

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

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4 Anne-Kathrin Happe^{1,2}, Georgina Alins³, Nico Blüthgen¹, Virginie Boreux⁴, Jordi
5 Bosch⁵, Daniel García⁶, Peter A. Hambäck⁷, Alexandra-Maria Klein⁴, Rodrigo
6 Martínez-Sastre⁸, Marcos Miñarro⁸, Ann-Kathrin Müller¹, Mario Porcel⁹, Anselm
7 Rodrigo⁵, Laura Roquer-Beni⁵, Ulrika Samnegård^{7,10}, Marco Tasin⁹, Karsten Mody¹

8

9 ¹Dept Biology, Technische Universität Darmstadt, Darmstadt, Germany, ²Earth
10 System Knowledge Platform, Alfred Wegener Institute Helmholtz Center for Polar
11 and Marine Research, Bremerhaven, Germany, ³Institut de Recerca i Tecnologia
12 Agroalimentàries, Lleida, Spain, ⁴Chair of Nature Conservation and Landscape
13 Ecology, University of Freiburg, Freiburg, Germany, ⁵CREAF, Universitat Autònoma
14 de Barcelona, Cerdanyola del Vallès, Spain, ⁶Unidad Mixta de Investigación en
15 Biodiversidad, Universidad de Oviedo, Oviedo, Spain, ⁷Dept Ecology, Environment
16 and Plant Sciences, Stockholm University, Stockholm, Sweden, ⁸Servicio Regional de
17 Investigación y Desarrollo Agroalimentario, Asturias, Spain, ⁹Dept Plant Protection
18 Biology, Swedish University of Agricultural Sciences, Alnarp, Sweden, ¹⁰Dept
19 Biology, Lund University, Lund, Sweden

20

21 Corresponding authors:

22 A.-K. Happe and K. Mody, Ecological Networks, Technische Universität Darmstadt,
23 Schnittspahnstr. 3, 64287 Darmstadt, Germany; Tel.: +49-6151-1675414. E-
24 mail: ahappe@posteo.net (Anne-K. Happe); mody@bio.tu-darmstadt.de (K. Mody).

25

27 **Abstract**

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

52 differs between countries. Our results indicate that organic management improves the
53 living conditions for effective predator communities.

54

55 **Keywords:** Agri-environmental scheme; Biological control; Integrated pest
56 management; Natural enemy; Organic management; Woody habitat

57

58 **Introduction**

59 Sustainable agricultural practices and enhanced habitat conservation at local and
60 landscape scales are considered key solutions to stop the accelerating degradation of
61 ecosystem services (IPBES, 2018). Biological control of agricultural pests is a
62 prominent example of nature's contribution to human welfare. Favourable local and
63 landscape factors can enhance predator communities and biological control
64 (Bengtsson et al., 2005; Bianchi et al., 2006; Tschumi et al., 2016). In taking
65 responsibility for sustainable land use and ecosystem services, we need to identify the
66 effects of factors that explain the variability in arthropod communities and their
67 potential services at different spatial scales, from climatic region, to landscape, to the
68 orchard itself and its immediate local surroundings.

69 The country scale comprises several factors beyond macroclimate and
70 biogeographic species pools. These include national policies on pesticides, differences
71 in landscape habitat loss, identity of common crops, and availability of public
72 advisory services. At the landscape scale, natural enemies benefit from a high
73 proportion of semi-natural habitats (Chaplin-Kramer and Kremen, 2012; but see
74 Hawro et al., 2015; Tschamtkke et al., 2005). However, landscape effects on natural
75 enemies also depend on taxon-specific mobility and dispersal capacity (Gallé et al.,
76 2018; Schweiger et al., 2005). For spiders, habitat diversity and landscape
77 composition are major determinants of occurrence at the landscape scale (Schweiger
78 et al., 2005). In contrast, less mobile predatory arthropods such as earwigs remain
79 mostly unaffected by the proportion of crop vs. non-crop cover in the landscape
80 | (Happe et al., 2018). ~~With respect to the function of natural enemies,~~ Landscape
81 | simplification as reflected by a high proportion of intensive agricultural cover reduces
82 | biological pest control (Rusch et al., 2016; Tschamtkke et al., 2016). ~~Ch~~

83 | eonsequentlyee, a reduced proportion of intensive agricultural land and a high
84 | landscape complexity are often regarded as of special relevance to enhance biological
85 | control (Jonsson et al., 2015). For example, in landscapes dominated by cultivated
86 | land, biological control of aphids in different annual crop systems can be reduced by
87 | 46% when compared with more heterogeneous landscapes (Rusch et al., 2016).

