



Predatory arthropods in apple orchards across Europe: Responses to agricultural management, adjacent habitat, landscape composition and country



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ABSTRACT

Local agri-environmental schemes, including hedgerows, flowering strips, organic management, and a landscape rich in semi-natural habitat patches, are assumed to enhance the presence of beneficial arthropods and their contribution to biological control in fruit crops. We studied the influence of local factors (orchard management and adjacent habitats) and of landscape composition on the abundance and community composition of predatory arthropods in apple orchards in three European countries. To elucidate how local and landscape factors influence natural enemy effectiveness in apple production systems, we calculated community energy use as a proxy for the communities' predation potential based on biomass and metabolic rates of predatory arthropods. Predator communities were assessed by standardised beating samples taken from apple trees in 86 orchards in Germany, Spain and Sweden. Orchard management included integrated production (IP; i.e. the reduced and targeted application of synthetic agrochemicals), and organic management practices in all three countries. Predator communities differed between management types and countries. Several groups, including beetles (Coleoptera), predatory bugs (Heteroptera), flies (Diptera) and spiders (Araneae) benefited from organic management depending on country. Woody habitat and IP supported harvestmen (Opiliones). In both IP and organic orchards we detected aversive influences of a high-quality surrounding landscape on some predator groups: for example, high covers of woody habitat reduced earwig abundances in German orchards but enhanced their abundance in Sweden, and high natural plant species richness tended to reduce predatory bug abundance in Sweden and IP orchards in Spain. We conclude that predatory arthropod communities and influences of local and landscape factors are strongly shaped by orchard management, and that the influence of management differs between countries. Our results indicate that organic management improves the living conditions for effective predator communities.

1. Introduction

Sustainable agricultural practices and enhanced habitat conservation

at local and landscape scales are considered key solutions to stop the accelerating degradation of ecosystem services (IPBES, 2018). Biological control of agricultural pests is a prominent example of nature's

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contribution to human welfare. Favourable local and landscape factors can enhance predator communities and biological control (Bengtsson et al., 2005; Bianchi et al., 2006; Tschumi et al., 2016). In taking responsibility for sustainable land use and ecosystem services, we need to identify the effects of factors that explain the variability in arthropod communities and their potential services at different spatial scales, from climatic region, to landscape, to the orchard itself and its immediate local surroundings.

The country scale comprises several factors beyond macroclimate and biogeographic species pools. These include national policies on pesticides, differences in landscape habitat loss, identity of common crops, and availability of public advisory services. At the landscape scale, natural enemies benefit from a high proportion of semi-natural habitats (Chaplin-Kramer and Kremen, 2012; but see Hawro et al., 2015; Tschamtko et al., 2005). However, landscape effects on natural enemies also depend on taxon-specific mobility and dispersal capacity (Gallé et al., 2018; Schweiger et al., 2005). For spiders, habitat diversity and landscape composition are major determinants of occurrence at the landscape scale (Schweiger et al., 2005). In contrast, less mobile predatory arthropods such as earwigs remain mostly unaffected by the proportion of crop vs. non-crop cover in the landscape (Happe et al., 2018). Landscape simplification as reflected by a high proportion of intensive agricultural cover reduces biological pest control (Rusch et al., 2016; Tschamtko et al., 2016). Consequently, a reduced proportion of intensive agricultural land and a high landscape complexity are often regarded as of special relevance to enhance biological control (Jonsson et al., 2015). For example, in landscapes dominated by cultivated land, biological control of aphids in different annual crop systems can be reduced by 46% when compared with more heterogeneous landscapes (Rusch et al., 2016).

Besides country and landscape effects, local factors such as adjacent habitat and orchard management influence natural enemies. At both landscape and local scales, the European Union subsidises agri-environmental schemes to enhance the ecological value of agro-ecosystems (Batáry et al., 2015). These schemes differ between countries and can, for example, protect diverse types of agro-ecosystems and cultural landscapes, support organic farmers, and enhance local habitat quality for natural enemies (e.g. in case of beetle banks and flower strips) (Batáry et al., 2015; Ekroos et al., 2014). Semi-natural woody habitats such as hedgerows or traditional orchards may shelter overwintering predatory arthropods such as coccinellid beetles and spiders (Elliott et al., 2002; Mestre et al., 2018). Improvement of local habitat quality in the orchard surroundings, for example by hedgerow restoration, can promote beneficial insects and natural pest control (Miñarro and Prida, 2013; Morandin et al., 2016). These habitats are more beneficial for predators than for pests and support predatory arthropods in fruit crops by enhancing habitat connectivity (Bailey et al., 2010). In addition to woody habitats, herbaceous plants may improve living conditions for natural enemies and the delivery of ecosystem services (Lichtenberg et al., 2017; Norris and Kogan, 2005). Flower-rich boundaries of crop orchards are particularly important for natural enemies that depend on pollen or nectar, which provide sugars and amino acids, for at least one part of their life cycle. These floral resources are essential for hoverflies, lacewings, hymenopteran parasitoids and omnivorous bugs such as anthocorids (Gurr et al., 2017; Wäckers and van Rijn, 2012). Herbal boundaries can also enhance the trait diversity of spiders, which may increase the biological control potential of spider communities (Gallé et al., 2018).

