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

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ABSTRACT

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

INTRODUCTION

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

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

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

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

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

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

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

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

MATERIAL AND METHODS

Study location and period

The study was conducted in spring barley fields surrounding the city of Uppsala (59.8° N, 17.6° E), south-central Sweden, from the end of May until the beginning of July 2011. We selected 10 fields with five under conventional management and five managed organically for a minimum consecutive period of ten years. Fields were arranged in pairs (i.e., one conventionally and one organically managed field) with a mean distance of 1.6 km (ranging from 1.1 to 2.2 km) within each pair. Conventional farming of spring barley in the study region are of comparatively low intensity and differences between conventional and organic farming methods mainly reside in the use of herbicides and inorganic fertilizers on conventionally managed fields whereas there is only a limited application of insecticides. Previous studies have indicated that differing farming systems did not affect abundances (Weibull *et al.* 2003) and had only a minimal effect on the food web structure of the same community of generalist predators as used in our study (Roubinet *et al.* 2017). Fields were selected along a gradient of landscape heterogeneity, ranging from highly homogeneous landscapes (i.e., landscapes with only a limited availability of semi-natural habitat) to highly heterogeneous landscapes (i.e., landscapes with a high availability, and variety, of semi-natural habitat). All field sampling was carried over a total of four weeks covering the two most critical periods for biological control of *R. padi* (Chiverton 1987): the colonization phase during the barley tillering stage (weeks 22 and 23) and a phase of population build-up during the barley stem extension and heading stage (weeks 25 and 26).

Sampling of predator abundance

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

Specimen collection for molecular gut content analysis

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

Molecular gut content analysis

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

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

Functional redundancy of predation

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

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

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

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

$$R_{ij} = p_{ij} * q_i * I_i$$

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

The level of functional redundancy of predation on prey group *j* within the predatory guild in each field and week was then calculated as diversity in the risk of predation by each predator, calculated as the exponential of the Shannon entropy $e^{H'}$:

$$e^{H'j} = \exp(-\Sigma R_{ij} * \ln(R_{ij}))$$

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

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

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

Predator diversity and predation evenness

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

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

where S is the number of predator species.

Quantification of landscape heterogeneity

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

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

Statistical analysis

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

Unlike estimations of goodness of fit for generalized linear models, which are based on the maximum likelihood theory for independent observations (McCullagh and Nelder 1989), the GEE method is based on the quasi-likelihood theory (Pan 2001), with no assumption being made about the distribution of response variables. Commonly used goodness of fit estimations derived under the likelihood theory, such as Akaike's information criterion (AIC; Akaike 1974), cannot be applied to GEE. Instead, a modified goodness of fit estimation based on AIC is applied, the quasi-likelihood under the independence model criterion (QIC; Pan 2001). The candidate models were ranked using QIC corrected for small sample sizes (QIC_c) (Pan 2001). Alternative models with 2 ΔQIC_c units in relation to the best model were considered to have substantial support (Pan 2001). The relative likelihood of each model was calculated using QIC_c weights (QIC_{cw}) with the weight of any particular model depending on the entire set of candidate models, varying from 0 (no support) to 1 (complete support) (Pan 2001). We used ANOVA to investigate the effects that N (i.e., the total number of species) and predation evenness had on the strength of the interaction between predator diversity and functional redundancy. Multivariable generalized linear modelling and ANOVA were carried out using IBM SPSS Statistics 24.0.

