

1 **Functional identity and diversity of animals predict ecosystem**  
2 **functioning better than species-based indices**

3 **Authors:** Vesna Gagic<sup>1,a</sup>, Ignasi Bartomeus<sup>1,2,a,\*</sup>, Tomas Jonsson<sup>1</sup>, Astrid Taylor<sup>1</sup>, Camilla  
4 Winqvist<sup>1</sup>, Christina Fischer<sup>3</sup>, Eleanor M. Slade<sup>4</sup>, Ingolf Steffan-Dewenter<sup>5</sup>, Mark Emmerson<sup>6</sup>,  
5 Simon G. Potts<sup>7</sup>, Teja Tschamtkke<sup>8</sup>, Wolfgang Weisser<sup>9</sup>, Riccardo Bommarco<sup>1</sup>

6 **Affiliations:**

7 <sup>1</sup>Swedish University of Agricultural Sciences, Department of Ecology, SE-75007 Uppsala, Sweden

8 <sup>2</sup> Estación Biológica de Doñana (EBD-CSIC), Dpto. Ecología Integrativa, E-41092 Sevilla, Spain.

9 <sup>3</sup> Technische Universität München, Restoration Ecology, Department of Ecology and Ecosystem  
10 Management, Emil-Ramann-Str. 6, 85354 Freising, Germany

11 <sup>4</sup> Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK

12 <sup>5</sup> Department of Animal Ecology and Tropical Biology, Biocentre, University of Würzburg, Am  
13 Hubland, 97074 Würzburg, Germany

14 <sup>6</sup> School of Biological Sciences, Queen's University Belfast, Medical Biology Centre, 97 Lisburn  
15 Road, Belfast, BT9 7BL, UK.

16 <sup>7</sup> School of Agriculture, Policy and Development, Reading University, Reading, RG6 6AR, UK

17 <sup>8</sup> Agroecology, University of Göttingen, Germany

18 <sup>9</sup> Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center  
19 for Food and Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-  
20 Carlowitz-Platz 2, 85354 Freising, Germany

21 <sup>a</sup> These authors made an equal contribution.

22 **Emails:** Vesna Gagic ([vesna.gagic@slu.se](mailto:vesna.gagic@slu.se)), Ignasi Bartomeus ([nacho.bartomeus@gmail.com](mailto:nacho.bartomeus@gmail.com)),  
23 Tomas Jonsson ([tomas.jonsson@slu.se](mailto:tomas.jonsson@slu.se)), Astrid Taylor ([astrid.Taylor@slu.se](mailto:astrid.Taylor@slu.se)), Camilla Winqvist  
24 ([camilla.winqvist@heby.se](mailto:camilla.winqvist@heby.se)), Christina Fischer ([christina.fischer@tum.de](mailto:christina.fischer@tum.de)), Eleanor Slade  
25 ([eleanor.slade@zoo.ox.ac.uk](mailto:eleanor.slade@zoo.ox.ac.uk)), Ingolf Steffan-Dewenter ([ingolf.steffan@uni-wuerzburg.de](mailto:ingolf.steffan@uni-wuerzburg.de)), Mark  
26 Emmerson ([m.emmerson@qub.ac.uk](mailto:m.emmerson@qub.ac.uk)), Simon Potts ([s.g.potts@reading.ac.uk](mailto:s.g.potts@reading.ac.uk)), Teja Tschardt  
27 ([ttschar@gwdg.de](mailto:ttschar@gwdg.de)), Wolfgang Weisser ([wolfgang.weisser@tum.de](mailto:wolfgang.weisser@tum.de)), Riccardo Bommarco  
28 ([riccardo.bommarco@slu.se](mailto:riccardo.bommarco@slu.se)),

29 \* **Correspondence to:** Ignasi Bartomeus, Estación Biológica de Doñana (EBD-CSIC), Avda.  
30 Américo Vespucio s/n, Isla de la Cartuja, E-41092 Sevilla, Spain +46 018-672 434.  
31 [nacho.bartomeus@gmail.com](mailto:nacho.bartomeus@gmail.com)

32 **Word count:** Abstract words 182; Main text words 5058; refs 60; Figures 2; Table 1.

33 **Author contributions:** IB and VG designed the research; AT, CW, CF, ES, SP, IS-D, ME, TT,  
34 WW, RB collected and provided data; VG and IB analyzed the data; VG, IB wrote the first draft of  
35 the manuscript, and all authors contributed substantially to revisions.

36 **Subject Area:** ecology

37 **Short title:** Functional diversity and ecosystem functioning

38 **Keywords:** functional traits, biodiversity, pollination, biocontrol, nutrient cycling, dung removal,  
39 seed burial, bioturbation

## 40 **Abstract**

41           Drastic biodiversity declines have raised concerns about the deterioration of ecosystem  
42 functions and have motivated much recent research on the relationship between species diversity  
43 and ecosystem functioning. A functional trait framework has been proposed to improve the  
44 mechanistic understanding of this relationship, but this has rarely been tested for organisms other  
45 than plants. We analyzed eight data-sets, including five animal groups, to examine how well a trait-  
46 based approach, compared with a more traditional taxonomic approach, predicts seven ecosystem  
47 functions below and above ground. Trait-based indices consistently provided greater explanatory  
48 power than species richness or abundance. The frequency distributions of single or multiple traits in  
49 the community were the best predictors of ecosystem functioning. This implies that the ecosystem  
50 functions we investigated were underpinned by the combination of trait identities (i.e., single-trait  
51 indices) and trait complementarity (i.e., multi-trait indices) in the communities. Our study provides  
52 new insights into the general mechanisms that link biodiversity to ecosystem functioning in natural  
53 animal communities and suggests that the observed responses were due to the identity and  
54 dominance patterns of the trait composition rather than the number or abundance of species *per se*.