Another factor acting at the local scale is organic management. It increases the abundance, diversity, and service of natural enemies in various perennial and annual crop systems (Lichtenberg et al., 2017; Muneret et al., 2018; Todd et al., 2011). However, its positive effect on the abundance of predatory arthropods, e.g. of spiders, differs between landscapes (Bengtsson et al., 2005). The interaction of landscape and local management is well predicted by the intermediate landscape complexity hypothesis, which states that organic management is more

beneficial at low and intermediate levels of landscape complexity, but less effective in highly-intensified and in natural landscapes (Tschamtko et al., 2012). Similarly, the impact of local habitat on the occurrence of natural enemies in orchards strongly depends on management (Lefebvre et al., 2016), but studies on interactions between management, adjacent habitat, and landscape factors on natural enemy communities are still rare (García et al., 2018; Martin et al., 2016). Comprehensive studies including these factors and their interactions are needed to develop agricultural practices and policies to promote effective and sustainable biological control across Europe.

In the production of apple, the most important European fruit crop (Eurostat, 2017), maintaining biological control is particularly important. Biological control by predatory arthropods in apple orchards has a high economic value as it may substantially reduce insecticide applications (Cross et al., 2015). Predators such as birds, earwigs, lacewings, bugs, coccinellids, syrphids and spiders have been identified as important biocontrol agents in apple orchards (Porcel et al., 2018; Simon et al., 2010; Solomon et al., 2000). They contribute crucially to the regulation of severe apple pests such as the rosy apple aphid *Dysaphis plantaginea* Passerini, the woolly apple aphid *Eriosoma lanigerum* Hausmann, and tortricid moths including the codling moth *Cydia pomonella* L. (Solomon et al., 2000). Hence, enhancement of these natural enemies can lower the level of pest pressure and decrease fruit damage (Cahenzli et al., 2017; Letourneau and Bothwell, 2008). Indirect positive effects from increased natural enemy abundance can even partly compensate for lower yield in organic apple orchards compared to integrated production (IP) orchards (Samnegård et al., 2018).

Here, we assess the effects of orchard management and features of adjacent habitats (local factors) as well as the effects of landscape composition (proportion of fruit orchard cover) and diversity (landscape factors) on predatory arthropods in the major apple production regions of three European countries (Spain, Germany, Sweden). Our aim is to identify favourable local and landscape factors to support predatory arthropods and to enhance their predation potential. We assess abundance of predatory arthropods in the study orchards and calculate their energy use by integrating predator body mass as a trait-based measure for predation potential (Perović et al., 2018). Energy use has been suggested as a proxy for prey consumption by predators and may serve as a currency for assessing ecosystem functioning (Brose et al., 2008; Hines et al., 2015).

We test the following hypotheses:

(1) The composition of predatory arthropod communities differs between countries and management types (organic vs. IP). (2) Responses to agricultural management and to local and landscape factors are taxon-specific: (a) most predatory arthropods (except earwigs) benefit from reduced orchard cover at the landscape scale and from enhanced landscape diversity; (b) a high cover of local, orchard-adjacent woody habitats as well as organic management support predatory arthropods but organic management may be more effective at intermediate levels of orchard cover; (c) abundance of flower-visiting predatory arthropods (e.g. bugs, lacewings and hoverflies) is higher in orchards with high local plant species richness. (3) Effects of local agri-environmental schemes and landscape factors differ between management types; they are more effective in supporting predatory arthropods in IP than in organic orchards. (4) Organic management, high quality local habitats, a reduced orchard cover at the landscape scale and increased landscape diversity enhance the overall biological control potential of predator communities, measured as community energy use.

2. Material and methods

2.1. Predator communities

Predator communities were surveyed in 2015 in 86 apple orchards in Spain, Germany and Sweden. Orchard management included integrated production (IP) and organic management (ORG). Survey

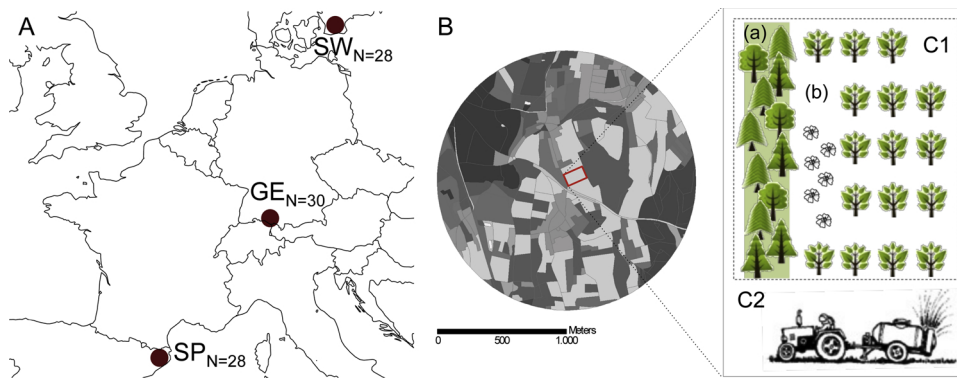


Fig. 1. Scales considered in this study: (A) country: Spain (SP), Germany (GE) and Sweden (SW); (B) landscape: composition and diversity within a 1 km radius around the orchard; (C) local scale: includes (C1) local habitat quality, i.e. (a) semi-natural woody habitat cover and (b) plant species richness, and (C2) orchard management (integrated production vs. organic management).

orchards were located in northeast Spain (Catalonia, hereafter ‘SP’; 14 IP and 14 ORG), southwest Germany (lake Constance region, Baden-Württemberg, hereafter ‘GE’; 15 IP and 15 ORG), and south Sweden (Skåne, hereafter ‘SW’; 14 IP and 14 ORG) (Fig. 1; see Table A1 for orchard characteristics). The minimum distance between orchards of different management types was 1 km in SP, 2 km in GE, and 0.3 km in SW. We conducted beating sampling on one branch of each of 24 randomly selected trees per orchard along one (SP and SW) or two (GE) transects. Branches were selected to occur at a standardized height of 1.2–1.5 m, and sampling targeted a branch section conforming to the diagonal width of the beating tray (0.60 m). Transects measured 40 m and started at the edge of the orchard. To cover different exposures, we sampled branches on both sides of each transect. We took samples when fruitlets were starting to grow (10–40% of final fruit size; SP: May 19–June 2; GE: June 15–22; SW: June 3–9) between 9 a.m. and 5 p.m. Arthropods were sorted from vegetation material and stored in 70% ethanol for quantification and identification under the stereo microscope. Predator abundance was calculated as the total number of predatory arthropods collected per orchard.