RESULTS

Habitat effects on functional redundancy of aphid predation

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

Differences in predation among prey groups

Aphids and springtails were commonly consumed by most predator species (32 out of 35 predator species preyed on aphids and 30 on springtails, respectively) whereas earthworms (21), true flies (18) and the intraguild prey groups of sheet-web spiders, *Bembidion* sp. and ladybird beetles (all 16; Table 2) were consumed by less predator species in the system. Predation evenness among predator species (i.e., similarity between proportions of specimens that had consumed a certain prey group) was high for aphids (Shannon evenness index =

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

Predator diversity and functional redundancy

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

DISCUSSION

Diversity metrics that combine measures of abundance and species richness with a quantification of functional niche overlap among species in a community allow for a more robust evaluation of the potential resilience of ecosystem processes to changing environmental conditions than metrics based solely on taxonomic diversity (Fonseca & Ganade 2001; Rosenfeld 2002). While previous studies have focussed on the importance of functional redundancy at the level of entire functional groups (e.g. Laliberté *et al.* 2010; Pillar *et al.* 2013; Sanders *et al.* 2018), the method we have presented here estimates functional redundancy based on process-specific functional niches of individual species within communities. This metric extends the utility of redundancy measures by allowing for a quantification of functional redundancy for more specific functions within species communities, e.g., predation on a specific prey species or pollination of a specific plant. In contrast to previous approaches that relied on abundance or frequency interaction measures alone to estimate redundancy within functional groups (e.g., Albrecht *et al.* 2013; Kaiser-Bunbury & Blüthgen 2015), our approach improves the accuracy and reliability of redundancy measures by a) quantifying the function directly via the dietary analysis and b) providing a link between abundance, function, and metabolic theory (Perović *et al.* 2018).

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

Models that included farming system (i.e., conventional and organic) in combination with landscape heterogeneity as predictor had additional support, indicating an effect of farming system on the results of our study. However, farming system as sole predictor had the least support of all models and revealed inconclusive results with parameter estimates covering both negative and positive values indicating that the variety of effects within both farming practices was greater than the difference between them. A likely explanation for this are differences in the amount and frequency of pesticide and fertilizer application within treatments that amount to alterations in their effects on the abundance of natural enemies, pest species, and alternative prey (Roubos *et al.* 2014; Staudacher *et al.* 2018).

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

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

If, however, an ecosystem process is provided by fewer species in a community, which, in addition, exhibit less functional niche overlap, the strength of the correlation between taxonomic diversity and process provision decreases. As demonstrated at the examples of predation on other prey groups, the effects of biodiversity on the functional redundancy of individual processes within functional groups depends on the level of functional niche overlap among species, in this case the level of predation evenness among predators. Functional redundancy of predation on aphids and springtails, prey groups that experienced a high predation evenness, showed a strong correlation between functional redundancy and predator diversity. Overall, the strength of this correlation decreased with decreasing predation evenness, down to ladybird beetles, where functional redundancy did not scale with predator diversity. These results show that management strategies tailored towards the protection of a high diversity of biocontrol agents have the potential to increase the resilience of individual ecosystem processes to future environmental change only under the condition of high functional niche overlap among service providers.

Functional redundancy within a community is, however, not the sole determinant of resilience of an ecosystem process to environmental stressors. Another critical component is the level of response diversity within a functional group, i.e. the extent to which functionally redundant species differ in their response to changes in environmental conditions (McNaughton 1977; Tilman 1999; Rosenfeld 2002). Response diversity can be assessed for multi-dimensional factors such as the effects of land-use on individual species (Cariveau *et al.* 2013) or with a focus on a specific ecological niche such as responses to changes in ambient temperature (Kühsel & Blüthgen 2015). High resilience can be expected only if functionally redundant species differ in their responses to environmental change to a degree high enough that some species within a functional group can continue to efficiently provide an ecosystem process when others are mitigated in their efficiency or lost entirely (McNaughton 1977; Tilman 1999; Kühsel & Blüthgen 2015). Hence, although the resilience of ecosystem processes to global change is likely to scale with functional redundancy, future work focused on predicting resilience to environmental stressors needs to combine estimations of functional redundancy with a measure of response diversity among service providers.

CONCLUSIONS

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

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REFERENCES

Albrecht, J., Berens, D.G., Blüthgen, N., Jaroszewicz, B., Selva, N. & Farwig, N. (2013). Logging and forest edges reduce redundancy in plant-frugivore networks in an old-growth European forest. *J. Ecol.*, 101, 990–999.