## 55 **Introduction**

56           Unprecedented species extinctions during the past decades have raised concerns about the  
57 consequences of biodiversity loss for the functioning of ecosystems and associated ecosystem  
58 services that are fundamental for human well-being [1]. Ample evidence shows that species  
59 richness and diversity can enhance ecosystem functioning [2, 3]. However, much variation in the  
60 relationship between biodiversity and functioning (BEF) remains to be explained. To improve  
61 predictions and mechanistic understanding of BEF it has been increasingly accepted that instead of  
62 focusing on the taxonomic identity of organisms, the diversity of functional traits of species within  
63 a community should be studied [2 - 5]. However, the usefulness of such trait-based compared to  
64 species-based approaches, as well as the relative importance of single vs. multiple traits for  
65 ecosystem functioning remained largely unexplored in organisms other than plants.

66           In early attempts to link species traits to ecosystem functioning, species were sorted into  
67 functional groups based on the similarity of their traits often according to experts' opinion (e.g.,  
68 [6]). Although this was a step forward and a useful exercise, the approach was criticized because  
69 functional groups failed to consider within-group variation in traits, and they rarely explained more  
70 variation in ecosystem functioning compared with randomly assembled groups of species [7].  
71 Recently, quantitative measures have been developed that use multivariate techniques to integrate  
72 multiple traits into a single continuous trait diversity index. These measures capture value, range, or  
73 distribution of functional traits in a community (hereafter “functional diversity”). They are  
74 promising tools that could increase our understanding of the mechanisms that drive ecosystem  
75 functioning [8 - 11]. However, most studies have used functional diversity merely as a proxy for  
76 ecosystem functioning, but without actually measuring the function and explicitly linking it to the  
77 functional diversity measure. For functional diversity measures to be useful for explaining  
78 ecosystem functioning, their predictive ability needs to be tested, and they should provide  
79 information beyond that given by measures based exclusively on species richness and abundances  
80 [5]. Here, we intend to fill this gap in BEF research by examining the relationship between trait- or

81 species-based indices and a number of animal provided ecosystems functions measured below- and  
82 above-ground.

83         There is an ongoing debate about which of the many functional diversity measures should  
84 best predict ecosystem functioning, and which mechanisms these relationships reflect [5]. We  
85 summarize the main mechanisms of ecosystem functioning that different trait-based indices  
86 emphasize (Figure 1). First, if differences among species are unimportant, the overall numerical or  
87 biomass abundance of organisms in a community might be better predictors than any of the  
88 measures that incorporate functional traits (Figure 1*a*). Thus, overall abundance provides a null  
89 model in which all species in the community are equally efficient regardless of the trait levels they  
90 have. Note that trait-based indices consider both, which traits are assumed to be important, but also  
91 their trait values (continuous traits, e.g., different values of body size) or levels (discrete traits, e.g.,  
92 diet ‘specialist’ or ‘generalist’). For simplicity we refer only to trait levels throughout. Second, if a  
93 single trait level is strongly linked to an ecosystem function, abundance of this trait level may best  
94 predict the functioning (the functional identity hypothesis) [12 - 14; Figure 1*b*]. Alternatively, the  
95 complementarity of different traits in the community may be important for the functioning in the  
96 ecosystem (the functional complementarity hypothesis) [4, 15]. In this case, indices that measure  
97 presence or absence of certain trait levels (i.e., functional richness, Figure 1*c*), or those that consider  
98 abundance of different trait levels in the community (Figure 1*d*) will explain most of the  
99 functioning. In the latter case, weighted functional diversity indices will best predict ecosystem  
100 functioning. It should be noted that only positive functional diversity-ecosystem functioning  
101 relationships indicate functional complementarity. Negative relationships reflect components of  
102 both functional identity and complementarity with only a few dominant trait levels being important.  
103 Hence, the functional identity and complementarity hypotheses are not mutually exclusive and  
104 several studies have found that a combination of the two explained most of the variation for several  
105 ecosystem functions [16 - 20]. Analyzing which functional diversity indices can best explain a set

106 of ecosystem functions may provide clues to the main drivers of these functions and increase our  
107 mechanistic understanding of the BEF relationship.

108         Most tests of how well multivariate functional diversity is linked to ecosystem functioning  
109 (Figure 1 *c* and *d*) have been conducted in small-scale, highly controlled plant communities. In  
110 addition, we have not been able to find any investigations of this relationship for terrestrial animals  
111 (see the literature summary in Table S1). Hence, we analyzed eight data sets collected from the field  
112 along land-use gradients, and covering five terrestrial animal groups and seven ecosystem functions  
113 above and below ground: bees (pollination), carabid beetles (biocontrol of crop pests, biocontrol of  
114 weeds), earthworms (bioturbation), soil nematodes (nutrient cycling) and dung beetles (dung  
115 removal, seed burial). Increased understanding of the BEF relationship in these systems is important  
116 because both species and functional diversity are under great threat from land-use intensification  
117 [21, 22]. Furthermore, sustainable development of human society in the face of rapidly increasing  
118 human populations will depend on the ways we manage these ecosystems and the services they  
119 provide. However, we do not attempt to describe direct effects of land-use on biodiversity or  
120 ecosystem functioning as this is done in numerous previous studies (e.g., [22 - 24]). Instead, we use  
121 the land-use gradients in order to assure we capture variability in different aspects of the community  
122 composition such that we can detect and assess its impacts on functioning.