2.2. Landscape composition and diversity

We assessed landscape categories (Fig. 1) based on official digital maps for SP and GE (Carreras and Diego, 2009; LGL, 2016; SIOSE, 2015), and spatial land-use data from the Swedish Board of Agriculture (Integrated Administrative Control System, IACS) for SW. The Geographic Information Systems and Remote Sensing software used were ArcView 10.3.1 and MiraMon. Landscape analysis targeted cover (%) of orchards (excluding orchard meadows), grassland, arable land and forest (Table A1) within a 1 km radius around the centre of each transect. To avoid collinearity, we used % orchard cover as a measure of landscape composition. A high proportion of fruit orchard cover can be seen as a measure for homogeneous landscape composition and as a proxy for high land-use intensity in the studied apple production regions (Samnegård et al., 2018). Additionally, to quantify landscape diversity, we calculated the Shannon diversity index, $SHDI = -\sum_{i=1}^R p_i \ln p_i$ where p_i is the proportion of landscape patches belonging to the i th type of land cover (Shannon, 1948). The SHDI is recommended for landscape analyses in an ecological context (Nagendra, 2002). Landscape categories used to calculate SHDI were % cover of orchards, grassland, arable land, forest, semi-natural habitat (e.g. orchard meadows, woody habitats), sealed land, water bodies and ‘other cover types’ within a 1 km radius.

2.3. Local habitat quality

Hedgerows, forest edges and other woody elements, including orchard meadows, were considered relevant semi-natural woody habitats at the local scale (Fig. 1). We calculated the cover (m^2) of these woody structures within a radius of 20 m from the first tree (orchard

edge) of the survey transects (Table A1). Local habitat quality and availability of floral resources was estimated by plant species richness in habitats adjacent to orchards (Fig. 1). We conducted vegetation surveys within a radius of 20 m from the first tree of the survey transects (orchard edge), during apple bloom. We assessed overall species richness of plants in the herb- and shrub-layer using six quadrats of 1 m^2 per orchard in GE and SW. In SP, plant species richness was assessed in three quadrats of 1 m^2 per habitat type (e.g. abandoned field, embankment, forest edge, grassy pathway, and hedgerow) and orchard. To account for differences in the number of quadrats per orchard in SP, we used sample-based rarefaction (Gotelli and Colwell, 2001).

2.4. Orchard management

All apple growers conducted standard pesticide treatments using air-assisted sprayers, following label recommendations and advice from local plant protection consultants. IP growers applied synthetic insecticides, fungicides and fertilizers following IOBC guidelines (Malavolta and Cross, 2009). ORG orchards were certified under European and national legislation (Council Regulation (EC) No 834/2007). ORG growers used natural plant extracts, microorganisms, viruses, mating disruption, and fungicides based on sulphur, copper and lime sulphur for pest and disease control (Table A2). ORG growers tilled tree rows instead of applying herbicides and used only organic fertilizers. Management intensity within categories IP and ORG differed between countries because national regulations restrict the use of some active compounds, e.g. Azadirachtin, Pyrethrin, Pirimor or Phosmet (Table A2). Growers can adjust management intensity within the range of national regulations but we did not get access to data on treatments for all orchards. Some extensive orchards in SW and two orchards in SP were uncertified but were considered organic because they were managed as under organic guidelines, with no chemical inputs.

2.5. Energy use of the predator community

Metabolic rate, i.e. the amount of energy expended by an organism at rest, has been identified as a key trait of arthropods in responding to the environment, affecting biological control services at local and landscape scales (Moretti et al., 2017; Perović et al., 2018). The energy use of the local predator community integrates each species abundance and body mass and can, to some extent, be used as a proxy of predation potential because individual metabolic rates determine consumption rates according to the metabolic theory of ecology (Brown et al., 2004). The community energy use of the local predator community is frequently used in the context of food webs (Brose et al., 2008; Thompson et al., 2012). Here, we apply it as an indicator for predation potential. It was calculated for each orchard based on dry body mass and abundance of collected specimens of each predator species (Table A3) using a metabolic model (Ehnes et al., 2011):

$$\ln C = \sum_{s=1}^S \left[\left(\ln i_s + a_s \ln M_s - E_s \left(\frac{1}{kT} \right) \right) \times A_s \right]$$

where C = predator community energy use (J h^{-1}), M_s = dry mass (g) of species s , k = Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$), T = average local summer temperature in Kelvin and A_s = total abundance of species s . Intercepts i_s , allometric exponents a_s and activation energies E_s (eV) are taxon-specific and differ for arachnids and insects (see Table 2 in Ehnes et al., 2011). The community energy use is thus summed across all S species and multiplied by their respective abundance.