Blüthgen, N. & Klein, A.M. (2011). Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. *Basic Appl. Ecol.*, 12, 282-291.

Brose, U., Ehnes, R.B., Rall, B.C., Vucic-Pestic, O., Berlow, E.L. & Scheu, S. (2008). Foraging theory predicts predator-prey energy fluxes. *J. Anim. Ecol.*, 77, 1072–1078.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.*, 48, 1079-1087.

Cannon, R.J.C. (1998). The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Glob. Chang. Biol.*, 4, 785–796.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59.

Cariveau, D.P., Williams, N.M., Benjamin, F.E. & Winfree, R. (2013). Response diversity to land use occurs but does not consistently stabilise ecosystem services provided by native pollinators. *Ecol. Lett.*, 16, 903–911.

Chiverton, P. A. (1987). Predation of Rhopalosiphum padi (Homoptera: Aphididae) by polyphagous predatory arthropods during the aphids' pre-peak period in spring barley. Ann Appl Biol 111:257–269.

Dormann, C.F., Gruber, B. & Fründ, J. (2008). Introducing the bipartite Package: Analysing Ecological Networks. *R News*, 8, 8–11.

Ehnes, R.B., Rall, B.C. & Brose, U. (2011). Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. *Ecol. Lett.*, 14, 993–1000.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., *et al.* (2003). Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.*, 1, 488-494.

Fonseca, C.R. & Ganade, G. (2001). Species functional redundancy, random extinctions and the stability of ecosystems. *J. Ecol.*, 89, 118–125.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., *et al.* (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proc. R. Soc. B Biol. Sci.*, 282, 20142620.

Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., *et al.* (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat Commun*, 4, 1340.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., *et al.* (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic Appl. Ecol.*, 11, 97–105.

Greenop, A., Woodcock, B.A., Wilby, A., Cook, S.M. & Pywell, R.F. (2018). Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis. *Ecology*, 99, 1771-1782.

Gurr, G. M., Wratten, S. D., Landis, D. A., & You, M. (2017). Habitat management to suppress pest populations: progress and prospects. *Annu. Rev. Entomol.*, 62, 91-109.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., *et al.* (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, 477, 199–202.

Jonsson, M., Bommarco, R., Ekbom, B., Smith, H.G., Bengtsson, J., Caballero-Lopez, B., *et al.* (2014). Ecological production functions for biological control services in agricultural landscapes. *Methods Ecol. Evol.*, 5, 243–252.

Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363-375.

Kaiser-Bunbury, C.N. & Blüthgen, N. (2015). Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB Plants*, 7, plv076.

Kaiser-Bunbury, C.N., Mougal, J., Whittington, A.E., Valentin, T., Gabriel, R., Olesen, J.M., *et al.* (2017). Ecosystem restoration strengthens pollination network resilience and function. *Nature*, 542, 223–227.

Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., *et al.* (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proc. Natl. Acad. Sci.*, 115, E7863–E7870.

Kühsel, S. & Blüthgen, N. (2015). High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. *Nat. Commun.*, 6, 7989.

Laliberté, E., Wells, J.A., Declerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., *et al.* (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol. Lett.*, 13, 76–86.

Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G. & Moreno, C.R. (2009). Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. *Annu. Rev. Ecol. Evol. Syst.*, 40, 573–592.

Macfadyen, S., Craze, P.G., Polaszek, A., van Achterberg, K. & Memmott, J. (2011). Parasitoid diversity reduces the variability in pest control services across time on farms. *Proc. R. Soc. B Biol. Sci.*, 278, 3387–3394.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.

McNaughton, S.J. (1977). Diversity and Stability of Ecological Communities: A Comment on the Role of Empiricism in Ecology. *Am. Nat.*, 111, 515–525.

Mori, A.S., Furukawa, T. & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biol. Rev.*, 88, 349–364.

Östman, Ö., Ekbom, B. & Bengtsson, J. (2003). Yield increase attributable to aphid predation by ground-living polyphagous natural enemies in spring barley in Sweden. *Ecol. Econ.*, 45, 149-158.

