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Dung beetles as drivers of ecosystem multifunctionality: are response and effect traits interwoven?

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(Article begins on next page)

1 **Running Head: Response and effect in dung beetles**

2 **Dung beetles as drivers of ecosystem multifunctionality: are response and effect traits**

3 **interwoven?**

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14

15 **Abstract**

16 Rapid biodiversity loss has emphasized the need to understand how biodiversity affects the

17 provisioning of ecological functions. Of particular interest are species and communities with versatile

18 impacts on multiple parts of the environment, linking processes in the biosphere, lithosphere, and

19 atmosphere to human interests in the anthroposphere (in this case, cattle farming). In this study, we

20 examine the role of a specific group of insects – beetles feeding on cattle dung – on multiple ecological

21 functions spanning these spheres (dung removal, soil nutrient content and greenhouse gas emissions).

22 We ask whether the same traits which make species prone to extinction (i.e. *response traits*) may also

23 affect their functional efficiency (as *effect traits*). To establish the link between response and effect

24 traits, we first evaluated whether two traits (body mass and nesting strategy, the latter categorized as

25 tunnelers or dwellers) affected the probability of a species being threatened. We then tested for a

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26 relationship between these traits and ecosystem functioning. Across Scandinavian dung beetle species,
27 75% of tunnelers and 30% of dwellers are classified as threatened. Hence, nesting strategy significantly
28 affects the probability of a species being threatened, and constitutes a response trait. Effect traits varied
29 with the ecological function investigated: density-specific dung removal was influenced by both
30 nesting strategy and body mass, whereas methane emissions varied with body mass and nutrient
31 recycling with nesting strategy. Our findings suggest that among Scandinavian dung beetles, nesting
32 strategy is both a response and an effect trait, with tunnelers being more efficient in providing several
33 ecological functions and also being more sensitive to extinction. Consequently, functionally important
34 tunneler species have suffered disproportionate declines, and species not threatened today may be at
35 risk of becoming so in the near future. This linkage between effect and response traits aggravates the
36 consequences of ongoing biodiversity loss.

37

38 **Keywords:** body mass, dung removal, endangered species; GHG emissions; nesting strategy; soil
39 nutrient content.

40 **1. Introduction**

41 During the last few decades, the accelerating rate of species extinction has intensified the need
42 to understand how biodiversity loss might alter the provisioning of ecological processes (Purvis and
43 Hector 2000; Naeem et al. 2012). Previous studies have shown that species are not equally affected by
44 environmental changes (Kopecky et al. 2013; Püttker et al. 2015), but instead differ in their sensitivity
45 to disturbance. Quite worryingly, the very same species which are particularly sensitive to disturbance
46 may also be especially important to ecosystem functions (Larsen et al. 2005). The functional
47 consequences of extinctions will therefore depend on the strength of the link between traits rendering
48 species more extinction-prone (so called *response traits*) and those that determine the functional
49 contribution of a species (so called *effect traits*) (Naeem and Wright 2003; Solan et al. 2004). As a
50 consequence of the links between species response and effect traits, the effects of environment change
51 on species compositions may translate into changes in ecosystem functioning due to changes in the
52 distribution of trait values represented in the modified versus original communities (Chapin et al.
53 2000).

54 Focusing on plants, Lavorel and Garnier (2002) proposed a general framework to account for
55 relationships between effect and response traits. In brief, these authors proposed that ecosystem
56 functioning is the end result of environmental filters operating at a hierarchy of scales which, by
57 selecting individuals with appropriate responses, result in assemblages with varying trait composition.
58 Functional linkages and trade-offs among traits, each of which relates to one or several processes, will
59 then determine whether or not an individual will pass a given filter, and whether ecosystem-level
60 effects can be easily deduced from the knowledge of the individual filters active in a given
61 environment. The last two decades have seen a plethora of studies addressing relationships between
62 response and effect traits (reviewed in Hevia et al. 2017). Of these, several have highlighted body mass
63 as a response trait which may make species prone to extinction (McKinney 1997; Pimm et al. 1988) –
64 and also affect functional efficiency, thereby rendering it an effect trait (Larsen et al. 2005).