88 | Besides country and landscape effects, local factors such as adjacent habitat
89 | and orchard management influence natural enemies. At both landscape and local
90 | scales, the European Union subsidises agri-environmental schemes to enhance the
91 | ecological value of agro-ecosystems (Batáry et al., 2015). These schemes differ
92 | between countries and can, for example, protect diverse types of agro-ecosystems and
93 | cultural landscapes, support organic farmers, and enhance local habitat quality for
94 | natural enemies (e.g. in case of beetle banks and flower strips) (Batáry et al., 2015;
95 | Ekroos et al., 2014). Semi-natural woody habitats such as hedgerows or traditional
96 | orchards may shelter overwintering predatory arthropods such as coccinellid beetles
97 | and spiders (Elliott et al., 2002; Mestre et al., 2018). Improvement of local habitat
98 | quality in the orchard surroundings, for example by hedgerow restoration, can
99 | promote beneficial insects and natural pest control (Miñarro and Prida, 2013;
100 | Morandin et al., 2016). These habitats are more beneficial for predators than for pests
101 | and support predatory arthropods in fruit crops by enhancing habitat connectivity
102 | (Bailey et al., 2010). In addition to woody habitats, herbaceous plants may improve
103 | living conditions for natural enemies and the delivery of ecosystem services
104 | (Lichtenberg et al., 2017; Norris and Kogan, 2005). Flower-rich boundaries of crop
105 | orchards are particularly important for natural enemies that depend on pollen or
106 | nectar, which provideing sugars and amino acids, for at least one partat-some-stage of
107 | their life cycle. These floral resources are essential for hoverflies, lacewings,

108 hymenopteran parasitoids and omnivorous bugs such as anthocorids (Gurr et al.,
109 | 2017; Wäckers and van Rijn, 2012). Herbal orchards boundaries can also enhance the
110 | trait diversity of spiders, which may increase the biological control potential of spider
111 | communities (Gallé et al., 2018).

112 | Another factor acting at the local scale is organic management. It increases the
113 | abundance, diversity, and service of natural enemies in various perennial and annual
114 | crop systems (Lichtenberg et al., 2017; Muneret et al., 2018; Todd et al., 2011).
115 | However, its positive effect on the abundance of predatory arthropods, e.g. of spiders,
116 | differs between landscapes (Bengtsson et al., 2005). The interaction of landscape and
117 | local management is well predicted by the intermediate landscape complexity
118 | hypothesis, which states that organic management is more beneficial at low and
119 | intermediate levels of landscape complexity, but less effective in highly-intensified
120 | and in natural landscapes (Tscharntke et al., 2012). Similarly, the impact of local
121 | habitat on the occurrence of natural enemies in orchards strongly depends on
122 | management (Lefebvre et al., 2016), but studies on interactions between management,
123 | adjacent habitat, and landscape factors on natural enemy communities are still rare
124 | (García et al., 2018; Martin et al., 2016). Comprehensive studies including these
125 | factors and their interactions are needed to develop agricultural practices and policies
126 | to promote effective and sustainable biological control across Europe.

127 | In the production of apple, the most important European fruit crop (Eurostat,
128 | 2017), maintaining biological control is particularly important. Biological control by
129 | predatory arthropods in apple orchards has a high economic value as it may
130 | substantially reduce insecticide applications (Cross et al., 2015). Predators such as
131 | birds, earwigs, lacewings, bugs, coccinellids, syrphids and spiders have been
132 | identified as important biocontrol agents in apple orchards (Porcel et al., 2018; Simon

133 et al., 2010; Solomon et al., 2000). They contribute crucially to the regulation of
134 severe apple pests such as the rosy apple aphid *Dysaphis plantaginea* Passerini, the
135 woolly apple aphid *Eriosoma lanigerum* Hausmann, and tortricid moths including the
136 codling moth *Cydia pomonella* L. (Solomon et al., 2000). Hence, enhancement of
137 these natural enemies can lower the level of pest pressure and decrease fruit damage
138 (Cahenzli et al., 2017; Letourneau and Bothwell, 2008). Indirect positive effects from
139 increased natural enemy abundance can even partly compensate for lower yield in
140 organic apple orchards compared to integrated production (IP) orchards (Samnegård
141 et al., 2018).