Pan, W. (2001). Akaike's Information Criterion in Generalized Estimating Equations.

Biometrics, 57, 120–125.

Peralta, G., Frost, C.M., Rand, T.A., Didham, R.K. & Tylianakis, J.M. (2014). Complementarity and redundancy of interactions enhance attack rates and spatial stability in host-parasitoid food webs. *Ecology*, 95, 1888–1896.

Perović, D.J., Gámez-Virués, S., Landis, D.A., Wäckers, F., Gurr, G.M., Wratten, S.D., *et al.* (2018). Managing biological control services through multi-trophic trait interactions: review and guidelines for implementation at local and landscape scales. *Biol. Rev.*, 93, 306–321.

Pillar, V.D., Blanco, C.C., Müller, S.C., Sosinski, E.E., Joner, F. & Duarte, L.D.S. (2013). Functional redundancy and stability in plant communities. *J. Veg. Sci.*, 24, 963–974.

R Core Team. (2017). R: A language and environment for statistical computing. *Environ. Stat. Comput.*

Rosenfeld, J.S. (2002). Functional redundancy in ecology and conservation. *Oikos*, 98, 156–162.

Roubinet, E., Birkhofer, K., Malsher, G., Staudacher, K., Ekbom, B., Traugott, M., *et al.* (2017). Diet of generalist predators reflects effects of cropping period and farming system on extra- and intraguild prey. *Ecol. Appl.*, 27, 1167–1177.

Roubinet, E., Jonsson, T., Malsher, G., Staudacher, K., Traugott, M., Ekbom, B., *et al.* (2018). High redundancy as well as complementary prey choice characterize generalist predator food webs in agroecosystems. *Sci. Rep.*, 8, 8054.

Roubos, C.R., Rodriguez-Saona, C., & Isaacs, R. (2014). Mitigating the effects of insecticides on arthropod biological control at field and landscape scales. *Biol. Control,* 75, 28–38.

Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G. & Ekbom, B. (2013). Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. *J. Appl. Ecol.*, 50, 345–354.

Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., *et al.* (2016). Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agric. Ecosyst. Environ.*, 221, 198–204.

Sanders, D., Thébault, E., Kehoe, R. & Frank van Veen, F.J. (2018). Trophic redundancy reduces vulnerability to extinction cascades. *Proc. Natl. Acad. Sci.*, 201716825.

Staudacher, K., Jonsson, M. & Traugott, M. (2016). Diagnostic PCR assays to unravel food web interactions in cereal crops with focus on biological control of aphids. *J. Pest Sci.,* 89, 281–293.

Staudacher, K., Rubbmark, O.R., Birkhofer, K., Malsher, G., Sint, D., Jonsson, M., & Traugott, M. (2018). Habitat heterogeneity induces rapid changes in the feeding behaviour of generalist arthropod predators. Funct. Ecol., 32, 809–819.

Thibaut, L.M. & Connolly, S.R. (2013). Understanding diversity-stability relationships: Towards a unified model of portfolio effects. *Ecol. Lett.*, 16, 140–150.

Thies, C. & Tscharntke, T. (1999). Landscape structure and biological control in agroecosystems. *Science,* 285, 893–895.

Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L., *et al.* (2012). Food webs: Reconciling the structure and function of biodiversity. *Trends Ecol. Evol.*, 27, 689-697.

Tilman, D. (1999). The ecological consequences of changes in biodiversity: A search for general principles. In: *Ecology*. pp. 1455–1474.

Toft, S. & Bilde, T. (2002). Carabid diets and food value. *Agroecology of Carabid Beetles* pp. 81–110.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T. A., Tylianakis, J.M., van Nouhuys, S. & Vidal, S. (2008) "Reprint of “Conservation biological control and enemy diversity on a landscape scale”[Biol. Control 43 (2007) 294–309]." *Biol Control* 45, 238-253

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010). Conservation of species interaction networks. Biol. Conserv., 143, 2270–2279.

