al. 2006) and constitute source habitats from which individuals can disperse into the landscape matrix (Chaplin-Kramer et al. 2011). The abundance of vegetation-dwelling phytophagous arthropods was also positively influenced by the proportion of woodlands, but only in OF fields. Organically farmed arable fields can be considered as an attractive environment for phytophagous taxa (Birkhofer et al. 2016), notably for food resources and habitat quality. Flying phytophagous arthropods easily move between woodlands and OF fields, and will benefit from the complementarity of trophic resources and nesting sites between semi-natural and crop habitats (Letourneau et al. 2009). The number of vegetation-dwelling omnivorous arthropods was negatively influenced by the proportion of organic farming surrounding fields. On the one hand many studies found an overall positive effect of the proportion of OF at landscape scale on the diversity of several taxa and many of them are generalist or omnivorous (e.g. butterflies, birds, ground beetles, plants and soil macroarthropods: Rundlöf et al. 2008; Diekötter et al. 2010; Gabriel et al. 2010). Moreover, the OF locally is known to be more diverse (local favorable habitat conditions, diverse resources...) leading to higher number of individuals consequently this effect is amplified on landscape level (i.e. additive effect).

On the other hand, our results are consistent with the (very) few studies that previously addressed this trophic group. Gosme et al. (2012) stated a negative effect of the proportion of OF at the landscape scale on crop pests and diseases. Winqvist et al. (2011) found that landscape heterogeneity had a negative effect on the abundance of omnivorous arthropods. These findings are consistent with our observation of decreasing abundance of omnivores with increasing proportion of OF in the landscape. These contrasting results reflect the heterogeneity in terms of trophic preferences among the Omnivorous taxa, which supports our initial argument regarding the very definition of this group, which is essentially more heterogeneous than other trophic groups such as predators. This can be seen in Fig. 5, where the negative linear relationship between the number of individuals and the percentage of OF in the landscape is not very strong. Looking at the distribution, we can see a non-linear regression suggesting a more complex relationship and the need of using higher taxonomic resolution and/or refining this trophic group by taking into account not only the diet preference but adding another trait for example, dispersal capacity. Our contrasting results in this regard suggest that the approach of taxonomic sufficiency (identification to higher taxonomic level, e.g. order, family) in studying arthropod communities at the landscape level, is a balanced method between cost-Effectiveness (time and resources) and power to detect significant effects ecological changes (Terlizzi et al. 2003).

Our study ultimately calls for more investigations of ecological interactions (e.g. trophic, competition ...) and their role in local community structure, and one of the underlying questions is how agricultural practices and landscape heterogeneity impact ecological interactions. In addition to showing the effects of local farming system and those of the landscape heterogeneity on arthropod communities, our study also highlights the interconnection between different spatial scales and the modulation of local effects by the landscape context, however the two component of landscape heterogeneity (i.e. configuration and composition) as defined in our study, were not tested for independence, thus limiting a strong conclusion on the magnitude of their respective effects. This highlights the fact that taking these aspects into account is therefore crucial in studying and understanding arthropod community dynamics in agroecosystems.

Acknowledgements We thank Jean-Luc Roger and Gérard Savary for help in carabids identification and Elsa Canard for help in the fieldwork.

Author contribution J.P. & M.P. organised the funding acquisition. E.A.D., J.P., M.P., S.A. general study design. E.A.D. data collection, analysis and wrote the main manuscript text. All authors reviewed the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. The study was funded by Région Bretagne, ARED 8960, Fondation pour la Recherche sur la Biodiversité, SOLUTION project

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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