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2 **Resilience of ecosystem processes: a new approach shows that functional redundancy of**
3 **biological control services is reduced by landscape simplification**

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5
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36 **ABSTRACT**

37

38 Functional redundancy can increase the resilience of ecosystem processes by providing
39 insurance against species loss and the effects of abundance fluctuations. However, due to the
40 difficulty of assessing individual species' contributions and the lack of a metric allowing for a
41 quantification of redundancy within communities, few attempts have been made to estimate
42 redundancy for individual ecosystem processes. We present a new method linking interaction
43 metrics with metabolic theory that allows for a quantification of redundancy at the level of
44 ecosystem processes. Using this approach, redundancy in the predation on aphids and other
45 prey by natural enemies across a landscape heterogeneity gradient was estimated. Functional
46 redundancy of predators was high in heterogeneous landscapes, low in homogeneous
47 landscapes, and scaled with predator specialisation. Our approach allows quantifying
48 functional redundancy within communities and can be used to assess the role of functional
49 redundancy across a wide variety of ecosystem processes and environmental factors.

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62 INTRODUCTION

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64 Biodiversity underpins vital ecosystem functions such as primary production and nutrient
65 cycling as well as ecosystem services that directly benefit humans such as biological pest
66 control and pollination, from here on collectively referred to as ecosystem processes (Isbell *et al.*
67 *2011*; Cardinale *et al.* 2012; Gamfeldt *et al.* 2013; Greenop *et al.* 2018). Taxonomic
68 diversity has traditionally been used to assess or infer relationships with ecosystem processes
69 (Cadotte *et al.* 2011; Gagic *et al.* 2015). However, in recent years it has become evident that
70 biodiversity effects on ecosystem processes are not sufficiently explained by taxonomic
71 diversity but often depend on the diversity of functional traits among species (McGill *et al.*
72 2006; Cadotte *et al.* 2011; Gagic *et al.* 2015). In particular, functional redundancy, the
73 diversity of functionally equivalent species, can have stabilizing effects on ecosystem
74 processes by enabling a functional group to compensate for the loss of species (insurance
75 hypothesis) and by dampening the effects of individual species fluctuations (portfolio effect)
76 (Rosenfeld 2002; Hooper *et al.* 2005). In theory, greater functional redundancy will thus lead
77 to greater resilience of ecosystem processes to environmental stressors as long as the
78 functionally redundant species responds differently to environmental conditions. This
79 response diversity depends, for example, on a species' climatic niche or its requirements for
80 resources (Elmqvist *et al.* 2003; Mori *et al.* 2013; Kühnel & Blüthgen 2015). Therefore, a
81 greater degree of functional redundancy within a group can ensure a higher probability that at
82 least some species continue to provide an ecosystem process when the contribution of others
83 is lost or reduced (McNaughton 1977; Hooper *et al.* 2005; Blüthgen & Klein 2011; Thibaut &
84 Connolly 2013).

85

86 The diversity–stability relationship and the effect of functional redundancy has mostly been
87 studied for entire communities (Albrecht *et al.* 2013; Pillar *et al.* 2013; Peralta *et al.* 2014;

88 Sanders *et al.* 2018). Metrics used in these studies quantified functional redundancy at the
89 level of an entire functional group, typically encompassing a combination of multiple traits or
90 functions for each species. For instance, Pillar *et al.* (2013) used twelve traits linked to
91 grazing intensity to quantify the level of functional redundancy in grassland communities,
92 Peralta *et al.* (2014) reported stabilizing effects of functional redundancy among parasitoids
93 on community-wide parasitism rates. However, there have so far been few attempts to assess
94 functional redundancy of specific ecosystem processes, e.g. targeting predation of a specific
95 prey or pollination of a specific plant. This is both because of the difficulty of assessing the
96 contribution of different species to a process and the lack of a metric that allows for a
97 quantification of functional redundancy within communities. Such a metric of functional
98 redundancy of specific ecosystem processes needs to be based on the diversity of process-
99 specific functional niches of individual species within a community, i.e. the relative
100 contribution of each species to the provision of an ecosystem process.

101
102 Equivalent to the concept of the ecological niche, a species' functional niche depends on
103 species-specific traits related to the process of interest such as *per capita* consumption or
104 pollination rates. Consequently, the potential of one species to compensate for the functional
105 loss of another is dependent on the degree of overlap in functional niches between them (i.e.,
106 how similar they are in their ability to provide a specific ecosystem process) (Rosenfeld
107 2002; Blüthgen & Klein 2011). The sum of functional niche overlap within a functional
108 group can be quantified as the degree of functional redundancy under current environmental
109 conditions (Rosenfeld 2002; Tylianakis *et al.* 2010; Kaiser-Bunbury *et al.* 2017).

110
111 Biological pest control, the regulation of pest species by naturally occurring predators,
112 parasitoids and pathogens, is one of the ecosystem services considered essential for
113 sustainable agricultural production (Östman *et al.* 2003; Letourneau *et al.* 2009; Jonsson *et al.*

114 2014). It is assumed that pest problems will increase in many parts of the world due to
115 climate change, as pest species might be able to complete more generations within a season
116 and new species are likely to colonize new regions (Cannon 1998; Zhu *et al.* 2017). At the
117 same time, the intensification of agriculture, particularly at the landscape level where a
118 spatial expansion of fields is realized at the expense of natural and semi-natural habitats, can
119 reduce the abundance and diversity of natural enemies and the efficiency of biological pest
120 control services (Rusch *et al.* 2013, 2016; Jonsson *et al.* 2014; but see Karp *et al.* 2018). To
121 date, the majority of investigations of the effects of the simplification of agricultural
122 landscapes on biological pest control have focused on immediate impacts on the efficiency of
123 pest control services (Letourneau *et al.* 2009). In contrast, the level of functional niche
124 overlap in biological pest control systems that would allow predictions about their long-term
125 stability remains largely unexplored with the exception of a small number of studies reporting
126 greater temporal stability in parasitism rates with increased parasitoid species richness
127 (Tylianakis *et al.* 2006; Veddeler *et al.* 2010; Macfadyen *et al.* 2011). As a consequence,
128 predictions about long-term effects of landscape simplification on the stability of biological
129 control through time and the potential to respond to possible increases in pest abundance in
130 the future remain difficult (Tscharntke *et al.* 2008; Gurr *et al.* 2017).