123         We tested which of the four groups of indices in Figure 1 best predicted ecosystem  
124 functioning in our data sets. More precisely, we explored (i) whether trait-based approaches offer  
125 greater explanatory power of ecosystem functioning than indices based only on species presence  
126 and abundance; (ii) whether single trait measures calculated as community weighted trait means  
127 (CWM, reflecting the functional identity hypothesis) explain ecosystem functioning better or worse  
128 than multivariate functional diversity measures (reflecting the functional complementarity  
129 hypothesis); and, (iii) whether the predictive power of multivariate functional diversity measures  
130 increases when the traits are weighted by numerical or biomass abundance of the species in the  
131 communities.

## 132 **Material and methods**

### 133 *Data description*

134           We analyzed eight field studies that included five animal groups (bees, carabid beetles,  
135 earthworms, soil nematodes, and dung beetles) which deliver seven key ecosystem functions  
136 (pollination, biocontrol of crop pests, biocontrol of weeds, bioturbation, nutrient cycling, dung  
137 removal, and seed burial). We focus on field studies because knowledge gained by them is an  
138 important complement to the numerous experimental studies in BEF research. Despite difficulties to  
139 demonstrate direct causal links [25], field studies better reflect the relative importance of  
140 mechanisms in real world situations that are governed by processes acting at other scales than the  
141 commonly investigated small-scale BEF experiments. The data we used had not been analyzed in  
142 this context previously. For each animal group we collected species' trait information from  
143 identification keys and from a number of published research papers and databases. We included  
144 traits which are often measured for a specific animal group and shown to be key traits in affecting  
145 the organisms' response to environmental change, and/or to have functional significance (see Text  
146 S1 for the discussion about the trait choice and list of traits and references). Adult specimens were  
147 identified to species, except for pollinators and nematodes where similar species not identifiable in  
148 the lab were assigned to the same morphspecies. Analyses were done independently for each  
149 separate data-set and ecosystem function.

150

151 *Pollination:* We analyzed three separate data-sets conducted in three crop systems (field beans,  
152 strawberries, and spring oilseed rape) in UK, Germany, and Sweden respectively [26]. Bees were  
153 sampled in 10 fields in each crop type by hand-netting along a fixed transect. Fields were located  
154 along a gradient of landscape complexity measured as percentage arable land. Functioning was  
155 measured as total weight of fruits on five to ten plants (depending on the crop) in 4 plots per field.

156

157 *Biocontrol of pests:* We analyzed data from studies replicated in six European regions: Ireland,  
158 West Germany, East Germany, Poland, and two provinces in Sweden: Uppsala and Scania [27]. In  
159 each country, eight cereal fields were located in contrasting landscapes with low vs. high levels of  
160 agricultural intensification. Carabid beetles were collected with five pitfall traps per field. To  
161 measure function delivery by ground-dwelling predators, enclosure experiments were used to  
162 calculate the difference between aphid population growth in full enclosure (excluding ground-  
163 dwelling and flying predators and parasitoids using cages and barriers), and aphid population  
164 growth when ground-dwelling predators (mainly carabids) had access to aphids (excluding flying  
165 predators and parasitoids using cages).

166

167 *Biocontrol of weeds:* We used data from a study conducted in Germany in 22 winter wheat fields  
168 selected along a gradient in landscape complexity measured as percentage arable land (11 paired  
169 fields, [28]). Carabids were sampled using four pitfall traps per field. Biocontrol of weeds was  
170 calculated for four common species: goosegrass (*Galium aparine* L.; Seed consumption Ga),  
171 creeping thistle (*Cirsium arvense* L. Scop.; Seed consumption Ca), rough-stalked meadow-grass  
172 (*Poa trivialis* L.; Seed consumption Pt), and loose silky bentgrass (*Apera spica-venti* L; Seed  
173 consumption As) separately. To measure percentage of seed loss due to ground-dwelling  
174 invertebrates, enclosure experiments were used to calculate the difference between percentage of  
175 remaining seeds from the initial seed number or seed weight in full enclosure (vertebrates and  
176 invertebrates excluded using cages with a small mesh size) and when only the vertebrates were  
177 excluded (using cages with a large mesh size) so that carabids had access to seeds.

178

179 *Bioturbation:* Earthworm communities were studied in cereal fields in the Swedish provinces of  
180 Uppland and Scania. In each province, earthworm communities were assessed in six sets of three  
181 farms that differed in farm management in close proximity to one another (see [29] for design of the



182 study). Earthworm communities were estimated from four soil samples (30×30×30 cm) per field,  
183 taken at least 20m from the field edges and with a 20m distance between each sample. Earthworms  
184 were carefully hand sorted. Bioturbation was measured as above-ground cast production estimated  
185 by measuring *in situ* cast production over time on four observation squares at each field (dry matter  
186 soil per unit area and time). Bioturbation is an important ecosystem function as it affects soil  
187 formation, water supply and flood and erosion control through its influence on pedogenesis and  
188 infiltration and storage of water in soil [30]. Earthworms actively participate to the process of  
189 bioturbation as they may ingest large amounts of soil and litter, and hence become major regulators  
190 of the dynamics of litter and SOM in the ecosystem [31].