To parameterize the model, we measured dry mass (mg) of one adult female (if available and sex could be identified; otherwise dry mass of an adult male, or an unidentified adult was used) of each species. The individual was dried until mass constancy was reached (at least 48 h at 45°C). Juvenile stages and morphospecies (species that could not be identified to species level but were morphologically distinct) were assigned a taxon-specific average dry mass (and metabolic rate) value (for example, unidentified coccinellid larvae would be assigned the average coccinellid dry mass; Table A3). To calculate the average of summer temperature in each region, we used the minimum and maximum average of the June mean daily temperature, based on data from the last 30 years (WMO, 2018) for WMO-listed cities closest to the study area: Lleida (SP; 22.3°C), Girona (SP; 20.5°C), Freiburg (GE; 18.0°C) and Malmö (SW; 15.5°C).

2.6. Statistical analysis

All statistical analyses were conducted using R version 3.3.2 (R Core Team, 2016). We first checked for effects of country (SP, GE and SW) and management (IP vs. ORG) on the predator community composition using the 'vegan' package (Oksanen et al., 2016). We applied the 'adonis' function to conduct a permutational multivariate analysis of variance (Anderson, 2001; Oksanen et al., 2016) based on Bray-Curtis dissimilarities, which were calculated from the relative abundance (proportion at orchard level) of each taxon. To test for homogeneity of multivariate dispersion (variance), we applied the 'betadisper' function (Anderson, 2006). Subsequently, we calculated indicator values of taxa (IndVal; the product of the relative frequency and relative average abundance in clusters) for each management type in each country separately (Dufrene and Legendre, 1997) using the 'indval' function of the 'labdsv' package (Roberts, 2016).

Nonmetric multidimensional scaling (NMDS) ordination plots visualised differences in community composition across management types and countries. For SP, we excluded one IP orchard from multivariate analysis because no predatory arthropods were found. We added arrows to indicate the grouping of predator taxa (predictors) using the 'vegan' function 'envfit' at $P \leq 0.001$ with 10,000 permutations. Some orchards had the same proportion value and overlapped in the ordination and therefore not all included orchards are displayed.

To assess management effects on the abundance of each predator group (spiders, beetles, earwigs, predatory flies, predatory bugs, lacewings, and harvestmen) between countries, we used generalised linear models (GLM) with Poisson distribution; accounting for overdispersion by using a quasi-GLM or negative binomial distribution when necessary. We included 'country' and 'management' as categorical predictors, allowing for first order interactions. Variability accounted for (% deviance explained = null deviance - residual deviance / null deviance) is presented to show the goodness of fit of the model. Whenever a variable with multiple levels was significant in the GLM, we applied post-hoc tests (Table A4) using the 'glht' function for multiple comparisons of means (simultaneous tests for general linear hypotheses) with Tukey contrasts.

We used GLMs to analyse the effects of local and landscape factors on predator abundance for each predator group in each country separately. We included management (IP vs. ORG), and the continuous

variables local woody habitat cover, local plant species richness, % cover of fruit orchards and landscape diversity (SHDI). We allowed first level interactions among management and other predictors. Given the expected quadratic response of management effect to landscape cover predicted by the intermediate landscape complexity hypothesis (Tschamtko et al., 2012), we additionally allowed for an interaction of management with the second order term of the two landscape variables, % cover of fruit orchards and SHDI. Subsequently, we excluded terms that were non-significant ($P > 0.05$) based on a stepwise backwards procedure to avoid model over-parameterisation.

We applied GLMs with Poisson distribution. In cases of overdispersion or heteroscedasticity of residuals between predictor levels, we either fitted GLMs with a negative binomial error distribution or generalised linear mixed-effects models (GLMM) (lme4 package; Bates et al., 2015) with Poisson distribution including orchard identity as an observation-level random effect (Harrison, 2014). In case of zero inflation, we used the AD model builder of the 'glmmADMB' package (Skaug et al., 2016).

To test the effect of local and landscape factors on community energy use (J h^{-1}), we applied linear models. Energy use was log-transformed, adding a value corresponding to half the value of the smallest amount of energy use in the case of zero energy use. We calculated rarefied plant species richness for SP using the function 'rarefy' in the 'vegan' package (Oksanen et al., 2016). We tested for collinearity between predictors by calculating variance inflation factors (VIF; Naimi et al., 2014). When we detected collinearity ($\text{VIF} > 3$) after scaling, strongly correlated variables or their interactions were dropped (Zuur et al., 2010). We checked distributions and Spearman rank correlations between all relevant response variables as well as local and landscape variables (Figs. A4-6). Normality and homoscedasticity of residuals were checked by visual inspection using the 'DHARMA' package (Hartig, 2017) for all but zero-inflated models (not implemented in the 'DHARMA' package). Finally, we used the car package (Fox and Weisberg, 2011) to conduct likelihood ratio tests to establish the significance of the main factors in all GLMs, GLMMs and linear models. Fig. 2 and figures in the appendix were visualized using the 'ggplot2' package (Wickham, 2016).