131
132 Here, we present a method to quantify the level of functional redundancy for individual
133 ecosystem processes within functional groups. We exemplify the approach by estimating
134 redundancy in the mortality risk of aphids and six other prey groups varying in their level of
135 predator specialisation to biocontrol agents in barley fields across a gradient of landscape
136 simplification. While previous approaches used abundance or interaction frequency to weight
137 different interaction partners for functional redundancy (e.g., Albrecht *et al.* 2013; Kaiser-
138 Bunbury & Blüthgen 2015), our method provides a link between these interaction metrics and
139 metabolic theory that aims to improve the accuracy and reliability of redundancy measures

140 (Brose *et al.* 2008; Perović *et al.* 2018). To achieve this, we combined data collected on the
141 gut content of field-sampled predators (based on molecular gut content analysis, MGCA)
142 with predator abundance data (activity density in pitfall traps) and their estimated metabolic
143 rate. Using this approach, we estimated the mortality risk of Bird cherry-oat aphids
144 (*Rhopalosiphum padi*), the most important agricultural pest in our study system, and
145 quantified the level of functional redundancy of aphid predation as the diversity in mortality
146 risk of aphids to each predator calculated as the exponential of the Shannon entropy ($e^{H'}$). We
147 then tested whether agricultural intensification is affecting the potential resilience of
148 biological pest control to future changes in environmental conditions by comparing the level
149 of functional redundancy of predation on aphids across landscapes of different levels of
150 intensification. In addition, using the same approach as for predation on aphids, we quantified
151 the level of functional redundancy of predation on six other prey groups to explore the
152 relationship between our metric of functional redundancy and ‘classic’ taxonomic
153 biodiversity along a gradient of predator specialisation.

154

155 **MATERIAL AND METHODS**

156

157 **Study location and period**

158

159 The study was conducted in spring barley fields surrounding the city of Uppsala (59.8° N,
160 17.6° E), south-central Sweden, from the end of May until the beginning of July 2011. We
161 selected 10 fields with five under conventional management and five managed organically for
162 a minimum consecutive period of ten years. Fields were arranged in pairs (i.e., one
163 conventionally and one organically managed field) with a mean distance of 1.6 km (ranging
164 from 1.1 to 2.2 km) within each pair. Conventional farming of spring barley in the study
165 region are of comparatively low intensity and differences between conventional and organic

166 farming methods mainly reside in the use of herbicides and inorganic fertilizers on
167 conventionally managed fields whereas there is only a limited application of insecticides.
168 Previous studies have indicated that differing farming systems did not affect abundances
169 (Weibull *et al.* 2003) and had only a minimal effect on the food web structure of the same
170 community of generalist predators as used in our study (Roubinet *et al.* 2017). Fields were
171 selected along a gradient of landscape heterogeneity, ranging from highly homogeneous
172 landscapes (i.e., landscapes with only a limited availability of semi-natural habitat) to highly
173 heterogeneous landscapes (i.e., landscapes with a high availability, and variety, of semi-
174 natural habitat). All field sampling was carried over a total of four weeks covering the two
175 most critical periods for biological control of *R. padi* (Chiverton 1987): the colonization
176 phase during the barley tillering stage (weeks 22 and 23) and a phase of population build-up
177 during the barley stem extension and heading stage (weeks 25 and 26).

178

179 **Sampling of predator abundance**

180

181 Sampling in each field was conducted along a 100-m transect located approximately 20 m
182 from, and in parallel with, one randomly selected field margin. We measured the activity
183 density of two taxonomic groups of ground-dwelling arthropod predators, spiders (Araneae:
184 Linyphiidae and Lycosidae) and carabid beetles (Coleoptera: Carabidae) using wet pitfall
185 traps. We placed six pitfall traps (11.5 cm diameter × 11 cm depth; Noax Lab, Farsta,
186 Sweden) at equal distances along the 100 m transect. Pitfall traps were filled with water and a
187 small quantity of detergent (Yes, Procter & Gamble, Stockholm, Sweden). Traps were open
188 for the entire sampling period and emptied weekly.

189

190 **Specimen collection for molecular gut content analysis**

191

192 Depending on predator abundance in the respective field, we placed 12 – 35 dry pitfall traps
193 (11.5 cm diameter × 11 cm depth) evenly along each transect. The number of pitfall traps
194 per transect was adjusted depending on initial trapping success rates to achieve a
195 reasonable sample size of each target predator. Dry pitfall traps were open for one 24 h
196 period during each of the four weeks. We placed clay balls (Weibulls, Åby, Sweden) as
197 refugia in the traps to minimize the likelihood of predation events (Sunderland et al. 2005,
198 King et al. 2008). Upon emptying the traps, all predators were placed in separate 1.5 ml
199 microtubes (Sarstedt, Nümbrecht, Germany), frozen on dry ice, and stored at -80°C until
200 subsequent identification and DNA extraction. Because not every specimen collection event
201 resulted in the collection of a sufficient number of individuals of each predator species for
202 subsequent gut content identification, ten data points were omitted from the analysis.

203

204 **Molecular gut content analysis**

205

206 Following morphological species identification, each sample was subjected to whole-body
207 DNA extraction and processed using previously established DNA-based molecular gut-
208 content multiplex PCR assays (Staudacher *et al.* 2016) (for sampling and bioassay specificity,
209 material description and measures taken to prevent DNA contamination, see Roubinet *et al.*
210 2017). We processed 4,493 specimens belonging to 20 species of ground-dwelling spiders
211 and 15 species of carabid beetles. Molecular assays provided presence/absence-data in each
212 predator gut for the most abundant, and important, extraguild prey groups for generalist
213 predators in cereal crops of Northern and Central Europe (Toft & Bilde 2002): bird cherry-oat
214 aphid (*R. padi*), true flies (Diptera), thrips (Thysanoptera), earthworms (Lumbricidae) and
215 springtails (Collembola). In addition, the predators were tested for nine taxa of intraguild
216 prey: seven-spot ladybird (*Coccinella septempunctata*), lacewings (Chrysopidae), sheet-web
217 spiders (Linyphiidae), wolf spiders (Lycosidae), other spiders, and four ground beetles

218 (*Bembidion* spp., *Harpalus* spp., *Poecilus* spp., and *Pterostichus* spp.). A detailed analysis of
219 the whole food web based on this analysis can be found in Roubinet *et al.* (2018). Here, we
220 focus on predation on the seven most frequently detected prey groups in the food web: bird
221 cherry-oat aphids, springtails, earthworms, true flies, seven-spot ladybirds, sheet-web spiders
222 and *Bembidion* spp.