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

153

154 We test the following hypotheses:

155 (1) The composition of predatory arthropod communities differs between countries
156 and management types (organic vs. IP). (2) Responses to agricultural management
157 and to local and landscape factors are taxon-specific: (a) most predatory arthropods

158 (except earwigs) benefit from reduced orchard cover at the landscape scale and from
159 enhanced landscape diversity; (b) a high cover of local, orchard-adjacent woody
160 habitats as well as organic management support predatory arthropods but organic
161 management may be more effective at intermediate levels of orchard cover; (c)
162 abundance of flower-visiting predatory arthropods (e.g. bugs, lacewings and
163 hoverflies) is higher in orchards with high local plant species richness. (3) Effects of
164 local agri-environmental schemes and landscape factors differ between management
165 types; they are more effective in supporting predatory arthropods in IP than in organic
166 orchards. (4) Organic management, high quality local habitats, a reduced orchard
167 cover at the landscape scale and increased landscape diversity enhance the overall
168 biological control potential of predator communities, measured as community energy
169 use.

170

171 **Material and Methods**

172

173 *Predator communities*

174 Predator communities were surveyed in 2015 in 86 apple orchards in Spain, Germany
175 and Sweden. Orchard management included integrated production (IP) and organic
176 management (ORG). Survey orchards were located in ~~northeast~~^{NE} Spain (Catalonia,
177 hereafter 'SP'; 14 IP and 14 ORG), ~~SW~~^{southwest} Germany (lake Constance region,
178 Baden-Württemberg, hereafter 'GE'; 15 IP and 15 ORG), and ~~south~~^S Sweden (Skåne,
179 hereafter 'SW'; 14 IP and 14 ORG) (Fig. 1; see Table A1 for orchard characteristics).
180 The minimum distance between orchards of different management types was 1 km in
181 SP, 2 km in GE, and 0.3 km in SW. We conducted beating sampling on one
182 ~~representative~~ branch of each of 24 randomly selected trees per orchard along one (SP

183 and SW) or two (GE) transects. Branches were selected to occur at a standardized
184 height of 1.2 – 1.5 m, and sampling targeted a branch section conforming to the
185 diagonal width of the beating tray (0.60 m). Transects measured 40 m and started at
186 the edge of the orchard. To cover different exposures, we sampled branches on both
187 sides of each transect. We took samples when fruitlets were starting to grow (10 -
188 40% of final fruit size; SP: May 19 - June 2; GE: June 15 - 22; SW: June 3 - 9)
189 between 9 am and 5 pm. Arthropods were sorted from vegetation material and stored
190 in 70% ethanol for quantification and identification under the stereo microscope.
191 Predator abundance was calculated as the total number of predatory arthropods
192 collected per orchard.

193

194 *Landscape composition and diversity*

195 We assessed landscape categories (Fig. 1) based on official digital maps for SP and
196 GE (Carreras and Diego, 2009; LGL, 2016; SIOSE, 2015), and spatial land-use data
197 from the Swedish Board of Agriculture (Integrated Administrative Control System,
198 IACS) for SW. The Geographic Information Systems and Remote Sensing software
199 used were ArcView 10.3.1 and MiraMon. Landscape analysis targeted cover (%) of
200 orchards (excluding orchard meadows), grassland, arable land and forest (Table A1)
201 within a 1 km radius around the centre of each transect. To avoid collinearity, we used
202 % orchard cover as a measure of landscape composition. A high proportion of fruit
203 orchard cover can be seen as a measure for homogeneous landscape composition and
204 as a proxy for high land-use intensity in the studied apple production regions
205 (Samnegård et al., 2018). Additionally, to quantify landscape diversity, we calculated
206 the Shannon diversity index, $SHDI = - \sum_{i=1}^R p_i \ln p_i$, where p_i is the proportion of
207 landscape patches belonging to the i th type of land cover (Shannon, 1948). The SHDI is

208 recommended for landscape analyses in an ecological context (Nagendra, 2002).
209 Landscape categories used to calculate SHDI were % cover of orchards, grassland,
210 arable land, forest, semi-natural habitat (e.g. orchard meadows, woody habitats),
211 sealed land, water bodies and 'other cover types' within a 1 km radius.