191

192 *Nutrient cycling:* Soil surveys from 44 agricultural sites in the Netherlands were analyzed [32]. In  
193 each field, 320 soil cores were randomly collected and mixed. Nematodes were extracted from 100g  
194 sub-samples. 150 randomly chosen individual nematodes were identified per site. As a measure  
195 of ecosystem function we used total amount of phosphorous (P total) in soil as a proxy for nutrient  
196 cycling. Nematode abundance is strongly correlated to soil P and through their micro-bioturbation  
197 activity high nematode abundances might contribute to high P retention [33].

198

199 *Dung removal and seed burial:* We used data collected from six forest sites in Sabah, Malaysian  
200 Borneo (two old-growth forest, two low-intensity selectively logged forest and two high-intensity  
201 logged forest) [34]. Dung beetles were sampled using 10 dung-baited pitfall traps per site. Dung  
202 removal was measured by placing a pile of cattle dung at each of the 10 points one month after the  
203 trapping and collecting the remaining dung after 24 hours. Plastic beads of three sizes (small,  
204 medium, large) were used as seed mimics and placed in the dung to measure seed removal rates.

205

207 For each community we calculated several biodiversity indices (Table 1) divided into the  
208 four groups shown in Figure 1. For indices that were weighted by numerical or biomass abundance,  
209 we used the subscripts “/n” and “/b” respectively. Biomass abundance of each species in a  
210 community was obtained by multiplying the number of individuals of each species by its average  
211 body mass. For bees and carabid beetles, average body masses were estimated from a measure of  
212 body size using allometric relationships (based on intertegular distance for bees [35]; total body  
213 length for carabids [36]). For earthworms, nematodes, and dung beetles we used body mass  
214 measurements; dry body mass measured directly or fresh weight converted to dry body mass. For  
215 earthworms and nematodes, body mass was estimated separately for field populations of adults and  
216 juveniles, and then weighted by their proportional numerical abundances.

217 First, we calculated species-based indices from species presence, and numerical or biomass  
218 abundance ( $S_x$ , where  $x$  is the diversity index used): species richness ( $S_{rich}$ ), Pielou’s evenness  
219 based on species numerical or biomass abundance ( $Seve/n$  and  $Seve/b$ ), Shannon diversity index  
220 based on numerical or biomass abundance ( $S_{sh}/n$  and  $S_{sh}/b$ ), and total abundance or biomass of the  
221 community ( $Stot/n$  and  $Stot/b$ ).

222 Second, we calculated single trait-based indices, i.e., community weighted means for each  
223 trait in a community (Figure 1b), weighted by their relative numerical ( $CWM_x/n$ , [37]) or biomass  
224 abundances (our adjusted index,  $CWM_x/b$ ), where  $x$  is the name of the trait or a trait dominant level  
225 for categorical traits. If a trait was categorical, we used the frequency of the most abundant trait  
226 level in the community.

227 Multi-trait indices are often described by three independent groups of measures [38] –  
228 functional richness, functional evenness and functional diversity [11, 39], which capture different  
229 aspects of the functional diversity [11]. Each group of measures can be calculated in several  
230 different ways, but there is no consensus on which index within each group performs best. To test

231 our question about relative importance of weighted vs. non-weighted FD indices we calculated 14  
232 commonly used multivariate functional diversity measures, which we divided into two groups. The  
233 first group considers only the presence or absence of trait levels (two functional richness indices  
234 FRx, Figure 1c). The second group comprises twelve functional diversity indices weighted by  
235 numerical and biomass abundance (FDx/n and FDx/b, Figure 1d), therefore including both  
236 functional divergence and functional evenness measures. All indices are based on a species per  
237 species trait-distance matrix. Given that all datasets contain traits coded as categorical variables, all  
238 distance matrices based on species traits were calculated using Gower distance with Podani's  
239 extension to ordinal variables [11, 40, 41].

240 For the two functional richness measures (FRx) we first calculated a measure based on  
241 dendrograms (FRdendr, [8]). The dendrogram was constructed using the UPGMA clustering  
242 algorithm, as it yielded a dendrogram with the highest cophenetic correlation with our original  
243 distance matrices and has also been identified to perform best in most cases [41]. The cophenetic  
244 correlation measures how faithfully a dendrogram preserves the original pairwise distances. Second,  
245 we estimated the minimum volume required to contain a set of points in trait-space (FRminvol,  
246 [11]). A Cailliez correction was applied when the species-by-species distance matrix could not be  
247 represented in a Euclidean space [42]. However, the quality of the reduced space was not as high as  
248 the quality measured as cophenetic correlation for the dendrogram-based approach (quality  
249  $FRminvol = 0.51 \pm 0.11$ , quality  $FRdendr = 0.8 \pm 0.04$ ).

250 Next, we calculated the twelve functional diversity measures weighted by numerical or  
251 biomass abundance (FDx). The first four indices (FDdendr.wc/n, FDdendr.wc/b, FDdendr.ac/n,  
252 FDdendr.ac/b) are weighted versions of FRdendr implemented specifically for this paper. In order  
253 to construct the weighted indexes, before summing the branches of a dendrogram, each branch is  
254 weighted by the relative numerical or biomass abundance of each species within the community  
255 (FDdendr.wc/n, FDdendr.wc/b). Hence, for each terminal branch, the weighting is done according  
256 to the abundance of the terminal species in this branch, but for each internal branch, the weighting