3. Results

We sampled 1509 predatory arthropods in 86 orchards. The arthropods were identified as belonging to 91 species in 77 genera. Additional 17 morphospecies belonged to unidentified genera (resulting in 108 species in total; Fig. A1, Table A3). The predators belonged to seven arthropod groups: spiders (Araneae, 40 spp.), beetles (Coleoptera, 24 spp.), earwigs (Dermaptera, 2 spp.), predatory flies (Diptera, 28 spp.), predatory bugs (Heteroptera, 9 spp.), lacewings (Neuroptera, 3 spp.), and harvestmen (Opiliones, 2 spp.). Overall, predator abundance was higher in ORG than in IP orchards (Table A3). Orchards in GE showed higher predator abundances than in SP and SW (Table 1, Fig. 2). Specifically, in SP, we found less than half as many predatory arthropods than in GE or SW (Table 1, Fig. 2). Spiders were abundant in all countries, with *Araniella opisthographa* Kulczyński being the most abundant species and *Philodromus* Walckenaer being the most abundant genus. Other frequent taxa were bugs, mainly anthocorids and mirids, beetles, mainly cantharids, adult and larval coccinellids, and predatory dipterans, mainly dolichopodids, empidids, hybotids and larval syrphids. In SP, we found more *Forficula pubescens* Gené earwigs than *F. auricularia* L, but earwigs were generally rare in the samples. In GE and SW all earwigs were *F. auricularia* (Table A3). In GE, earwigs and predatory bugs comprised a large proportion of the predator community (Fig. 2). Dipterans were more abundant in SW than in the other countries (Table 1). Lacewings and harvestmen had low abundances in most orchards (Fig. 2, Table 1). As expected, there were strong positive correlations between abundance and predator community energy use in each country (SP: $\rho = 0.86$, $P < 0.001$; GE: $\rho = 0.54$, $P = 0.002$; SW: $\rho = 0.71$, $P < 0.01$).

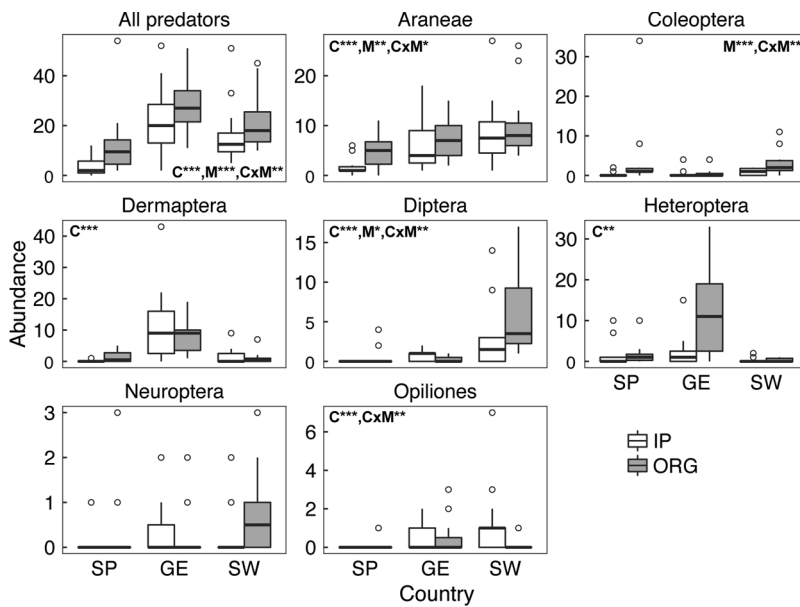


Fig. 2. Abundance (number of individuals per 24 trees per orchard) of seven predator taxa in apple orchards in Spain (SP), Germany (GE) and Sweden (SW). Effects of country (C) and management (M; integrated production 'IP' vs. organic 'ORG') on the abundance of each taxon are indicated within each plot (see Table A4 for summary statistics and post-hoc tests). Empty circles indicate outliers.

3.1. Predator responses to management in different countries

The interaction between country and management was significant for all predators (summed up over all groups) and for four out of seven predator groups (Fig. 2, Table A4). Depending on the country, the predator community composition differed between ORG and IP orchards (ADONIS: $pseudo-F_{5,79} = 2.51$, $P = 0.018$, $R^2 = 0.32$, Fig. 3). Dispersion among groups (multivariate spread) was homogeneous (beta-dispersion: $pseudo-F_{5,79} = 1.78$, $P = 0.126$). The analysis of indicator values for orchard management in each country revealed only one indicator taxon for IP orchards in SW: Opiliones: 0.5 (9), $P_{adj} = 0.027$; IndVal with frequency in parentheses. For ORG orchards, several indicator taxa were observed: three in SP (Coleoptera: 0.7 (14), $P_{adj} = 0.018$; Araneae: 0.6 (23), $P_{adj} = 0.047$, Dermaptera: 0.5 (8), $P_{adj} = 0.026$), one in GE (Heteroptera: 0.7 (22), $P_{adj} = 0.015$), two in SW (Coleoptera: 0.7 (21), $P_{adj} = 0.060$; Diptera: 0.7 (23), $P_{adj} = 0.060$).

3.2. Country-specific responses to local and landscape factors

Effects of local and landscape factors differed between countries and predatory arthropod groups (Table 1). We observed no consistent response of predatory arthropod groups to either of the tested local and landscape factors or to interactions between management and other factors across all three countries. In SP, high orchard cover at the landscape scale was associated with predator abundance in IP but not in ORG orchards, where predator abundance was constantly high (Fig. A2). Landscape diversity did not explain variability in predator abundance in any of the countries. We did not find a management-dependent peak in predator abundances at intermediate levels of orchard cover or intermediate landscape diversity. Local woody habitat cover influenced only two predator groups, earwigs and harvestmen. It enhanced harvestmen abundances in GE but showed contrasting effects on earwig abundances in different countries. It was associated with high earwig abundance in SW but with reduced abundance in GE (Table 1). In SP, woody habitat cover was very low (Table A1) and did not influence predator abundances. Local plant species richness (Table A5) in adjacent habitats reduced the abundance of predatory bugs in Spanish IP orchards (SP: $P = 0.010$, Table 1; Fig. A2). The effect of plant species richness was similar but not statistically significant for Heteroptera in Swedish IP and ORG orchards ($P = 0.070$; Table 1). The analysis of local and landscape factors confirmed the sensitivity of predatory

arthropods to orchard management (as already suggested by indicator values) for all predator groups except for beetles in SP (Table 1). However, most predator groups were influenced in only one or two countries, and the effects of management were not consistent (Table 1). In SP, the positive influence of ORG management on predator groups was reflected in predator community energy use. However, effects of management on energy use were not always similar to effects on abundance. Energy use was generally less sensitive than abundance (Table 1).