Tylianakis, J.M., Tscharntke, T. & Klein, A.M. (2006). Diversity, ecosystem function, and stability of parasitoid-host interactions across a tropical habitat gradient. *Ecology*, 87, 3047–3057.

Veddeler, D., Tylianakis, J., Tscharntke, T. & Klein, A.M. (2010). Natural enemy diversity reduces temporal variability in wasp but not bee parasitism. *Oecologia*, 162, 755–762.

Weibull, A.C., Östman, Ö. & Granqvist, Å. (2003). Species richness in agroecosystems: The effect of landscape, habitat and farm management. *Biodivers. Conserv.*, 12, 1335–1355.

Zhu, G., Gariepy, T.D., Haye, T. & Bu, W. (2017). Patterns of niche filling and expansion across the invaded ranges of Halyomorpha halys in North America and Europe. *J. Pest Sci. (2004).*, 90, 1045–1057.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). Generalised Estimation Equations. In: *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, pp. 295–321.

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

Model	**QIC_c**	**ΔQIC_c**	**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)

Table 2: Subset of prey groups of ground-dwelling arthropod predators in spring barley fields in central Sweden used in the analysis. Total number of predator species tested positive for consumption of each prey group, predation evenness among predator species and parameter estimates (PE) derived from generalized estimating equations (GEE) for the relationship between biodiversity and functional redundancy of predation on each respective prey group are shown. Significant correlations (i.e., 95% confidence intervals not crossing 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 files	extraguild	18	0.70	**0.23 (0.07-0.39)**
Sheet-web spiders	intraguild	16	0.73	**0.35 (0.20-0.49)**
Bembidion sp.	intraguild	16	0.69	**0.27 (0.12-0.42)**
Seven-spot ladybird	intraguild	16	0.63	0.17 (-0.10-0.44)

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

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

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

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

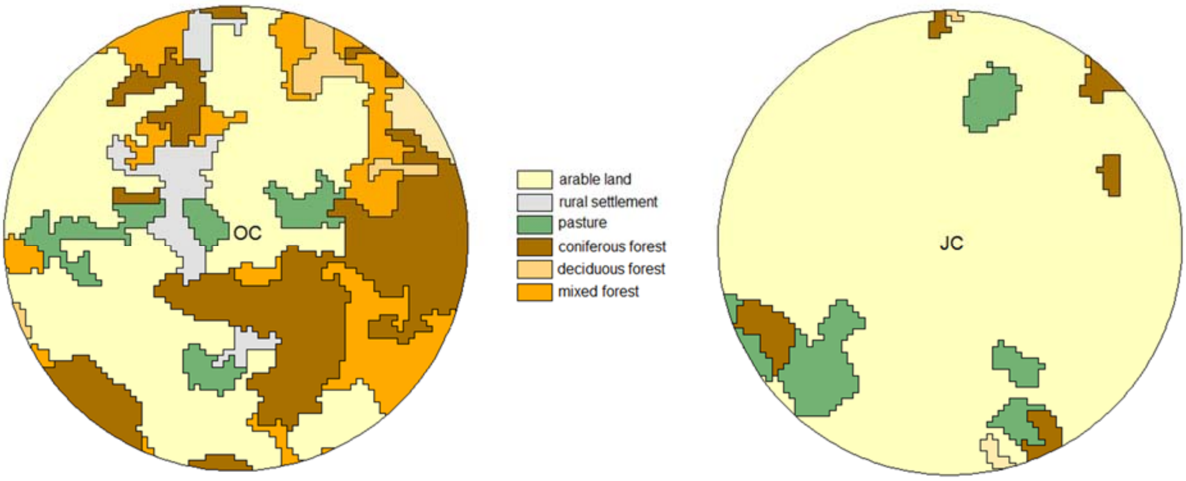

Figure 1.