257 is done by the average of the abundances of all the species descending form this internal branch.  
258 This index is highly correlated with the weighting procedure proposed in [43], but has the  
259 advantage that instead of building a different dendrogram for each community, it builds a single  
260 dendrogram for all communities, which is the recommended approach [41]. The next two indices  
261 are constructed in the same way, but weighted by the mean relative proportion of numerical or  
262 biomass abundance of each species with respect to the species with highest numerical or biomass  
263 abundance across all communities (FDdendr.ac/n, FDdendr.ac/b). While the first index relates to the  
264 evenness of species in a community, the second one takes into account the relative numerical or  
265 biomass abundances in a community with respect to all the other analyzed communities. The  
266 remaining eight indices are based on the convex hull space: functional divergence (FDdiv/n,  
267 FDdiv/b, [11]), functional dispersion (FDdis/n, FDdis/b, [10]), and Rao's quadratic entropy  
268 (FDRao/n, FDRao/b [44]). Functional dispersion and Rao's quadratic entropy are highly correlated,  
269 but we included both to enable comparison with other studies that have used these indices. Finally,  
270 we calculated two measures of functional evenness (FDeve/n, FDeve/b; [11]).

271

## 272 *Statistical analysis*

273 For each dataset we ranked the indices according to their relative performance in explaining  
274 functioning. For that, we focus only on the explanatory power (measured as  $R^2$ ) of different indices.  
275 First, we used linear mixed-effect models and calculated their marginal  $R^2$  [45]. For each  
276 ecosystem function (response variable), we built one single-variable model for each of the diversity  
277 indices (explanatory variable). For datasets that included observations that were collected at  
278 multiple times within a region or a field we included these (Field or Region) as random factors. The  
279 residuals from all models were plotted and visually inspected. When necessary, data were  
280 transformed by  $\log_{10}(x+1)$  or arcsine square root to meet model assumptions of normality. To meet  
281 the assumptions of homoscedasticity we used a constant variance function when necessary. We only

282 provide p-values in the appendix for completeness, and we do not interpret them as indicators of  
283 statistical significance due to the risk of Type I errors from multiple testing on the same data.  
284 Indices were ranked according to the  $R^2$  value obtained and a relative rank bounded between 0 and 1  
285 was calculated for each dataset, with 0 being the best ranked index.

286 To compare the relative performance among groups of indices, we used linear mixed effects model  
287 to regress the arcsine square root transformed relative rank of the indices within each of the 14  
288 datasets (response variable) against its category (factor with four levels: species based indices -  $S_x$ ,  
289 functional richness - $FR_x$ , functional diversity- $FD_x$  and community weighted means- $CWM_x$ ), and  
290 weighting method (factor with two levels: biomass or numerical abundance). Given that  $FDR_{ao}$  and  
291  $FD_{dis}$  are mathematically correlated, we excluded  $FD_{dis}$  from this comparison. We used “dataset”  
292 in the random structure to control for multiple calculations of the indices belonging to the same  
293 group in each dataset. We used General linear hypothesis testing (“glht” function) with two-tailed  
294 test and Hochberg correction for multiple testing [46] for post-hoc comparisons among groups of  
295 indices. Note that studies are conducted at different scales (within vs. across regions) with a  
296 consequence of having more confidence in the results for highly replicated designs (i.e. biocontrol  
297 of pests and nutrient cycling). However, we do not correct for this as each dataset contributes with  
298 only one set of values to the linear model.

299

### 300 *Influence of traits on functional diversity-ecosystem functioning relationship*

301 All included traits were chosen *a priori* based on the authors' ecological knowledge. To test  
302 whether our choice of traits had a large influence on the observed effect of functional diversity  
303 measures on ecosystem functioning, we used a jack-knife approach for the functional diversity  
304 predictors ( $FR_x$  or  $FD_x$ ) that explained most variance.

305 We built models with all traits included, and we then removed one trait at a time from the  
306 full model. We calculated the difference in explanatory power ( $\Delta R^2$ ) between the full model and the

307 model without a given trait. Negative  $\Delta R^2$ 's reflect traits that are important in explaining the  
308 relationship between diversity and function, while positive values indicate traits that, when  
309 excluded, improved the model. All calculations of diversity indices and statistical analyses were  
310 performed in R (version 2.15.1, [47]) using packages “nlme” [48], “MuMIn” [49], “FD” [10, 50],  
311 “multcomp” [51] and our own R script. The R function to calculate all indices used in our analysis  
312 is available at <https://github.com/ibartomeus/fundiv>.

313 All relevant data including all indices calculated for each dataset can be found in Dataset S1.

## 314 **Results**

### 315 *Performance of functional diversity in predicting ecosystem functioning*

316 We compared explanatory power between groups of biodiversity indices: species-based vs.  
317 trait-based, single-trait vs. multiple traits, community weighted vs. non-weighted indices, and  
318 indices weighted by numerical vs. biomass abundance. We found large differences in the average  
319 performance between the index groups ( $F_{3,478} = 11.16$ ,  $p < 0.0001$ ). Post-hoc comparison among  
320 relative ranks of indices groups revealed that weighted trait-based indices, both community  
321 weighted means (CWM<sub>x</sub>) and functional diversity (FD<sub>x</sub>), performed consistently better than  
322 species-based indices (S<sub>x</sub>) across all data sets studies (difference in means: S<sub>x</sub>-CWM<sub>x</sub> =  $0.23 \pm$   
323  $0.04$ ,  $p < 0.0001$ ; S<sub>x</sub>-FD<sub>x</sub> =  $0.13 \pm 0.05$ ,  $p = 0.02$ ; Figure 2, Table S2). However, non-weighted  
324 functional richness (FR<sub>x</sub>) did not perform better than species-based indices (S<sub>x</sub>-FR<sub>x</sub> =  $0.10 \pm 0.07$ ,  
325  $p = 0.36$ ), while single-trait measures (CWM<sub>x</sub>) were on average better ranked than functional  
326 diversity measures (CWM<sub>x</sub>-FD<sub>x</sub> =  $-0.10 \pm 0.04$ ,  $p = 0.02$ ). Multi-trait functional diversity measures  
327 weighted by numerical abundance (FD/n) performed equally good as measures weighted by  
328 biomass abundance (FD/b;  $F_{1,478} = 0.078$ ,  $p = 0.93$ ). Note that the lower the relative rank, the better  
329 the performance of the index is.