4. Discussion

4.1. Predator responses to management in different countries

We expected the responses of the predator communities to apple management to be consistent across Europe. Instead, predator communities showed country-specific differences in their sensitivity to management. Total predator abundance differed between management types only in Spain (SP) (significantly) and Germany (GE) (marginally significant), with higher abundances in ORG. This finding can be partly explained by country-specific differences in management intensity in both management types (IP and ORG), such as the restricted use of several insecticides in Sweden (SW) for both management types. However, lack of pesticide data at the orchard level in SW limits our understanding of management intensity in this region (Table A2). Alternatively, some of the different responses of the regional predator communities to management may be explained by latitudinal differences. These differences may for example influence predator and prey faunas, tree cultivar, and predominant land-cover types and local habitats (Mody et al., 2017; Nyffeler and Sunderland, 2003).

However, predator community responses to management at the country scale can be better understood when considering specific taxonomic groups (Fig. 2). It has been proven that predators such as lacewings, coleopterans, earwigs, and bugs are sensitive to insecticides applied in apple orchards (Fountain and Harris, 2015; Mills et al., 2016). Sub-lethal effects of both organic and synthetic pesticides on predatory bugs and other predatory arthropods are well known (Biondi et al., 2012; Desneux et al., 2007; Müller, 2018). Porcel et al. (2018) reported enhanced natural enemy abundance (and increased biological control of aphids) in organic apple orchards compared to conventional apple orchards; predatory bugs, which played a key role in regulating

Table 1

Effects of local and landscape factors¹ on (A) abundance of seven predatory arthropod groups and on (B) energy use of the predator community in apple orchards in Spain (SP), Germany (GE) and Sweden (SW); for each predator group, total abundance across sites for each country (number of individuals in all orchards) and the number of orchards in which the predator group was recorded (in parentheses) are indicated in bold. Effects on (B) total energy use by the predator community in bold as well. Orchard cover (%) was assessed at landscape scale (within 1 km), orchard management (IP vs. organic), plant species richness and woody habitat cover (m²) at local scale (within 20 m). χ^2 - and *P*-values² are given for reduced models (stepwise-backward selection) with estimates \pm S.E. in parentheses. 'NA' indicates that no analysis was possible, 'n.s.' that no significant effect was found.

	SP (N = 28)	GE (N = 30)	SW (N = 28)
(A) Abundance			
All predatory arthropods	224 (27)^a	755 (30)^b	530 (28)^a
Management	$\chi^2 = 16.07$ (1.25 \pm 0.31) <i>P</i> < 0.001 ***	$\chi^2 = 3.27$ (0.37 \pm 0.20) <i>P</i> = 0.070	n.s.
Orchard cover (%) ¹	$\chi^2 = 3.17$ (0.43 \pm 0.23) <i>P</i> = 0.075	n.s.	n.s.
Management \times orchard cover (%) ¹	$\chi^2 = 7.08$ (-0.84 \pm 0.31) <i>P</i> = 0.008 **	n.s.	n.s.
Araneae	89 (23)^a	201 (30)^a	261 (28)^a
Management	$\chi^2 = 10.69$ (1.11 \pm 0.35) <i>P</i> = 0.001 **	n.s.	n.s.
Coleoptera	58 (14)^{c, d}	13 (7)^c	55 (21)^a
Management	n.s.	n.s.	$\chi^2 = 9.52$ (1.17 \pm 0.39) <i>P</i> = 0.002 **
Dermoptera	21 (8)^a	290 (26)^a	36 (14)^c
Management	$\chi^2 = 11.72$ (3.00 \pm 1.12) <i>P</i> < 0.001 ***	n.s.	$\chi^2 = 6.89$ (-2.08 \pm 0.79) <i>P</i> = 0.009 **
Woody habitat cover ¹	n.s.	$\chi^2 = 9.73$ (-0.003 \pm 0.001) <i>P</i> = 0.002 **	$\chi^2 = 4.87$ (1.00 \pm 0.45) <i>P</i> = 0.027 *
Diptera	6 (2)^c	15 (13)^c	136 (23)^b
Management	n.s.	$\chi^2 = 3.00$ (-1.01 \pm 0.58) <i>P</i> = 0.083	$\chi^2 = 3.93$ (0.92 \pm 0.46) <i>P</i> = 0.047 *
Heteroptera	43 (15)^b	213 (22)^a	9 (7)^c
Management	$\chi^2 = 7.54$ (2.83 \pm 0.87) <i>P</i> = 0.006 **	$\chi^2 = 11.8$ (1.63 \pm 0.46) <i>P</i> < 0.001 ***	n.s.
Plant species richness ¹	$\chi^2 = 13.20$ (-2.18 \pm 0.60) <i>P</i> < 0.001 ***	n.s.	$\chi^2 = 3.27$ (-0.90 \pm 0.50) <i>P</i> = 0.070
Management \times plant species richness ¹	$\chi^2 = 6.66$ (1.76 \pm 0.68) <i>P</i> = 0.010 **	n.s.	n.s.
Neuroptera	6 (4)^c	9 (7)^c	15(10)^c
Opiliones	1 (1)	14 (9)^c	18 (9)^c
Management	NA	n.s.	$\chi^2 = 6.05$ (-2.76 \pm 1.12) <i>P</i> = 0.014 *
Woody habitat cover ¹	NA	$\chi^2 = 3.94$ (0.78 \pm 0.39) <i>P</i> = 0.047 *	n.s.
(B) Energy use			
Management	9.83 J h⁻¹	55.1 J h⁻¹	17.9 J h⁻¹
	<i>F</i> _{1,26} = 23.95 (1.59 \pm 0.33) <i>P</i> = < 0.001***	n.s.	n.s.
Woody habitat cover ¹	n.s.	<i>F</i> _{1,28} = 3.08 (-0.002 \pm 0) <i>P</i> = 0.09	n.s.