223

224 **Functional redundancy of predation**

225

226 We defined functional redundancy of predation as the diversity in the mortality risk for prey
227 among predator species within the predator community. It is thus dependent on the predation
228 pressure exerted by individual predators. The predator-specific predation pressure is a
229 function of the respective predator's probability of feeding on a specific prey species, its
230 feeding rate, and abundance. We calculated the probability of predation by any given
231 predator in the predator community during each week of survey in each field using the
232 presence/absence-data derived from MGCA. Because energy requirements are an important
233 factor contributing to the intensity and frequency of predation events (Brose *et al.* 2008;
234 Thompson *et al.* 2012), we approximated the feeding rate of individual predators as a
235 function of their metabolic rate. Theory predicts that the metabolic rate scales with a 3/4
236 power to body mass and feeding rates of consumers follow the same mass-dependence
237 (Brown *et al.* 2004). We therefore calculated the metabolic rate I of predator i as a proxy for
238 its consumption rate:

239

$$I_i = I_0 * M_i^{3/4}$$

240 where I_0 is a taxon-specific normalization constant (data derived from Ehnes *et al.* 2011) and
241 M the average dry body mass of predator i . Predator abundance was calculated from activity
242 density in wet pitfall traps.

243

244 We then calculated the risk of predation R for prey group j by predator i at each location for
245 each week of survey by combining the metabolic rate of predator i with its abundance and the
246 probability of predation on prey group j :

$$247 \quad R_{ij} = p_{ij} * q_i * I_i$$

248 where p_{ij} is the probability of predator i feeding on prey j and q_i is the activity density of
249 predators belonging to species i . As a consequence, dissimilarity in R_{ij} between species can
250 result from dissimilarity in the parameters p_{ij} , q_i , and/or I_i . However, these parameters can
251 also compensate each other and thus minimize the risk of over- or underestimation of the
252 importance of a single parameter: species A may have low p_{ij} but high q_i , species B may have
253 high p_{ij} and low q_i , and yet both can yield a similar R_{ij} .

254
255 The level of functional redundancy of predation on prey group j within the predatory guild in
256 each field and week was then calculated as diversity in the risk of predation by each predator,
257 calculated as the exponential of the Shannon entropy e^H :

$$258 \quad e^{H_j} = \exp(-\sum R_{ij} * \ln(R_{ij}))$$

259 This approach of re-transformed entropy corresponds to the ‘effective diversity’ proposed by
260 Jost (2006) which follows a linear distribution and has a doubling property that allows for a
261 direct comparison of redundancy between communities. A community with an e^H value of 2
262 is considered to have double redundancy of a community with an e^H value of 1, a community
263 with an e^H value of 4 doubles the redundancy of a community with an e^H value of 2, etc. The
264 value of e^H approaches zero in dissimilar communities and equals N (i.e., the total number of
265 species) in communities consisting entirely of species that are identical in their functional
266 niche dimensions. As a result, e^H penalizes communities of lower species richness, i.e., in
267 case two communities exhibit identical niche overlap among members but community A
268 consists of twice as many species as community B, e^H of community A is double the one of
269 community B.

270

271 Our redundancy metric defines the quantitative overlap of species within a functional group
272 such as predatory arthropods for a specific target function such as aphid biocontrol. The
273 specific functional performance of each potential predator species depends on its activity
274 density and its average probability to prey on a specific target. Predator species that represent
275 similar predation risks, e.g. similar abundance, prey consumption rate and specialization,
276 exhibit a greater functional niche overlap than predators that are heterogeneous in these
277 parameter combinations. Functional redundancy thus increases both with the evenness among
278 predator niches and with the richness of potential predators in a community. Analogous
279 redundancy metrics can be defined across different functional groups or targets and compared
280 across different environments, for which our comparison of aphid biocontrol across arable
281 fields in variable landscapes may serve as a model case.

282

283 Calculations of $e^{H'}$, the biodiversity of predators and the predation evenness (see below) on
284 each specific prey group among predators (see below) were conducted in R (version 3.4.2; R
285 Core Team 2017) using the ‘specieslevel’ function within the *bipartite* package (version 2.08;
286 Dormann *et al.* 2008).

287

288 **Predator diversity and predation evenness**

289

290 We quantified the diversity of the entire ground-dwelling arthropod predator community in
291 each field and week of survey by calculating the Shannon entropy (H') based on the activity
292 densities recorded by wet pitfall trapping. We calculated the level of evenness of predation on
293 each prey group in the predator community as the diversity in the proportion of individuals
294 within each predator species that tested positive for the respective prey group, expressed as
295 Shannon evenness (E):

296
$$E = H' / \ln(S)$$

297 where S is the number of predator species.

298
299 **Quantification of landscape heterogeneity**

300
301 We obtained raster-based land use data from the Swedish Land Cover Database *Svenska*
302 *Marktäckedata* (SMD) for the reference year of 2012 to quantify the structural and
303 compositional heterogeneity of the landscape surrounding each transect. SMD accounts for
304 57 classes of vegetation and land use with a resolution of 25 x 25 m. Classes found in our
305 study area were merged into eight larger habitat categories: arable land, pasture, grassland,
306 rural settlement, and the woodland categories deciduous forest, coniferous forest, mixed
307 forest, and cleared forest.