330 Interestingly, species richness and abundance did not only obtain low rankings, but their  
331 explanatory power was on average less than half of that of FD indices (Table S2). Shannon

332 diversity and species evenness tended to explain most functions better than species richness and  
333 abundance. Within the weighted multi-trait functional diversity measures, FDeve and FDdiv were  
334 the best performers. In fact, in 9 of 14 cases they ranked as the overall best predictors. Notably, the  
335 direction of the effects of biodiversity indices on ecosystem functioning was positive in the majority  
336 of cases, the exception being a few FD indices (Table S2).

### 337 *Influence of traits on functional diversity-ecosystem functioning relationship*

338 Jack-knife analysis showed that our results are relatively robust with respect to the choice of  
339 traits included (see Figure S1). Changes in  $R^2$  after excluding any trait were small and mainly  
340 negative. The few exceptions were ‘dung manipulation strategy’ for large seed burial by dung  
341 beetles, ‘light preference’ for consumption of *Apera spica-venti* seeds by carabid beetles, and ‘body  
342 length’ and ‘trophic level’ for nutrient cycling by nematodes. Traits with high negative values are  
343 highly influential because they increase the explanatory power. In contrast, we only found one trait,  
344 ‘hibernation’, which induced large positive  $R^2$ -changes in the consumption of *Apera spica-venti*  
345 seeds and *Galium aparine* seeds by carabid beetles, indicating that this trait reduces the model  
346 performance (Figure S1).

347

## 348 **Discussion**

349 Indices solely based on the numbers and abundances of species were consistently poor at  
350 predicting ecosystem functioning across the seven ecosystem functions investigated here.  
351 Moreover, they performed worse than indices using a trait-based approach, both in previous studies  
352 of plants (Table S1), and in our current analysis of animals. As in many plant studies, single-trait  
353 indices (CWMx) were often ranked as the best predictors of ecosystem functioning in our analyses  
354 on animals. Hence, functioning is in the majority of cases maximized by a single trait. However, we  
355 also found that multi-trait functional diversity measures (e.g., FDeve, FDdiv) can best predict

356 functions provided by some animal groups. Thus, it appears that the distribution of functionally  
357 dissimilar traits is also relevant for several functions.

358         Despite the diversity of ecosystems and of organisms and ecosystem functions provided by  
359 animals investigated here, and by plants in previous studies, some general conclusions can be made.  
360 First, species numerical and biomass abundance appear to be poor sole predictors of the functions  
361 investigated, although they are often positively correlated with ecosystem functions (Figure 1a, e.g.,  
362 [52]). Second, non-weighted indices that have commonly been used as proxies of functional  
363 diversity were also poor predictors of ecosystem functioning. These include species richness, but  
364 also newly developed multi-trait indices of functional richness (FR<sub>x</sub>) that has been useful for  
365 analyzing community assembly [39]. This suggests that the number of species in a community, or  
366 the trait ranges they encompass, are insufficient to fully explain ecosystem functioning.

367         Current knowledge on the role of species richness for ecosystem functioning is mainly based  
368 on small-scale experiments [3]. There is increasing evidence that results from such studies do not  
369 always agree with findings from more realistic and species rich assemblages where skewed species  
370 abundance distributions have been suggested to play a key role [53, 54]. Our findings indicate that  
371 we need to integrate the abundance and distribution not only of species, but also of their trait levels  
372 within the community to better understand BEF relationships in terrestrial animal communities  
373 (Figure 1b,d). On one hand, we show that weighted functional diversity indices (especially  
374 functional evenness and divergence) in many cases were the best predictors of ecosystem  
375 functioning provided by animals, and this relationship was most often positive. This means that  
376 communities with a more even distribution of species across the trait space, will deliver higher  
377 levels of ecosystem functioning; a result that supports the functional complementarity hypothesis.  
378 On the other hand, we also found negative relationships between functional evenness and  
379 functioning in some cases, as well as single traits being consistently good predictors of functioning.  
380 This exemplifies that a dominant trait level of a single or just a few traits are needed to maximize  
381 functioning in some communities.



382           The functions studied here were performed by different taxa with different traits, and hence  
383 the mechanisms driving high functioning levels vary among functions. Given the exploratory nature  
384 of our analyses, we restrain from discussing specific traits and mechanisms for different organisms,  
385 but rather propose that our findings provide a starting point for future research in these  
386 communities. On a more general level, there are some interesting questions emerging from our  
387 study that future BEF research should focus on. First, why does functional identity often appear as  
388 the best mechanism and under which scenarios it interplays with functional complementarity? For  
389 example, a reason for the better support of the functional identity rather than functional  
390 complementarity hypothesis for some functions may be that ecosystem functions, such as predation  
391 of just one pest species, provide a narrow niche with less opportunity for niche partitioning than the  
392 predation of different species. Second, how can increasing the spatial and temporal scales, or the  
393 number of functions performed by the same animal group, increase the importance of functional  
394 diversity? For example, it appears that even when the same animal group (e.g. bees) is performing a  
395 given function (e.g., pollination) the key traits explaining functioning for a particular crop are  
396 specific for each plant. Hence, for pollination to be maximized at the landscape level and  
397 simultaneously for several crops, the functional diversity of the pollinator community would have  
398 to be increased. In this case, functional diversity will be more important than single-trait values as it  
399 provides insurance across varying conditions across space and time. However, the situation may be  
400 different when there are trade-offs between functions provided by the same community [15].