¹continuous variables were scaled to decrease VIF below 3; ²ANOVA type III; ^aGLM: negative binomial with log-link; ^bGLMM: poisson with log-link and observation level random effect in case of overdispersion; ^czero-inflation models glmmADMB with observation level random effect in case of overdispersion; ^dpositive effect of plant species richness on Coleoptera in Spain ($\chi^2 = 24.99$ (+), *P* < 0.001) if outlier is included (orchard E7: 33 years old).

the growth of aphid colonies, were the group that benefited most from organic management. Our results support these findings and point to at least three differences in insecticide application between countries (Table A2). (1) ORG management reduced abundances of earwigs and harvestmen in SW and had marginally significant negative effects on predatory flies in GE. The only commonly applied ORG-insecticide in SW known for side effects on earwigs was Pyrethrin (Peusens and

Gobin, 2008). Products based on this active ingredient were not permitted in SP and only rarely applied in GE. The application of neem (*Azadirachta indica*) products as ORG insecticides in GE and SP but not in SW may partly explain patterns of dipteran abundance. Azadirachtin, a component of neem oil that repels feeding and inhibits moulting, can harm dipterans, especially those in their larval stages (Schmutterer, 1997; Spollen and Isman, 1996). (2) Focusing on IP orchards, we found

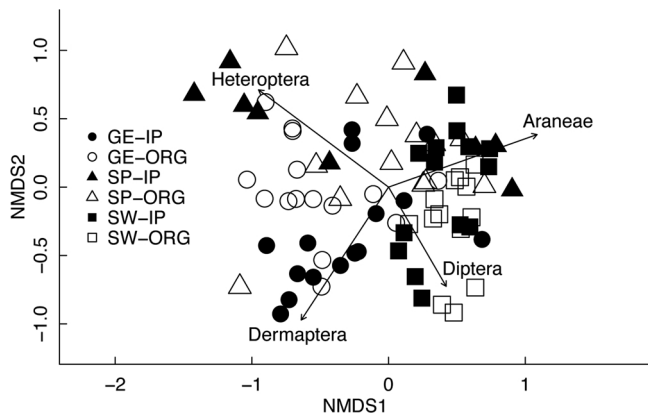


Fig. 3. Ordination of predatory arthropod communities in apple orchards in Spain (SP), Germany (GE) and Sweden (SW) for two management types: integrated production (IP) and organic management (ORG). Grouping of taxa (arrows) along the two first axes of the NMDS (stress = 16.8%, 20 procrustes). Arrow length indicates the strength of predictors (taxa) fitted onto the ordination for $P \leq 0.001$.

lower predator abundances for spiders and earwigs in SP that can be explained as side effects of synthetic insecticides. IP growers in SP (exclusively) applied several insecticides containing the active compounds Chlorpyrifos or Deltamethrin, both known for their harmful side effects on spiders (Markó et al., 2009; Pekár and Beneš, 2008), and Phosmet, which belongs to the group of organophosphates, known for their harmful side effects on earwigs (Malagnoux et al., 2015a; Peusens and Gobin, 2008). (3) Regular application of Pirimicarb and Thiacloprid in IP may explain a positive effect of ORG on bugs in GE (van de Veire et al., 2002; van de Veire and Tirry, 2003).

However, the absence of spray information at the orchard level limits our capacity to link agrochemical applications to predator abundance. In addition, soil management in the tree row (herbicide application in IP; mulching and mechanical weed control or tillage in ORG) can affect epigeic predators and earwigs (Miñarro et al., 2009; Moerkens et al., 2012). The non-consistent response of earwigs to management in SW and SP may have been triggered by differences in regional management and in species composition. In SP, we found two earwig species, whereas only one species was present in SW (and GE). The two species found in SP markedly differed in their sensitivity to management: *Forficula auricularia* was common in both IP and ORG orchards, whereas *F. pubescens* was much less abundant in IP orchards (Happe et al., 2018). On the other hand, earwigs' sensitivity to tillage during hibernation and below-ground brood care may explain lower *F. auricularia* abundances in ORG orchards in SW (Moerkens et al., 2012). When interpreting abundance patterns of predatory arthropods, it should be considered that species richness and regional species composition differed not only for earwigs but also for other focal groups such as predatory flies and spiders (Fig. A1, Table A3). In addition to the toxic effects of pesticides, differences between ORG and IP may be partly explained by the higher pest densities in ORG orchards, which may support larger predator populations (Samnegård et al., 2018).