212

213 *Local habitat quality*

214 Hedgerows, forest edges and other woody elements, including orchard meadows,
215 were considered relevant semi-natural woody habitats at the local scale (Fig. 1). We
216 calculated the cover (m²) of these woody structures within a radius of 20 m from the
217 first tree (orchard edge) of the survey transects (Table A1). Local habitat quality and
218 availability of floral resources was estimated by plant species richness in habitats
219 adjacent to orchards (Fig. 1). We conducted vegetation surveys within a radius of 20
220 m from the first tree of the survey transects (orchard edge), during apple bloom. We
221 assessed overall species richness of plants in the herb and shrub layer using six
222 quadrats of 1 m² per orchard in GE and SW. In SP, plant species richness was
223 assessed in three quadrats of 1 m² per habitat type (e.g. abandoned field, embankment,
224 forest edge, grassy pathway, and hedgerow) and orchard. To account for differences
225 in the number of quadrats per orchard in SP, we used sample-based rarefaction
226 (Gotelli and Colwell, 2001).

227

228 *Orchard management*

229 All apple growers conducted standard pesticide treatments using air-assisted sprayers,
230 following label recommendations and advice from local plant protection consultants.
231 IP growers applied synthetic insecticides, fungicides and fertilizers following IOBC
232 guidelines (Malavolta and Cross, 2009). ORG orchards were certified under European

233 and national legislation (Council Regulation (EC) No 834/2007). ORG growers used
234 natural plant extracts, microorganisms, viruses, mating disruption, and fungicides
235 based on sulphur, copper and lime sulphur for pest and disease control (Table A2).
236 ORG growers tilled tree rows instead of applying herbicides and used only organic
237 fertilizers. Management intensity within categories IP and ORG differed between
238 countries because national regulations restrict the use of some active compounds, e.g.
239 Azadirachtin, Pyrethrine, Pirimor or Phosmet (Table A2). Growers can adjust
240 management intensity within the range of national regulations but we did not get
241 access to data on treatments for all orchards. Some extensive orchards in SW and two
242 orchards in SP were uncertified but were considered organic because they were
243 managed as under organic guidelines, with no chemical inputs.

244

245 *Energy use of the predator community*

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

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

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

264 To parameterize the model, we measured dry mass (mg) of one adult female
 265 (if available and sex could be identified; otherwise dry mass of an adult male, or an
 266 unidentified adult was used) of each species. The individual was dried until mass
 267 constancy was reached (at least 48 hours at 45 °C). Juvenile stages and
 268 morphospecies (species that could not be identified to species level but were
 269 morphologically distinct) were assigned a taxon-specific average dry mass (and
 270 metabolic rate) value (for example, unidentified coccinellid larvae would be assigned
 271 the average coccinellid dry mass; Table A3). To calculate the average of summer
 272 temperature in each region, we used the minimum and maximum average of the June
 273 mean daily temperature, based on data from the last 30 years (WMO, 2018) for
 274 WMO-listed cities closest to the study area: Lleida (SP; 22.3 °C), Girona (SP; 20.5
 275 °C), Freiburg (GE; 18.0 °C) and Malmö (SW; 15.5 °C).

276

277 *Statistical analysis*

278 All statistical analyses were conducted using R version 3.3.2 (R Core Team, 2016).
 279 We first checked for effects of country (SP, GE and SW) and management (IP vs.
 280 ORG) on the predator community composition using the 'vegan' package (Oksanen et

281 al., 2016). We applied the ‘adonis’ function to conduct a permutational multivariate
282 analysis of variance (Anderson, 2001; Oksanen et al., 2016) based on Bray-Curtis
283 dissimilarities, which were calculated from the relative abundance (proportion at
284 orchard level) of each taxon. To test for homogeneity of multivariate dispersion
285 (variance), we applied the ‘betadisper’ function (Anderson, 2006). Subsequently, we
286 calculated indicator values of taxa (IndVal; the product of the relative frequency and
287 relative average abundance in clusters) for each management type in each country
288 separately (Dufrêne and Legendre, 1997) using the ‘indval’ function of the ‘labdsv’
289 package (Roberts, 2016).

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

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

306 'glht' function for multiple comparisons of means (simultaneous tests for general
307 linear hypotheses) with Tukey contrasts.

308 We used GLMs to analyse the effects of local and landscape factors on
309 predator abundance for each predator group in each country separately. We included
310 management (IP vs. ORG), and the continuous variables local woody habitat cover,
311 local plant species richness, % cover of fruit orchards and landscape diversity (SHDI).
312 We allowed first level interactions among management and other predictors. Given
313 the expected quadratic response of management effect to landscape cover predicted
314 by the intermediate landscape complexity hypothesis (Tscharntke et al., 2012), we
315 additionally allowed for an interaction of management with the second order term of
316 the two landscape variables, % cover of fruit orchards and SHDI. Subsequently, we
317 excluded terms that were non-significant ($P > 0.05$) based on a stepwise backwards
318 procedure to avoid model over-parameterisation.