401           The choices we make in BEF research, such as which traits and indices to use, can strongly  
402 affect the observed relationship between functional diversity and ecosystem functioning [5]. First,  
403 the trait selection is extremely important for characterizing trait-based indices, especially for single-  
404 trait measures, such as CWM. Preferably, we should use *a priori* knowledge based on experimental  
405 manipulations investigating which traits are likely to drive different functions, but this information  
406 is rarely available for animals. However, we found that most multi-trait functional diversity indices  
407 were weakly affected by trait choice (see also [55]), and while excluding traits worsen explanatory

408 power in some cases, it rarely increased it. We propose that the jack-knife approach can be used to  
409 exclude or weight traits that contribute little to predicting functioning. Second, we show that the  
410 choice of weighted vs. non-weighted indices is important. Weighted indices always explained  
411 ecosystem functions better, demonstrating the importance of considering the abundance distribution  
412 of traits in communities. Weighting by biomass should be superior to weighting by numerical  
413 abundance in cases where the process is size-based, often by being related to metabolic rate of  
414 individuals (i.e. individual's performance increase with body size). However, we found no clear  
415 preference for indices scaled by biomass vs. numerical abundances in the communities we  
416 investigated.

417         Several new avenues have been proposed to better quantify functional diversity and increase  
418 the predictive power of biodiversity-functioning relationships: taking into account single and multi-  
419 trait indices simultaneously, phylogenetic diversity [56], within-species trait variability [57], abiotic  
420 factors [58], and nonlinearities in the response [3]. We show that the power to predict ecosystem  
421 functions using trait distributions in natural communities is relatively low (< 50%). This is not  
422 surprising given that most ecosystem functions, such as crop pollination and thereby yield  
423 production, depend on multiple abiotic and biotic processes including several organism groups [59,  
424 60]. Direct links between organisms and functions, like between aphid predation and predators, are  
425 stronger than indirect links, like between P retention and nematodes. However, we show that for  
426 predicting ecosystem functioning, trait-based measures are substantially better than measures of  
427 species richness and abundances, commonly used by researchers and policy makers. Our study thus  
428 provides new insights into general mechanisms that link biodiversity to ecosystem functioning in  
429 natural animal communities and suggests that the observed responses were due to the identity and  
430 dominance patterns of the trait composition rather than to the number or abundance of species *per*  
431 *se*. Hence, using trait-based approach in BEF research is a promising step forward and may greatly  
432 increase our understanding and aid management of multiple ecosystem functions.

433 **Acknowledgments:** We thank Piotr Ceryngier, Michael Kuhlmann and Stuart Roberts for providing  
434 data. We also thank two anonymous reviewers for their insightful comments on the manuscript.

435 **Data accessibility.** The data reported in this paper is deposited at:

436 <http://datadryad.org/review?doi=doi:10.5061/dryad.177g0>

437 **Funding statement:** Funding was provided by the Swedish Research Council FORMAS to the  
438 project “SAPES - Multifunctional agriculture: harnessing biodiversity for sustaining agricultural

439 production and ecosystem services”. SP and ISD were supported by EC FP7 grant no. 244090,

440 STEP Project (Status and Trends of European Pollinators, [www.step-project.net](http://www.step-project.net)), and TT by the

441 DFG and BMBF. The funders had no role in study design, data collection and analysis, decision to

442 publish, or preparation of the manuscript.