65 Dung beetles (Coleoptera: Scarabaeoidea) contribute to a wide range of ecosystem services,
66 including dung removal rates, nutrient cycling and seed dispersal (e.g. Nichols et al. 2008; Beynon et
67 al. 2012). Biotic interactions involving dung beetles have also been suggested to affect greenhouse gas
68 (GHG) emissions (Pentillä et al. 2013; Iwasa et al. 2015; Slade et al. 2016a; Piccini et al. in press) and
69 nutrient transfer from the dung to the soil (Kazuhira et al. 1991; Yamada et al. 2007; Nervo et al.
70 2017). Through their activity, dung beetles change the soil composition of microorganisms (Slade et al.
71 2016b) and the availability of nutrients with significant impacts on plant biomass (Nervo et al. 2017)
72 and protein content (Bang et al. 2005). Thus, the functional activity of dung beetles ties together key
73 parts of the total environment: being part of the biosphere, they rely on and directly promote the
74 functioning of the anthroposphere (by feeding on and decomposing the dung of domestic cattle), and
75 mitigate processes between the anthroposphere and the atmosphere (by affecting emissions of
76 greenhouse gases from cattle dung) and the lithosphere (by affecting the release of nutrients from the
77 dung to the soil).

78 Dung beetles are frequently classified according to their nesting habits: dwellers (syn.
79 endocoprids) are species that spend their full life cycle within the dung pats, and tunnelers (syn.
80 paracoprids) are species that reproduce in dung which they remove and bury (Cambefort & Hanski
81 1991). Globally, dung beetle diversity is facing many pressures (e.g. global warming, pastoral
82 abandonment, habitat loss, modification and fragmentation, chemicals), leading to potential population
83 declines, range contractions and species extinctions (Lobo et al. 2001; Carpaneto et al. 2007; Rosenlew
84 & Roslin, 2008). These declines have negative impacts on ecosystem functioning (Nichols et al. 2008).
85 Current concerns about the decline of dung beetles are particularly focused on large-bodied species,
86 which have been suggested to be both the most extinction-prone (Larsen et al. 2008) and the most
87 functionally efficient (Larsen et al. 2005; Lähteenmäki et al. 2015). In some cases, large-bodied species
88 are also functionally important for ecosystems (Solan et al. 2004; Larsen et al. 2005; Slade et al. 2007).
89 For example, larger-bodied beetles (i.e. *Geotrupes*) account for the 61% of overall dung removal in

90 Finland (Kaartinen et al. 2013). In other cases, a direct link between size and efficiency has been
91 challenged by experiments comparing multi-species dung beetle assemblages, including large tunnelers
92 versus assemblages encompassing dwellers only (Nervo et al. 2014) and rollers only (Slade et al.
93 2007). In these studies, large tunnelers have been proven to be more efficient, not only in dung
94 removal, but also in soil nutrient cycling (Nervo et al. 2017) and seed dispersal (Slade et al. 2007).

95 In this study, we target the dung beetle fauna of Sweden. We ask what traits make species
96 particularly effective in sustaining a given function. We then examine whether the dung beetle species
97 most prone to extinction are also the functionally most important, thereby aggravating the
98 consequences of biodiversity loss. More specifically we ask: 1) What traits make species prone to
99 extinction, as reflected by their current threat status; 2) Are threatened species more functionally
100 efficient than non-threatened species; 3) What traits make dung beetle species functionally efficient; 4)
101 Do the traits that make species more vulnerable also affect their functional efficiency; and 5) Is a
102 species particularly efficient in promoting one ecological function also efficient in promoting others?

103

104 **2. Materials and methods**

105 *2.1 Study area and mesocosm design*

106 Many dung beetle species have suffered extensive population declines in Scandinavia (Roslin et
107 al. 2014). Our experiment was conducted on the island of Öland (S-E Sweden), an area supporting
108 substantial dung beetle diversity. Preliminary studies have shown that several dung beetle species
109 which are rare or declining elsewhere are locally common in Öland (Roslin et al. 2014).