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

326 To test the effect of local and landscape factors on community energy use (J h^{-1})
327 ¹), we applied linear models. Energy use was log-transformed, adding a value
328 corresponding to half the value of the smallest amount of energy use in the case of
329 zero energy use. We calculated rarefied plant species richness for SP using the
330 function 'rarefy' in the 'vegan' package (Oksanen et al., 2016). We tested for

331 collinearity between predictors by calculating variance inflation factors (VIF; Naimi
332 et al., 2014). When we detected collinearity ($VIF > 3$) after scaling, strongly
333 correlated variables or their interactions were dropped (Zuur et al., 2010). We
334 checked distributions and Spearman rank correlations between all relevant response
335 variables as well as local and landscape variables (Figs. A4-6). Normality and
336 homoscedasticity of residuals were checked by visual inspection using the
337 ‘DHARMA’ package (Hartig, 2017) for all but zero-inflated models (not implemented
338 in the ‘DHARMA’ package). Finally, we used the car package (Fox and Weisberg,
339 2011) to conduct likelihood ratio tests to establish the significance of the main factors
340 in all GLMs, GLMMs and linear models. Figure 2 and figures in the appendix were
341 visualized using the ‘ggplot2’ package (Wickham, 2016).

342

343 **Results**

344 We sampled 1,509 predatory arthropods in 86 orchards. The arthropods were
345 identified as belonging to 91 species in 77 genera. Additional 17 morphospecies
346 belonged to unidentified genera (resulting in 108 species in total; Fig. A1, Table A3).
347 The predators belonged to seven arthropod groups: spiders (Araneae, 40 spp.), beetles
348 (Coleoptera, 24 spp.), earwigs (Dermaptera, 2 spp.), predatory flies (Diptera, 28 spp.),
349 predatory bugs (Heteroptera, 9 spp.), lacewings (Neuroptera, 3 spp.), and harvestmen
350 (Opiliones, 2 spp.). Overall, predator abundance was higher in ORG than in IP
351 orchards (Table A3). Orchards in GE showed higher predator abundances than in SP
352 and SW (Table 1, Fig. 2). Specifically, in SP, we found less than half as many
353 predatory arthropods than in GE or SW (Table 1, Fig. 2). Spiders were abundant in all
354 countries, with *Araniella opisthographa* Kulczyński being the most abundant species
355 and *Philodromus* Walckenaer being the most abundant genus. Other frequent taxa

356 were bugs, mainly anthocorids and mirids, beetles, mainly cantharids, adult and larval
357 coccinellids, and predatory dipterans, mainly dolichopodids, empidids, hybotids and
358 larval syrphids. In SP, we found more *Forficula pubescens* Gené earwigs than *F.*
359 *auricularia* L, but earwigs were generally rare in the samples. In GE and SW all
360 earwigs were *F. auricularia* (Table A3). In GE, earwigs and predatory bugs
361 comprised a large proportion of the predator community (Fig. 2). Dipterans were
362 more abundant in SW than in the other countries (Table 1). Lacewings and
363 harvestmen had low abundances in most orchards (Fig. 2, Table 1). As expected, there
364 were strong positive correlations between abundance and predator community energy
365 use in each country (SP: $\rho = 0.86$, $P < 0.001$; GE: $\rho = 0.54$, $P = 0.002$; SW: $\rho = 0.71$,
366 $P < 0.01$).