4.2. Country-specific responses to local and landscape factors

Intensive orchard management may alter or even counteract other local factors as well as landscape factors (Tschamtkke et al., 2016), and landscape features may alter the effectiveness of local habitat and organic management in supporting biological control (Jonsson et al., 2015; Tschamtkke et al., 2012). In this study, orchard management directly influenced the abundance of six out of seven predatory arthropod groups (sometimes in opposite directions, Table 1). Yet, interactions between management and local or landscape factors were only evident in two cases. Firstly, plant species richness was associated with low

predatory bug abundance in IP but not in ORG, indicating that effects of local habitat are management-dependent. Secondly, ORG management enhanced predator abundance only at low levels of orchard cover in Spanish landscapes. The intermediate landscape complexity hypothesis highlights the effectiveness of ORG management to support biodiversity at intermediate cover levels of semi-natural habitats and non-crop areas, which provide arthropod biodiversity to crops through spillover effects (Batáry et al., 2010; Tschamtkke et al., 2012). High levels of orchard cover at landscape scale reduced the availability and accessibility of semi-natural habitats. This may be of special relevance in IP orchards, where predatory arthropods are subjected to greater hazards. A peak in predator abundance in ORG orchards at intermediate levels of landscape diversity or orchard cover was not evident.

At the local scale, woody habitat had mixed effects on predator abundances. High local woody habitat coverage enhanced earwig abundance in SW (but reduced it in GE), and harvestmen abundance in GE. In the context of augmenting biological control, woody habitat quality has often been characterised in terms of woody plant species richness, cover and connectivity (Dainese et al., 2016; Malagnoux et al., 2015b). For example, linyphid spiders have been reported to use continuous unbroken hedgerows with a high diversity of woody species as source habitats, spilling over to neighbouring crops (Garratt et al., 2017). Differences in quality of woody structures may have driven the contrasting responses of earwigs and harvestmen to woody elements in the three countries. On the other hand, plant species richness did not alter earwig or harvestmen abundances in either country (Table 1). It may be that regional differences in the response of the two groups were triggered by spillover constrained by the density of prey in the woody habitat. Results for harvestmen (and lacewings) should be interpreted cautiously because the number of individuals was low (Table 1).

Other studies have provided evidence that enhancing local plant diversity by establishing flower strips improves living conditions for beneficial arthropods (Batáry et al., 2015; Letourneau et al., 2011; Lichtenberg et al., 2017). A high local flower richness is especially important for natural enemies in orchards that lack woody habitats in the vicinity (Saunders and Luck, 2018). Contrary to these findings, we observed negative influences of plant species richness on predatory bugs in SW (marginally significant), and no effects on the other groups. Some particularly prominent bugs in apple orchards (e.g. anthocorids, Table A3) use floral nectar and pollen as a food resource (Wäckers and van Rijn, 2012). However, plant species richness did reduce rather than enhance bug abundance and the response of bugs to plant species richness was inconsistent among countries. The presence and flower cover of a few favoured plant species may be more relevant than total plant species richness (Wäckers and van Rijn, 2012). On the other hand, bugs could be more attracted by flower-rich adjacent habitats than by intensively managed IP orchards. Results for orchards in SP could support this explanation: In SP high plant species richness was associated with low bug abundance in IP but not in ORG orchards (Fig. A2). Management intensity may reduce the attractiveness of the orchard as a habitat, especially if food resources for beneficial arthropods are affected. For instance, insecticide applications can diminish prey insects, and weed control may reduce plant species richness and flower cover (Cross et al., 2015; Miñarro, 2012; Simon et al., 2010). In this case, high-quality adjacent habitats, such as sown flower strips, can potentially provide a suitable if not a better environment for a wide range of herbivores. As a result, natural enemies may not disperse from the adjacent habitat into the crop (Holland et al., 2016; Tschamtkke et al., 2016). This could also explain the lower earwig abundance in orchards with enhanced woody habitat cover in GE (Happe et al., 2018).

Effects of local and landscape factors on overall predation potential (measured as energy use) mainly resembled the response of the largest and most abundant taxon in each country. Such large, abundant predatory arthropods (e.g. spiders in SP and earwigs in GE) are likely to contribute strongly to biological control of their specific prey taxa. In general, community energy use was less sensitive than abundance to

local and landscape factors, reflecting body mass distribution (Fig. A3). The effectiveness of predators is well predicted by mean predator body size with larger predators showing higher per capita consumption rates (Emmerson and Raffaelli, 2004; Rusch et al., 2016). Positive influence of higher abundance and biomass on biological control is necessarily constrained in cold climates by energetic demand (Londoño et al., 2015; Schneider et al., 2012). Energy use may therefore be more relevant than abundance and biomass to describe the biological control potential of predator communities along a geographical gradient with large climatic differences.

5. Conclusion

Our results suggest that management plays an important role in shaping communities of predatory arthropods in orchards across Europe. ORG management enhanced abundance of some predator groups depending on country but only a few generalist predator groups benefited from high quality local habitat. Landscape composition and interactions of orchard management with local and landscape factors seemed to be less relevant for predators than local management and habitat quality. Predation potential (energy use by the predator community) can be enhanced by ORG management but it remains largely unaffected by local and landscape factors. We conclude that conservation measures and agri-environmental schemes to foster effective predator communities in apple orchards need to be well adapted to the target region. They should take the taxonomic identity of predatory arthropods and region-specific management intensity into account. The local knowledge of growers and their advisers on specific site conditions and requirements from ecosystem services may be the key to more targeted and dynamic management strategies.

Author contributions

JB, NB, DG, AKH, PAH, AMK, KM, MM, AR and MT conceived the ideas for the paper and designed the studies; GA, JB, LRB, VB, AKH, PAH, AKM, MP, AR, MT and US collected the data; AKH analysed the data and led the writing of the manuscript with substantial input from PAH and KM. All authors contributed to the development of ideas and drafts and provided final approval to publication.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <https://doi.org/10.1016/j.agee.2018.12.012>.

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