308
309 We used the 'buffer' tool in ArcGIS (version 10.5.1) to create a circular polygon of 1 km
310 radius with the centre of each transect as the centroid of the respective polygon (Fig. 1). We
311 selected a 1 km radius because it has been identified as a relevant scale to understand
312 population dynamics of arthropod predators in crop fields (Thies & Tschardtke 1999; Rusch
313 *et al.* 2016). We quantified land-use intensity within each polygon in three different ways:
314 We calculated the exponential of Shannon H' as a measure of landscape diversity ($e^{H'}$) within
315 each polygon to quantify variance in the proportion of area covered by each of the five
316 habitat categories. Furthermore, we quantified the patchiness of the landscape as an
317 additional measure of landscape heterogeneity. Landscape patchiness was expressed in two
318 ways: the number of distinct habitat patches irrespective of habitat type, and the cumulative
319 length of borders between habitat patches of the five habitat categories.

320
321 **Statistical analysis**

322

323 We investigated the effects of landscape heterogeneity and farming system on the functional
324 redundancy of aphid predation using multivariable generalized linear modelling with
325 generalized estimating equations (GEE) (Zuur *et al.* 2009). Because each field was subject to
326 repeated measures, activity density for each predator species was correlated along the time
327 axis. By employing an autoregressive correlation matrix (AR1) error structure, GEE allows
328 for a specification of each data point as a repeated measure that takes into account this lack of
329 independence (Zuur *et al.* 2009). Within the AR1 error structure, a correlation matrix is
330 specified for observations within a cluster (i.e., predator *j* on field *i*), whereas separate
331 clusters are assumed to be independent while sharing the same correlation matrix. Landscape
332 heterogeneity (i.e., landscape diversity and patchiness) was used as a covariate and farming
333 system (i.e., conventional or organic) as fixed factor in the analysis. Because the different
334 measures of landscape heterogeneity were highly correlated, they were not included in the
335 same model.

336

337 Unlike estimations of goodness of fit for generalized linear models, which are based on the
338 maximum likelihood theory for independent observations (McCullagh and Nelder 1989), the
339 GEE method is based on the quasi-likelihood theory (Pan 2001), with no assumption being
340 made about the distribution of response variables. Commonly used goodness of fit
341 estimations derived under the likelihood theory, such as Akaike's information criterion (AIC;
342 Akaike 1974), cannot be applied to GEE. Instead, a modified goodness of fit estimation based
343 on AIC is applied, the quasi-likelihood under the independence model criterion (QIC; Pan
344 2001). The candidate models were ranked using QIC corrected for small sample sizes (QIC_c)
345 (Pan 2001). Alternative models with 2 Δ QIC_c units in relation to the best model were
346 considered to have substantial support (Pan 2001). The relative likelihood of each model was
347 calculated using QIC_c weights (QIC_{cw}) with the weight of any particular model depending on

348 the entire set of candidate models, varying from 0 (no support) to 1 (complete support) (Pan
349 2001). We used ANOVA to investigate the effects that N (i.e., the total number of species)
350 and predation evenness had on the strength of the interaction between predator diversity and
351 functional redundancy. Multivariable generalized linear modelling and ANOVA were carried
352 out using IBM SPSS Statistics 24.0.

353

354 **RESULTS**

355

356 *Habitat effects on functional redundancy of aphid predation*

357

358 The best predictor of functional redundancy of aphid predation on the landscape scale was the
359 number of distinct habitat patches in the landscape surrounding the spring barley fields (QIC
360 = 165.2, $QIC_{cw} = 0.39$; Table 1, Fig. 2). Functional redundancy of aphid predation correlated
361 positively with the number of distinct habitat patches and landscape diversity ($e^{H'}$) but not the
362 cumulative length of borders between habitat patches (Table 1). The model with farming
363 system as sole predictor had no support (Table 1).

364

365 *Differences in predation among prey groups*

366

367 Aphids and springtails were commonly consumed by most predator species (32 out of 35
368 predator species preyed on aphids and 30 on springtails, respectively) whereas earthworms
369 (21), true flies (18) and the intraguild prey groups of sheet-web spiders, *Bembidion* sp. and
370 ladybird beetles (all 16; Table 2) were consumed by less predator species in the system.

371 Predation evenness among predator species (i.e., similarity between proportions of specimens
372 that had consumed a certain prey group) was high for aphids (Shannon evenness index =

373 0.94) and springtails (0.96) but, in comparison, lower for earthworms (0.74), true flies (0.70),
374 sheet-web spiders (0.73), *Bembidion* sp. (0.69), and ladybird beetles (0.63; Table 2).

375

376 *Predator diversity and functional redundancy*

377

378 We found a strong positive correlation between the diversity of predators in each field and
379 the functional redundancy of both predation on aphids ($B = 0.93 \pm 0.07$; GEE, Wald $\chi^2 =$
380 187.9 , $p < 0.001$) and springtails ($B = 1.01 \pm 0.08$; GEE, Wald $\chi^2 = 122.3$, $p < 0.001$; Table
381 2, Fig. 3). Functional redundancy correlated positively with predator diversity in all other
382 prey groups, with the exception of ladybird beetles ($B = 0.17 \pm 0.14$; GEE, Wald $\chi^2 = 1.6$,
383 $p = 0.21$; Table 2, Fig. 3). The strength of the correlation between functional redundancy and
384 predator diversity decreased with decreasing predation evenness among predators (Table 2;
385 Fig. 4). Overall, the interaction strength between predator diversity and functional
386 redundancy correlated positively with both the number of predators feeding on the respective
387 prey group (ANOVA, $F = 64.2$, $p > 0.001$) and predation evenness among predators
388 (ANOVA, $F = 189.7$, $p < 0.001$).