367

368 *Predator responses to management in different countries*

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

381

382 *Country-specific responses to local and landscape factors*

383 Effects of local and landscape factors differed between countries and predatory
384 arthropod groups (Table 1). We observed no consistent response of predatory
385 arthropod groups to either of the tested local and landscape factors or to interactions
386 between management and other factors across all three countries. In SP, high orchard
387 cover at the landscape scale was associated with predator abundance in IP but not in
388 ORG orchards, where predator abundance was constantly high (Fig. A2). Landscape
389 diversity did not explain variability in predator abundance in any of the countries. We
390 did not find a management-dependent peak in predator abundances at intermediate
391 levels of orchard cover or intermediate landscape diversity. Local woody habitat
392 cover influenced only two predator groups, earwigs and harvestmen. It enhanced
393 harvestmen abundances in GE but showed contrasting effects on earwig abundances
394 in different countries. It was associated with high earwig abundance in SW but with
395 reduced abundance in GE (Table 1). In SP, woody habitat cover was very low (Table
396 A1) and did not influence predator abundances. Local plant species richness (Table
397 A5) in adjacent habitats reduced the abundance of predatory bugs in Spanish IP
398 orchards ~~as well as in Swedish IP and ORG orchards~~ (SP: $P = 0.010$, [Table 1](#); Fig.
399 [A2](#); ~~SW: $P = 0.070$; Table 1~~). [The effect of plant species richness was similar but not](#)
400 [statistically significant for Heteroptera in Swedish IP and ORG orchards \(\$P = 0.070\$;](#)
401 [Table 1\)](#). The analysis of local and landscape factors confirmed the sensitivity of
402 predatory arthropods to orchard management (as already suggested by indicator
403 values) for all predator groups except for beetles in SP (Table 1). However, most
404 predator groups were influenced in only one or two countries, and the effects of
405 management were not consistent (Table 1). In SP, the positive influence of ORG

406 management on predator groups was reflected in predator community energy use.
407 However, effects of management on energy use were not always similar to effects on
408 abundance. Energy use was generally less sensitive than abundance (Table 1).

409

410 **Discussion**

411 *Predator responses to management in different countries*

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

427 However, predator community responses to management at the country scale
428 can be better understood when considering specific taxonomic groups (Fig. 2). It has
429 been proven that predators such as lacewings, coleopterans, earwigs, and bugs are
430 sensitive to insecticides applied in apple orchards (Fountain and Harris, 2015; Mills et

431 al., 2016). Sub-lethal effects of both organic and synthetic pesticides on predatory
432 bugs and other predatory arthropods are well known (Biondi et al., 2012; Desneux et
433 al., 2007; Müller, 2018). Porcel et al. (2018) reported enhanced natural enemy
434 abundance (and increased biological control of aphids) in organic [apple orchards](#)
435 compared to conventional apple orchards; predatory bugs, which played a key role in
436 regulating the growth of aphid colonies, were the group that benefited most from
437 organic management. Our results support these findings and point to at least three
438 differences in insecticide application between countries (Table A2). (1) ORG
439 management reduced abundances of earwigs and harvestmen in SW and had
440 marginally significant negative effects on predatory flies in GE. The only commonly
441 applied ORG-insecticide in SW known for side effects on earwigs was Pyrethrine
442 (Peusens and Gobin, 2008). Products based on this active ingredient were not
443 permitted in SP and only rarely applied in GE. The application of neem (*Azadirachta*
444 *indica*) products as ORG insecticides in GE and SP but not in SW may partly explain
445 patterns of dipteran abundance. Azadirachtin, a component of neem oil that repels
446 feeding and inhibits moulting, can harm dipterans, especially those in their larval
447 stages (Schmutterer, 1997; Spollen and Isman, 1996). (2) Focusing on IP orchards, we
448 found lower predator abundances for spiders and earwigs in SP that can be explained
449 as side effects of synthetic insecticides. IP growers in SP (exclusively) applied several
450 insecticides containing the active compounds Chlorpyrifos or Deltamethrin, both
451 known for their harmful side effects on spiders (Markó et al., 2009; Pekár and Beneš,
452 2008), and Phosmet, which belongs to the group of organophosphates, known for
453 their harmful side effects on earwigs (Malagnoux et al., 2015a; Peusens and Gobin,
454 2008). (3) Regular application of Pirimicarb and Thiacloprid in IP may explain a

455 positive effect of ORG on bugs in GE (van de Veire et al., 2002; van de Veire and
456 Tirry, 2003).