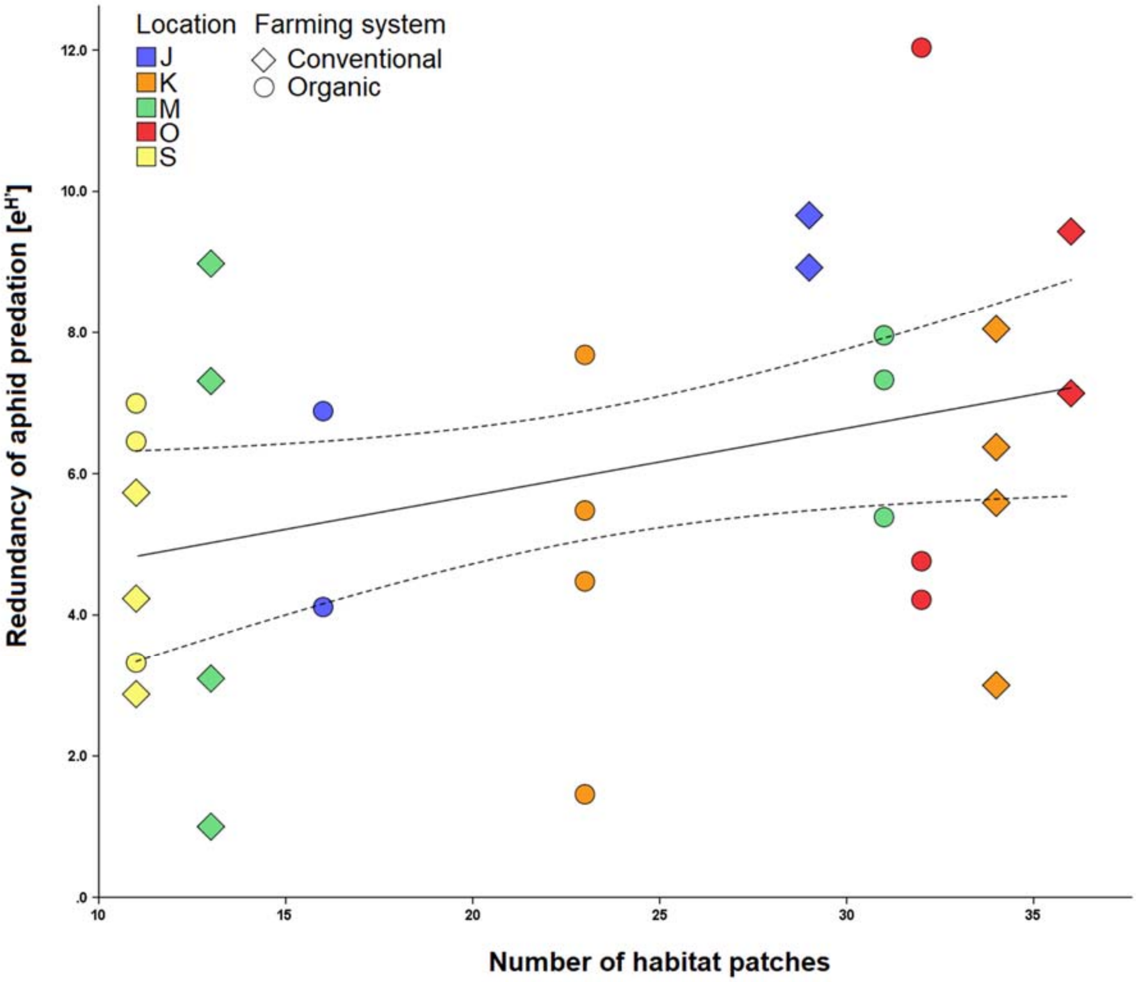

Figure 2.