389

390 **DISCUSSION**

391

392 Diversity metrics that combine measures of abundance and species richness with a
393 quantification of functional niche overlap among species in a community allow for a more
394 robust evaluation of the potential resilience of ecosystem processes to changing
395 environmental conditions than metrics based solely on taxonomic diversity (Fonseca &
396 Ganade 2001; Rosenfeld 2002). While previous studies have focussed on the importance of
397 functional redundancy at the level of entire functional groups (e.g. Laliberté *et al.* 2010; Pillar
398 *et al.* 2013; Sanders *et al.* 2018), the method we have presented here estimates functional

399 redundancy based on process-specific functional niches of individual species within
400 communities. This metric extends the utility of redundancy measures by allowing for a
401 quantification of functional redundancy for more specific functions within species
402 communities, e.g., predation on a specific prey species or pollination of a specific plant. In
403 contrast to previous approaches that relied on abundance or frequency interaction measures
404 alone to estimate redundancy within functional groups (e.g., Albrecht *et al.* 2013; Kaiser-
405 Bunbury & Blüthgen 2015), our approach improves the accuracy and reliability of
406 redundancy measures by a) quantifying the function directly via the dietary analysis and b)
407 providing a link between abundance, function, and metabolic theory (Perović *et al.* 2018).
408

409 To exemplify the approach, we tested whether the simplification of agricultural landscapes,
410 an environmental variable that has been linked to a reduction in biological pest control
411 services under current environmental conditions (Geiger *et al.* 2010; Rusch *et al.* 2013, 2016;
412 Jonsson *et al.* 2014), is reducing the level of functional redundancy among ground-dwelling
413 arthropod predators. We found functional redundancy of aphid predation by ground-dwelling
414 predators to be highest in the most heterogeneous landscapes (i.e., landscapes with a high
415 availability, and variety, of semi-natural habitat) and lowest in the most homogeneous
416 landscapes (i.e., landscapes with only a limited availability of semi-natural habitat).
417

418 Models that included farming system (i.e., conventional and organic) in combination with
419 landscape heterogeneity as predictor had additional support, indicating an effect of farming
420 system on the results of our study. However, farming system as sole predictor had the least
421 support of all models and revealed inconclusive results with parameter estimates covering
422 both negative and positive values indicating that the variety of effects within both farming
423 practices was greater than the difference between them. A likely explanation for this are
424 differences in the amount and frequency of pesticide and fertilizer application within

425 treatments that amount to alterations in their effects on the abundance of natural enemies,
426 pest species, and alternative prey (Roubos *et al.* 2014; Staudacher *et al.* 2018).

427

428 Because of the importance of functional redundancy for the resilience of ecosystem processes
429 (McNaughton 1977; Hooper *et al.* 2005; Blüthgen & Klein 2011; Thibaut & Connolly 2013),
430 agricultural landscapes of high intensification and corresponding low habitat complexity
431 might be at a higher risk of experiencing a reduction in biological pest control under
432 changing environmental conditions in the future. In contrast, agricultural landscapes of low
433 intensification and corresponding high habitat complexity are characterized by functional
434 groups providing pest control services of higher potential resilience in response to future
435 environmental stressors.

436

437 Predation on aphids was common among arthropod predators with 32 out of 35 species tested
438 positive for aphid consumption and was characterized by a high evenness and a positive
439 correlation between the redundancy of aphid predation and the species diversity of predators
440 in the spring barley fields. The reason for the strong dependency of redundancy of aphid
441 predation on the diversity of predators is the high proportion of predators feeding on aphids
442 and the evenness of predation among aphid predators (i.e., their level of functional niche
443 overlap). Under these circumstances, every predator species contributes similarly to the
444 process. Consequently, simple measures of taxonomic diversity can generate similar
445 information regarding the conditions of such ecosystem processes. For instance, the findings
446 that landscape simplification reduces redundancy of aphid predation are in line with previous
447 studies reporting negative effects of landscape simplification on the diversity of natural
448 predators and the pest control services they provide (Geiger *et al.* 2010; Rusch *et al.* 2013,
449 2016; Jonsson *et al.* 2014). Management strategies tailored towards the conservation of
450 biodiversity among predators that benefit service provision under current environmental

451 conditions would thus be equally beneficial for the preservation of resilience of aphid control
452 services to future disturbances.

453

454 If, however, an ecosystem process is provided by fewer species in a community, which, in
455 addition, exhibit less functional niche overlap, the strength of the correlation between
456 taxonomic diversity and process provision decreases. As demonstrated at the examples of
457 predation on other prey groups, the effects of biodiversity on the functional redundancy of
458 individual processes within functional groups depends on the level of functional niche
459 overlap among species, in this case the level of predation evenness among predators.

460 Functional redundancy of predation on aphids and springtails, prey groups that experienced a
461 high predation evenness, showed a strong correlation between functional redundancy and
462 predator diversity. Overall, the strength of this correlation decreased with decreasing
463 predation evenness, down to ladybird beetles, where functional redundancy did not scale with
464 predator diversity. These results show that management strategies tailored towards the
465 protection of a high diversity of biocontrol agents have the potential to increase the resilience
466 of individual ecosystem processes to future environmental change only under the condition of
467 high functional niche overlap among service providers.

468

469 Functional redundancy within a community is, however, not the sole determinant of
470 resilience of an ecosystem process to environmental stressors. Another critical component is
471 the level of response diversity within a functional group, i.e. the extent to which functionally
472 redundant species differ in their response to changes in environmental conditions
473 (McNaughton 1977; Tilman 1999; Rosenfeld 2002). Response diversity can be assessed for
474 multi-dimensional factors such as the effects of land-use on individual species (Cariveau *et*
475 *al.* 2013) or with a focus on a specific ecological niche such as responses to changes in
476 ambient temperature (Kühnel & Blüthgen 2015). High resilience can be expected only if

477 functionally redundant species differ in their responses to environmental change to a degree
478 high enough that some species within a functional group can continue to efficiently provide
479 an ecosystem process when others are mitigated in their efficiency or lost entirely
480 (McNaughton 1977; Tilman 1999; Kühnel & Blüthgen 2015). Hence, although the resilience
481 of ecosystem processes to global change is likely to scale with functional redundancy, future
482 work focused on predicting resilience to environmental stressors needs to combine
483 estimations of functional redundancy with a measure of response diversity among service
484 providers.