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

476

477 *Country-specific responses to local and landscape factors*

478 Intensive orchard management may alter or even counteract other local factors as well
479 as landscape factors (Tschardt et al., 2016), and landscape features may alter the

480 effectiveness of local habitat and organic management in supporting biological
481 control (Jonsson et al., 2015; Tschardtke et al., 2012). In this study, orchard
482 management directly influenced the abundance of six out of seven predatory
483 arthropod groups (sometimes in opposite directions, Table 1). Yet, interactions
484 between management and local or landscape factors were only evident in two cases.
485 Firstly, plant species richness was associated with low predatory bug abundance in IP
486 but not in ORG, indicating that effects of local habitat are management-dependent.
487 Secondly, ORG management enhanced predator abundance only at low levels of
488 orchard cover in Spanish landscapes. The intermediate landscape complexity
489 hypothesis highlights the effectiveness of ORG management to support biodiversity at
490 intermediate cover levels of semi-natural habitats and non-crop areas, which provide
491 arthropod biodiversity to crops through spillover effects (Batáry et al., 2010;
492 Tschardtke et al., 2012). High levels of orchard cover at landscape scale reduced the
493 availability and accessibility of semi-natural habitats. This may be of special
494 relevance in IP orchards, where predatory arthropods are subjected to greater hazards.
495 A peak in predator abundance in ORG orchards at intermediate levels of landscape
496 diversity or orchard cover was not evident.

497 At the local scale, woody habitat had mixed effects on predator abundances.
498 High local woody habitat coverage enhanced earwig abundance in SW (but reduced it
499 in GE), and harvestmen abundance in GE. In the context of augmenting biological
500 control, woody habitat quality has often been characterised in terms of woody plant
501 species richness, cover and connectivity (Dainese et al., 2016; Malagnoux et al.,
502 2015b). For example, linyphid spiders have been reported to use continuous unbroken
503 hedgerows with a high diversity of woody species as source habitats, spilling over to
504 neighbouring crops (Garratt et al., 2017). Differences in quality of woody structures

505 may have driven the contrasting responses of earwigs and harvestmen to woody
506 elements in the three countries. On the other hand, plant species richness did not alter
507 earwig or harvestmen abundances in either country (Table 1). ~~Perhaps~~ It may be that,
508 regional differences in the response of the two groups were triggered by spillover
509 constrained by the density of prey in the woody habitat. Results for harvestmen (and
510 lacewings) should be interpreted cautiously because the number of individuals was
511 low (Table 1).

512 Other studies have provided evidence that enhancing local plant diversity by
513 establishing flower strips improves living conditions for beneficial arthropods (Batáry
514 et al., 2015; Letourneau et al., 2011; Lichtenberg et al., 2017). A high local flower
515 richness is especially important for natural enemies in orchards that lack woody
516 habitats in the vicinity (Saunders and Luck, 2018). Contrary to these findings, we
517 observed negative influences of plant species richness on predatory bugs in SW
518 (marginally significant), and no effects on the other groups. Some particularly
519 prominent bugs in apple orchards (*e.g.* anthocorids, Table A3) use floral nectar and
520 pollen as a food resource (Wäckers and van Rijn, 2012). However, plant species
521 richness did ~~rather~~ reduce rather than enhance bug abundance and the response of
522 bugs to plant species richness was inconsistent among countries. The presence and
523 flower cover of a few favoured plant species may be more relevant than total plant
524 species richness (Wäckers and van Rijn, 2012). On the other hand, bugs could be
525 more attracted by flower-rich adjacent habitats than by intensively managed IP
526 orchards. Results for orchards in SP could support this explanation: Results for
527 ~~orchards~~ in SP ~~—where~~ high plant species richness was associated with low bug
528 abundance in IP but not in ORG orchards (Fig. A2) ~~—could support this explanation.~~
529 Management intensity may reduce the attractiveness of the orchard as a habitat,

530 especially if food resources for beneficial arthropods are affected. For instance,
531 insecticide applications can diminish prey insects, and weed control may reduce plant
532 species richness and flower cover (Cross et al., 2015; Miñarro, 2012; Simon et al.,
533 2010). In this case, high-quality adjacent habitats, such as sown flower strips, can
534 potentially provide a suitable if not a better environment for a wide range of
535 herbivores. As a result, natural enemies may not disperse from the adjacent habitat
536 into the crop (Holland et al., 2016; Tschardt et al., 2016). This could also explain
537 the lower earwig abundance in orchards with enhanced woody habitat cover in GE
538 (Happe et al., 2018).

539 Effects of local and landscape factors on overall predation potential (measured
540 as energy use) mainly resembled the response of the largest and most abundant taxon
541 in each country. Such large, abundant predatory arthropods (e.g. spiders in SP and
542 earwigs in GE) are likely to contribute strongly to biological control of their specific
543 prey taxa. In general, community energy use was less sensitive than abundance to
544 local and landscape factors, reflecting body mass distribution (Fig. A3). The
545 effectiveness of predators is well predicted by mean predator body size with larger
546 predators showing higher per capita consumption rates (Emmerson and Raffaelli,
547 2004; Rusch et al., 2016). Positive influence of higher abundance and biomass on
548 biological control is necessarily constrained in cold climates by energetic demand
549 (Londoño et al., 2015; Schneider et al., 2012). Energy use may therefore be more
550 relevant than abundance and biomass to describe the biological control potential of
551 predator communities along a geographical gradient with large climatic differences.