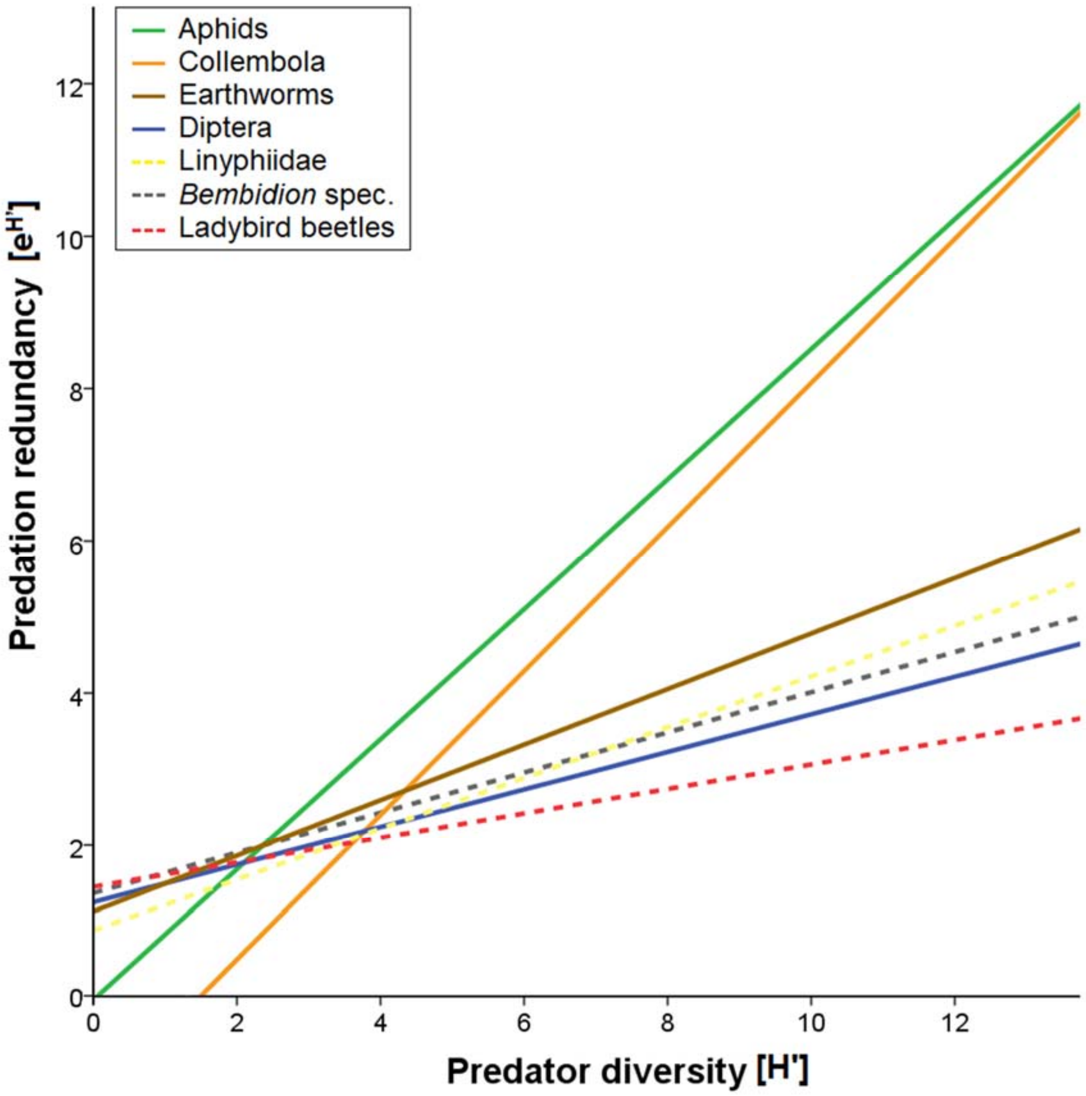
Aphids
Collembola
Earthworms
Diptera
Linyphiidae
Bembidion spec.
Ladybird beetles
Predation redundancy [e^H']
Predator diversity [H']
0
2
4
6
8
10
12
0
2
4
6
8
10
12

Figure 3.