485

486 **CONCLUSIONS**

487

488 We have described a method to estimate functional redundancy of individual ecosystem
489 processes that combines classic interaction metrics used in previous approaches with
490 metabolic theory. We have demonstrated the utility of this method at the example of
491 functional redundancy among natural predators in barley fields when providing pest control
492 services by feeding on aphids and when feeding on other prey groups. In addition to previous
493 studies reporting benefits of increased habitat complexity on the biodiversity of natural
494 enemies and their pest control services under current environmental conditions, our results
495 show that complex habitat compositions in agricultural landscapes can increase the potential
496 resilience of biological pest control to future environmental change. Our findings demonstrate
497 that ecosystem processes that are characterized by a high level of generalism (i.e., a high
498 functional niche overlap among service providers) can be improved by management
499 approaches that aim to protect, or increase, biodiversity of functional groups. In contrast to
500 previous approaches, where functional redundancy has mostly been defined at the level of
501 entire functional groups, the metric presented here allows for a quantification of process-

502 specific functional redundancy and is applicable to a wide variety of functional groups,
503 ecosystem processes and environmental factors.

504

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506

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512

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681 **Table 1:** Model selection results for candidate sets of generalized estimating equations (GEE)
682 for habitat effects within 1 km radius on the level of functional redundancy of predation on
683 aphids in spring barley fields in central Sweden. Listed are models with an $AIC \leq 2.0$ and
684 models including only one predictor. Parameter estimates (PE) and 95% confidence intervals
685 are presented for each factor when it was the sole predictor. Significant interactions (i.e., 95%
686 confidence intervals not crossing zero) are highlighted in bold. Farming system includes
687 conventional and organic management. QICc is the quasi-likelihood under the independence
688 model criterion corrected for small sample sizes. $\Delta QICc$ is the difference in QICc in relation
689 to the best model. QICcw is the relative likelihood of the respective model. All models
690 include the random factors field and sampling session in an autoregressive correlation matrix
691 (AR1) error structure.

692

Model	QIC_c	$\Delta QICc$	QIC_{cw}	PE (95% CI)
Habitat patches	165.2		0.40	0.09 (0.04-0.14)
Habitat patches x Farming system	166.4	1.2	0.21	
Habitat patches + Farming system	166.9	1.7	0.17	
Cumulative border length	169.2	4.0	0.05	<0.001
Landscape diversity (e^H)	181.7	16.5	<0.01	0.69 (0.10-1.37)
Farming system	190.8	25.6	<0.01	0.28 (-1.25-1.82)

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708 **Table 2:** Subset of prey groups of ground-dwelling arthropod predators in spring barley
709 fields in central Sweden used in the analysis. Total number of predator species tested positive
710 for consumption of each prey group, predation evenness among predator species and
711 parameter estimates (PE) derived from generalized estimating equations (GEE) for the
712 relationship between biodiversity and functional redundancy of predation on each respective
713 prey group are shown. Significant correlations (i.e., 95% confidence intervals not crossing
714 zero) are highlighted in bold.

Prey group	Prey class	Predator species feeding on prey group	Predation evenness among predators (E)	PE (95%CI)
Bird cherry-oat aphid	extraguild	32	0.94	0.93 (0.79-1.06)
Springtails	extraguild	30	0.92	1.01 (0.83-1.19)
Earthworms	extraguild	21	0.74	0.39 (0.08-0.69)
True flies	extraguild	18	0.70	0.23 (0.07-0.39)
Sheet-web spiders	intraguild	16	0.73	0.35 (0.20-0.49)
<i>Bembidion</i> sp.	intraguild	16	0.69	0.27 (0.12-0.42)
Seven-spot ladybird	intraguild	16	0.63	0.17 (-0.10-0.44)

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729 **Figure 1:** Example of high (Field OC; Shannon $H' = 1.51$, 36 habitat patches) and low (Field
730 JO; Shannon $H' = 0.45$, 15 habitat patches) landscape heterogeneity within a 1 km radius
731 from the centre of pitfall trap transects in spring barley fields in central Sweden.

732

733 **Figure 2:** Relationship between the number of distinct habitat patches within a 1 km radius
734 from the centre of pitfall trap transects and functional redundancy of aphid predation in
735 spring barley fields in central Sweden. Functional redundancy is the diversity in mortality
736 risk to predators within the predatory guild calculated as the exponential of the Shannon
737 entropy [$e^{H'}$]. The regression and 95% confidence interval are fitted by generalized estimating
738 equations.

739

740 **Figure 3:** Relationship between redundancy of predation and the diversity of ground-
741 dwelling arthropod predators in spring barley fields in central Sweden. Lines indicate
742 regressions fitted by generalized estimating equations. Solid lines indicate extraguild and
743 dashed lines intraguild predation, respectively.

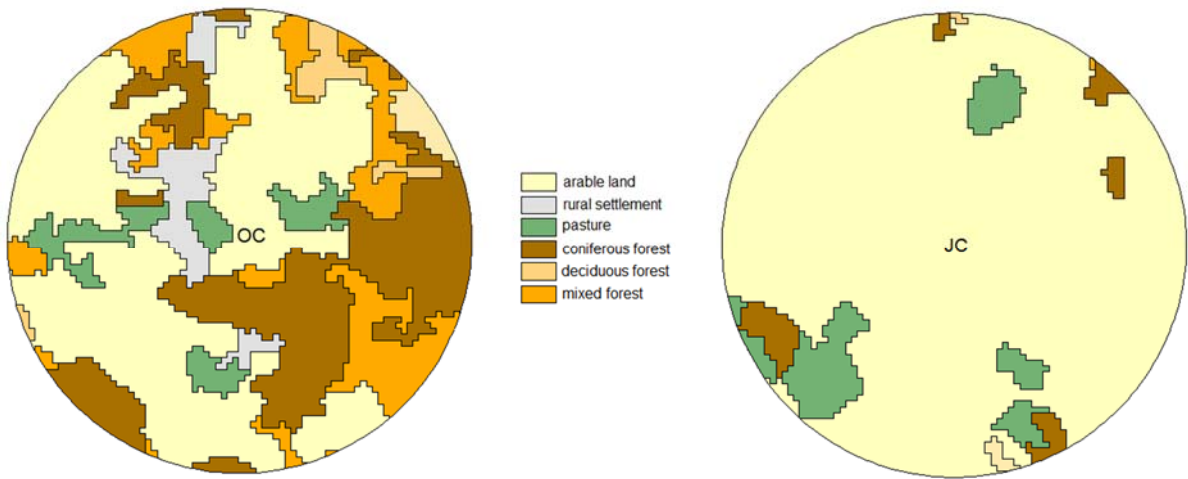
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745 **Figure 4:** Relationship between estimated effects of predator diversity on functional
746 redundancy (parameter estimates derived from generalized estimating equations) and
747 predation evenness of ground-dwelling arthropod predators [H'] in spring barley fields in
748 central Sweden. Filled squares indicate extraguild and empty squares intraguild predation,
749 respectively.