552

553 *Conclusion*

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

568

569 **Author contributions**

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

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591

592 **Appendix A. Supplementary data**

593 | Supplementary material related to this article can be found, in the
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931 | Table 1. Effects of local and landscape factors¹ on (A) abundance of seven predatory
932 | arthropod groups and on (B) energy use of the predator community in apple orchards
933 | in Spain (SP), Germany (GE) and Sweden (SW); for each predator group, total
934 | abundance across sites for each country (number of individuals in all orchards) and
935 | the number of orchards in which the predator group was recorded (in parentheses) are
936 | indicated in bold. Effects on (B) total energy use by the predator community in bold
937 | as well. Orchard cover (%) was assessed at landscape scale (within 1 km), orchard
938 | management (IP vs. organic), plant species richness and woody habitat cover (m²) at
939 | local scale (within 20 m). χ^2 - and *P*-values² are given for reduced models (stepwise-
940 | backward selection) with estimates \pm S.E. in parentheses. ‘NA’ indicates that no
941 | 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 $\chi^2 = 16.07$	755 (30)^b $\chi^2 = 3.27$	530 (28)^a
Management	(1.25 \pm 0.31) <i>P</i> < 0.001 *** $\chi^2 = 3.17$	(0.37 \pm 0.20) <i>P</i> = 0.070	n.s.
Orchard cover (%) ¹	(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 $\chi^2 = 10.69$	201 (30)^a	261 (28)^a
Management	(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 $\chi^2 = 9.52$
Management	n.s.	n.s.	(1.17 \pm 0.39) <i>P</i> = 0.002 **
Dermaptera	21 (8)^a $\chi^2 = 11.72$	290 (26)^a	36 (14)^c $\chi^2 = 6.89$
Management	(3.00 \pm 1.12) <i>P</i> < 0.001 ***	—	(-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)	$\chi^2 = 3.93$ (0.92 \pm 0.46)

		$P = 0.083$	$P = 0.047 *$
Heteroptera	43 (15)^b $\chi^2 = 7.54$	213 (22)^a $\chi^2 = 11.8$	9 (7)^c
Management	(2.83±0.87) $P = 0.006 **$	(1.63±0.46) $P < 0.001 ***$	n.s.
Plant species richness ¹	$\chi^2 = 13.20$ (-2.18±0.60) $P < 0.001 ***$	n.s.	$\chi^2 = 3.27$ (-0.90±0.50) $P = 0.070$
Management × plant species richness ¹	$\chi^2 = 6.66$ (1.76±0.68) $P = 0.010 **$	n.s.	n.s.
Neuroptera	6 (4)^c	9 (7)^c	15(10)^c
Opiliones	1 (1)	14 (9)^c	18 (9)^c $\chi^2 = 6.05$
Management	NA	n.s.	(-2.76±1.12) $P = 0.014 *$
Woody habitat cover ¹	NA	$\chi^2 = 3.94$ (0.78±0.39) $P = 0.047 *$	n.s.
(B) Energy use	9.83 J h⁻¹ $F_{1,26} = 23.95$	55.1 J h⁻¹	17.9 J h⁻¹
Management	(1.59±0.33) $P = <0.001***$	n.s.	n.s.
Woody habitat cover ¹	n.s.	$F_{1,28} = 3.08$ (-0.002±0) $P = 0.09$	n.s.

¹continuous variables were scaled to decrease VIF below 3; ²ANOVA type III; ³GLM: negative binomial with log-link; ⁴GLMM: poisson with log-link and observation level random effect in case of overdispersion; ⁵zero-inflation models glmmADMB with observation level random effect in case of overdispersion; ⁶positive 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)

944 **Figure legends**

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946 | Figure 1. Scales considered in this study: (A) country: (Spain (SP), Germany (GE)
947 | and Sweden (SW)); (B) landscape: (composition and diversity within a 1 km radius
948 | around the orchard); (C) local scale: including local habitat quality (semi-natural
949 | woody habitat cover and plant species richness), and orchard management (integrated
950 | production vs. organic management).

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

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