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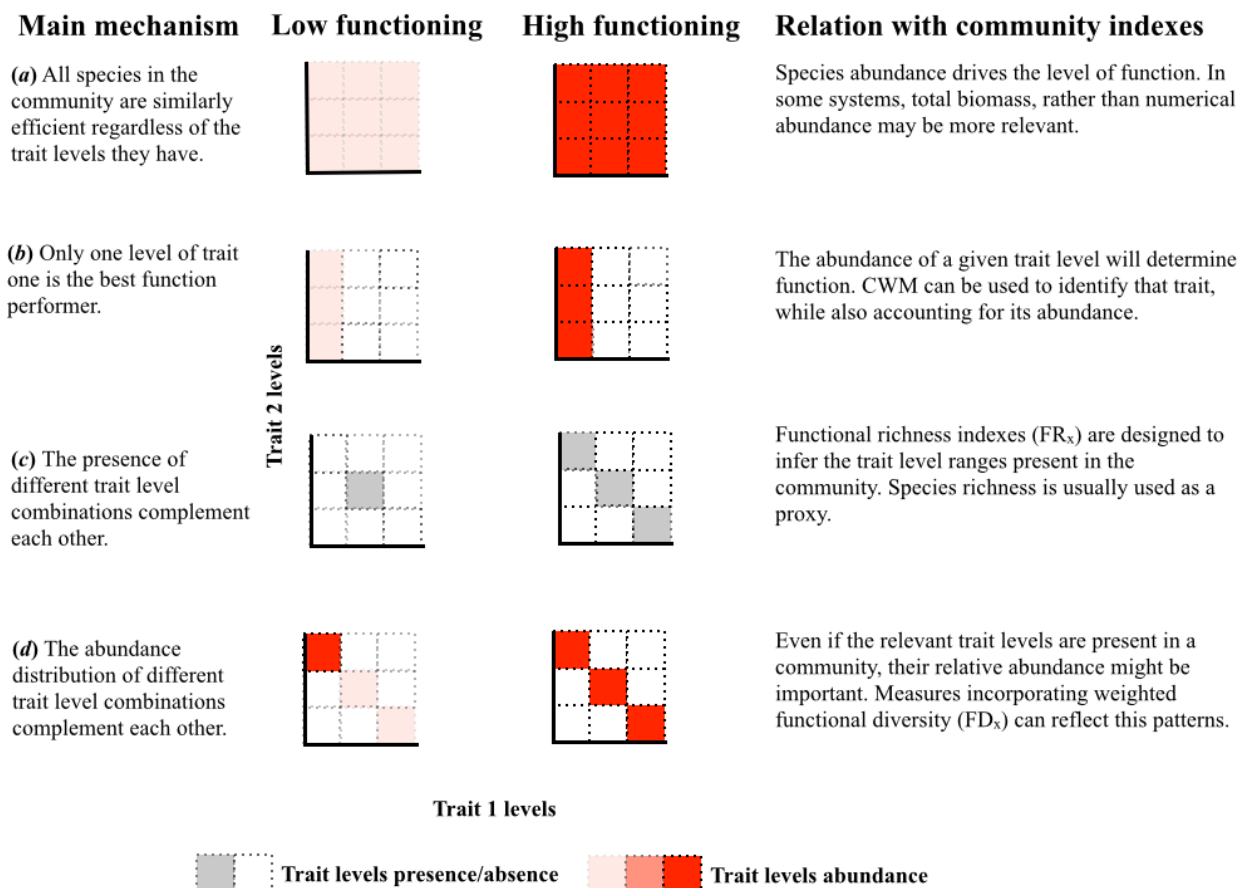
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589 **Figure 1. Main mechanisms linking traits to ecosystem function.** The x and y axes represent  
 590 different trait levels (e.g. ‘large body size’, ‘medium body size’ and ‘small body size’). For the  
 591 simplicity only two traits are presented. Darker colors indicate higher trait level abundance in the  
 592 community. Different mechanisms predict that high functioning levels can be achieved by having  
 593 (a) high abundance of any trait present in the community, (b) high abundance of the efficient trait  
 594 level of the relevant trait, (c) the presence of complementary trait levels combinations or (d) an even  
 595 distribution of complementary trait level combinations. Figures should be seen as simplified  
 596 examples and other trait combinations are possible. See text for explanation for the calculation of  
 597 indices.

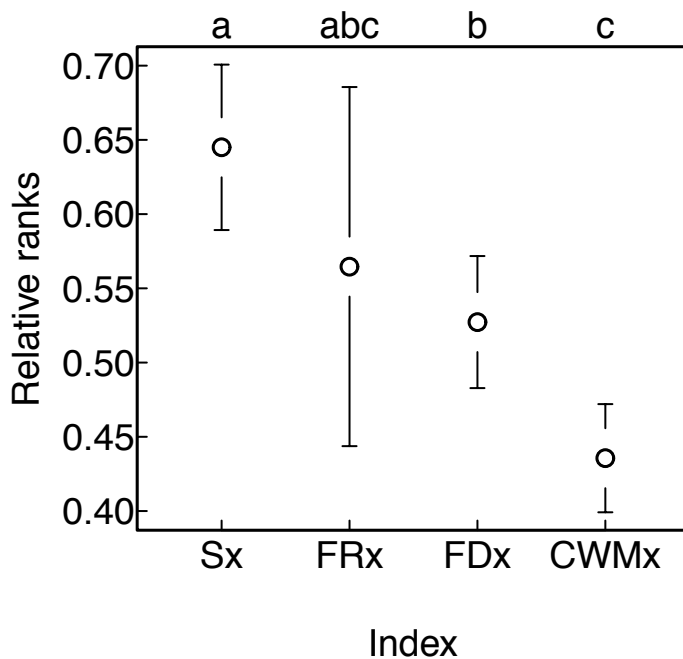


598

599 **Figure 2. Performance of different groups of diversity indices across ecosystem functions and**  
 600 **groups of organisms investigated.** The mean and standard error of the relative ranking of species-  
 601 based indices (S<sub>x</sub>, n= 94), functional richness (FR<sub>x</sub>, n= 28), functional diversity (FD<sub>x</sub>, n= 168) and



602 community weighted means (CWM<sub>x</sub>, n= 194). Different letters indicate post-hoc significant  
603 differences after correcting for multiple comparisons. Lower rank values indicate better explanatory  
604 power. See the text and the Table 1 for description of the ecosystem functions and codes for  
605 biodiversity indices and Table S2 for the results for all predictors.



606

607 **Figure S1.** Figure presenting  $\Delta R^2$ -s after the jack-knife approach is applied on the best multivariate  
608 functional diversity predictor in the system. Note that in the case where FDdiv was the best  
609 multivariate predictor and the trait data included only one continuous trait (i.e. carabid beetles), we  
610 used the second best predictor for the jack-knife approach due to the inability of FDdiv to be  
611 calculated with only categorical traits included.