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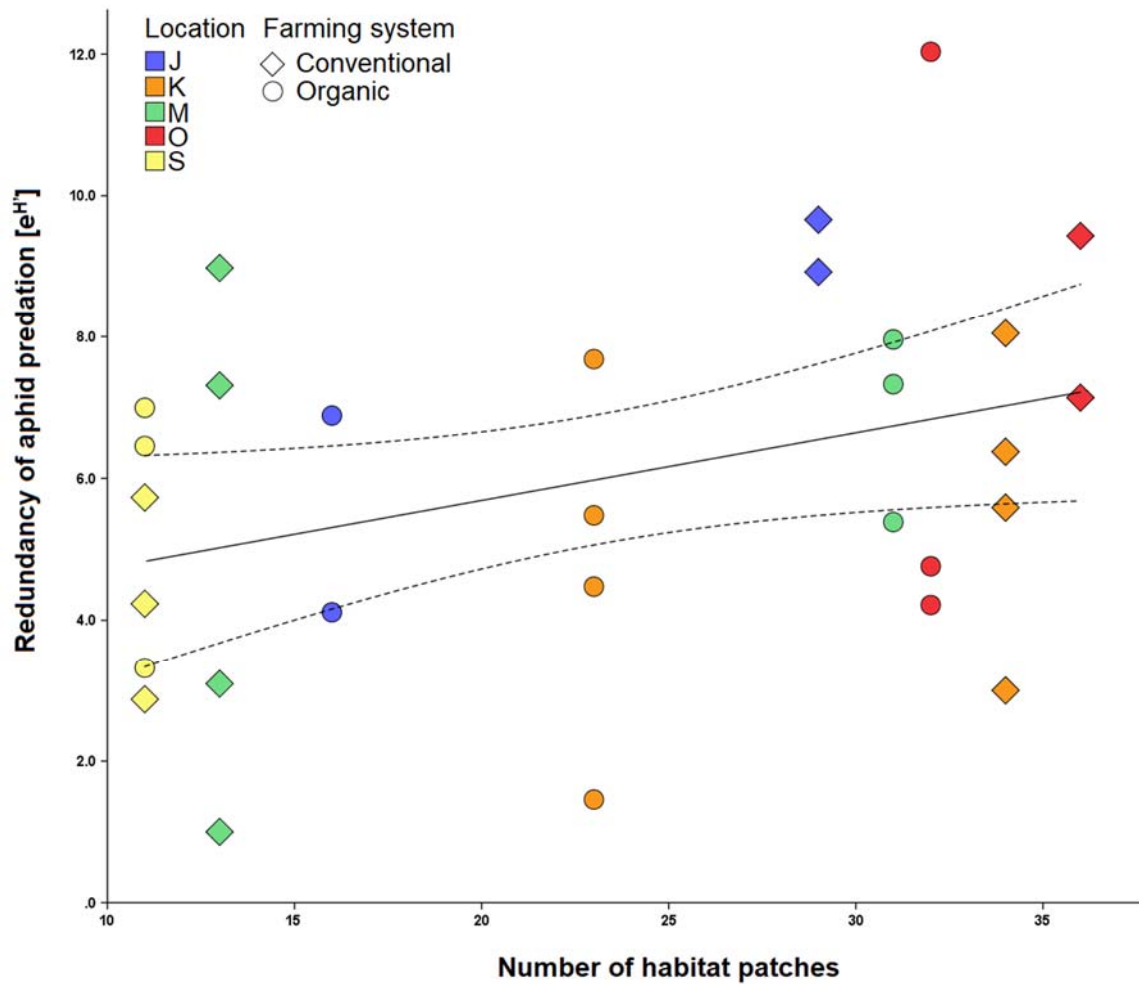
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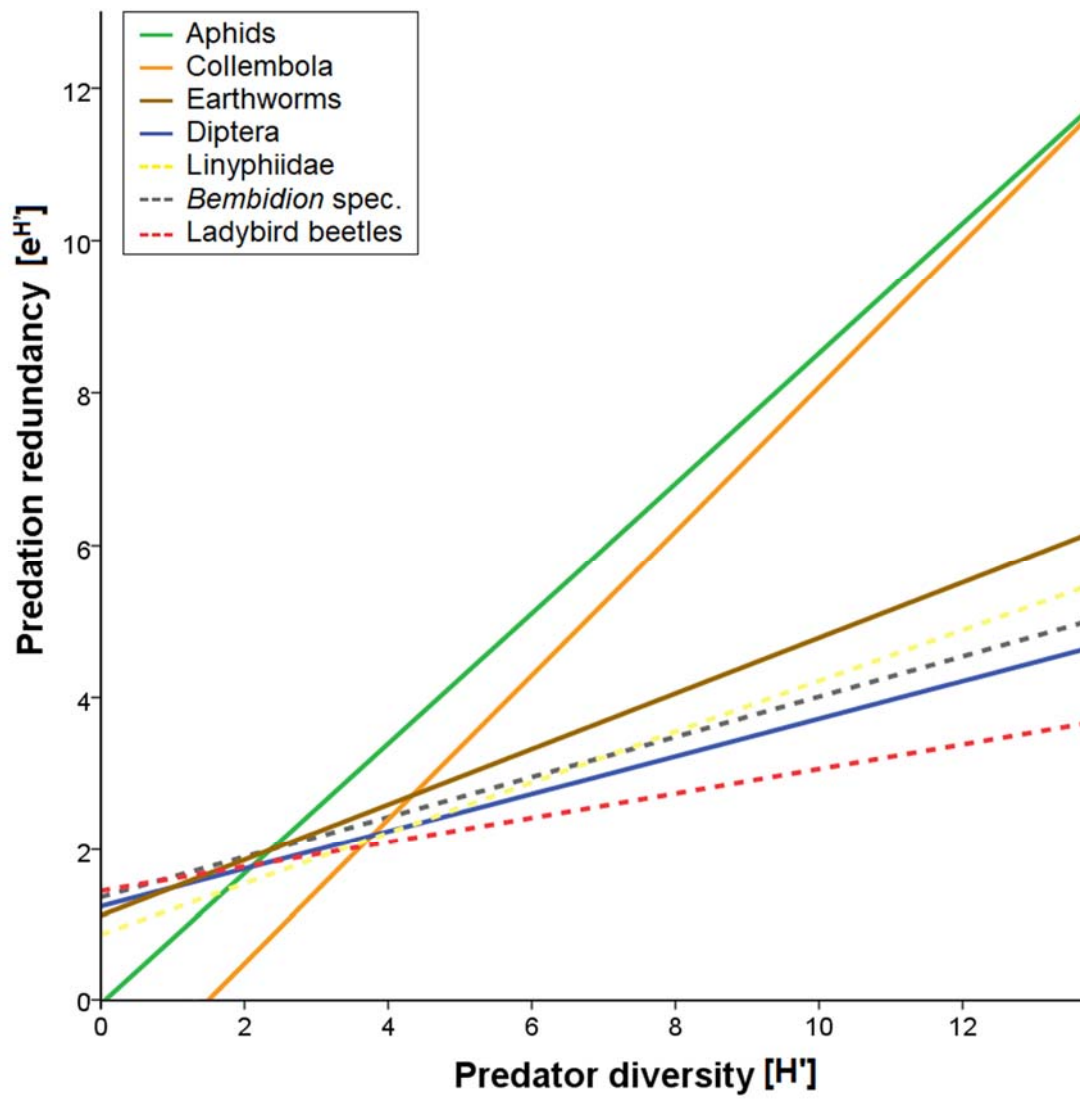