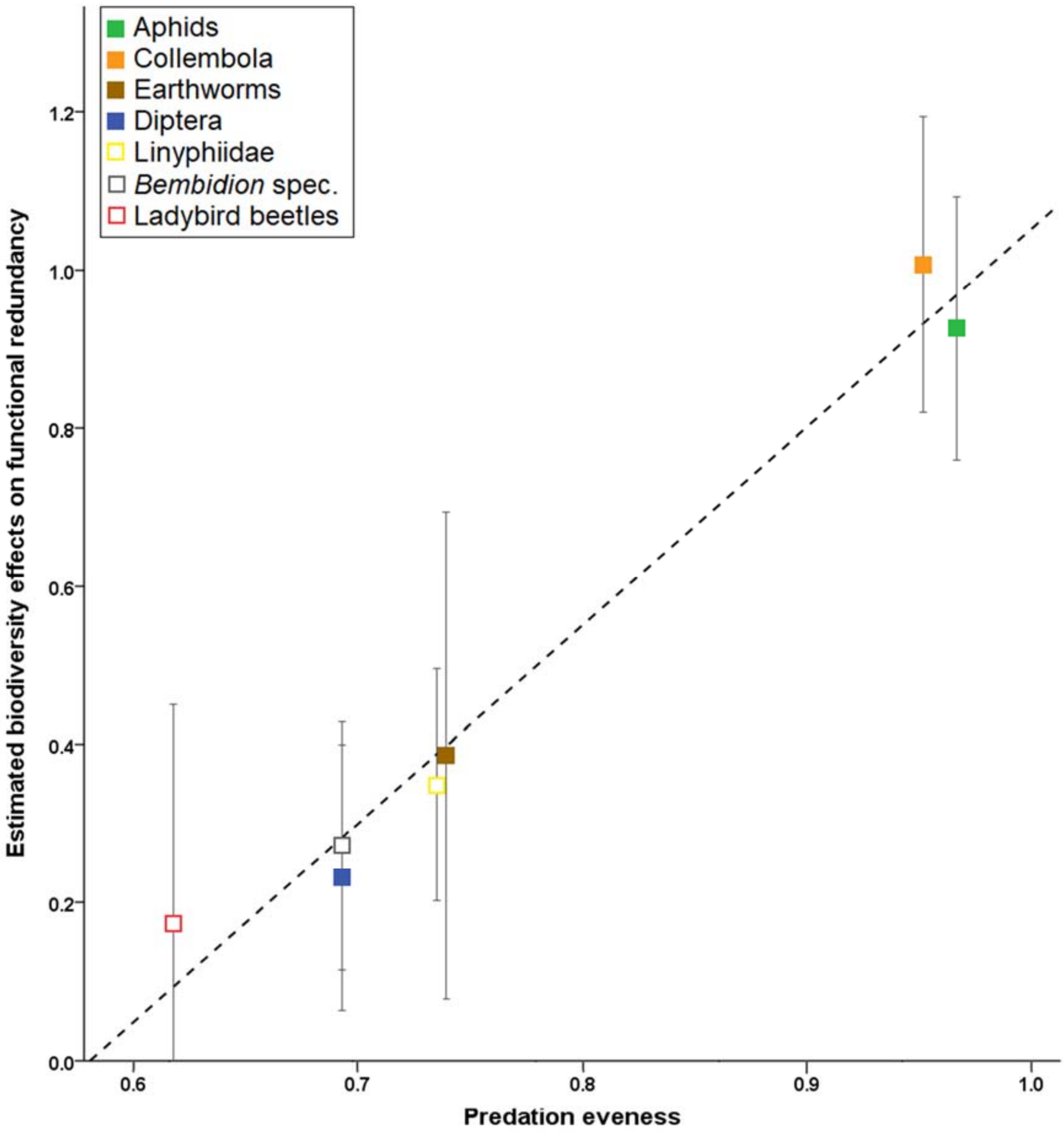
Aphids
Collembola
Earthworms
Diptera
Linyphiidae
Bembidion spec.
Ladybird beetles
Estimated biodiversity effects on functional redundancy
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.6
0.7
0.8
0.9
1.0
Predation eveness

Figure 4.