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754 **Figure 1.**

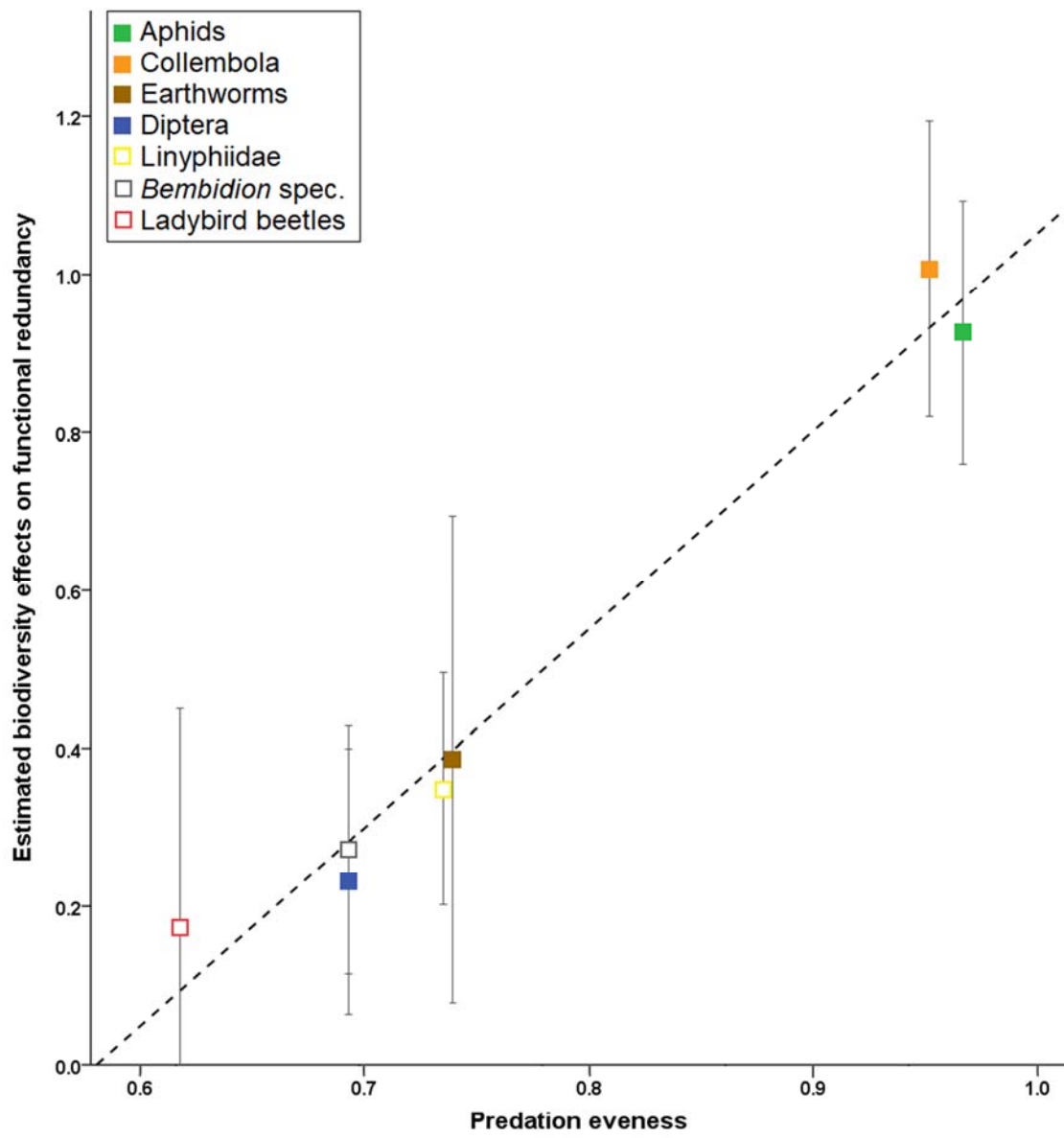
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757 **Figure 2.**



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 759 **Figure 3.**
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Figure 4.