110 To evaluate the functional efficiency of beetle species, we used a mesocosm design. Each
111 mesocosm was constructed as a metallic square enclosure of 1m width, 1m length and 25cm height, of
112 which 5 cm was inserted into the soil. The mesocosms were constructed on a uniform grass sward at
113 Station Linné (56° 37' 07" N, 16° 29' 57" E). Within the experimental unit, the spatial distribution of

114 specific assemblages (Appendix, Table A1) was randomized among a set of 36 mesocosms (33 dung
115 pats with dung beetles and 3 controls).

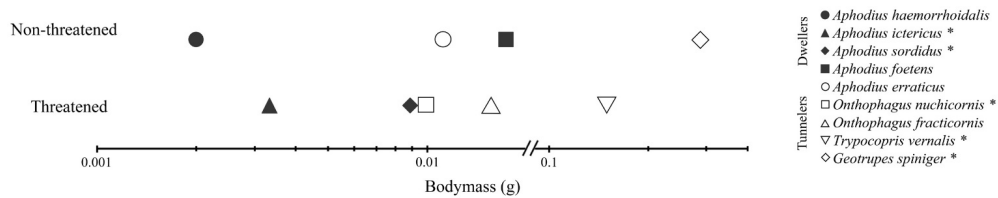
116 Dung beetles were collected manually and using pitfall traps baited with cattle dung. The
117 collections were made in August 2016 at five localities within an overall area of ca 55 km². We placed
118 15 pitfall traps for 24 hours at the localities identified in the Appendix (Table A2).

119 The methods of beetle collection conformed with all applicable laws, and explicit permission
120 for sampling in those areas was obtained from the farmers and from the responsible authority of
121 Gårdby Natural Reserve (Länsstyrelsen i Kalmar län). After capture, individuals were stored in moist
122 paper under cool conditions until used in the experiment.

123

124 2.2 Traits evaluated

125 Species were classified according to their threat status, individual body mass and nesting
126 strategy. We defined a species as threatened in Scandinavia if it was classified as “Near Threatened”
127 (NT), VUlnerable (VU), ENdangered (EN), CRitically endangered (CR) or Regionally Extinct (RE) in
128 Sweden and/or in at least three Nordic countries (Sweden, Norway, Denmark or Finland; Roslin et al.
129 2014). Five species collected fitted this description: *Aphodius sordidus* (Fabricius, 1775), *Aphodius*
130 *ictericus* (Laicharting, 1781), *Onthophagus fracticornis* (Preyssler, 1790), *Onthophagus nuchicornis*
131 (Linnaeus, 1758) and *Trypocopris vernalis* (Linnaeus, 1758). As a reference group, we selected four
132 non-threatened widespread species with a similar body mass to the selected 5 threatened species:
133 *Aphodius foetens* (Fabricius, 1787), *Aphodius haemorrhoidalis* (Linnaeus, 1758), *Aphodius erraticus*
134 (Linnaeus, 1758) and *Geotrupes spiniger* (Marsham, 1802) (Roslin et al. 2014). The species included
135 were further classified into two nesting strategies: tunnelers (5 species) and dwellers (4 species).
136 Together, they were chosen to represent a broad range of individual body size, from *A.*
137 *haemorrhoidalis* (0.002 g) to *G. spiniger* (0.28 g), with size roughly matched between threatened and
138 non-threatened species (Figure 1).



139

140

141 **Figure 1: Species used in the experiment.** Rows correspond to threat status (non-threatened species
 142 versus threatened ones), and a species' position along the x-axis reflects its body mass (note the axis
 143 break reflecting a seven-fold jump – 0.07g – in body mass). Nesting strategies are identified by
 144 symbols: filled symbols point to dwellers and open ones to tunnelers (the same symbols are used to
 145 identify the same species in Figs 2 and 5). An asterisk (*) identifies species for which the body mass
 146 was estimated by the method described in Materials and Methods. For the other species, body mass was
 147 derived from Piccini (unpublished data) and Nervo et al. (2014).

148

149 2.3 Experimental design

150 To compare the functional efficiency of threatened versus non-threatened dung beetle species,
 151 and of species with different traits (nesting strategy and body mass), we established monocultures of 9
 152 species: 3 threatened and 2 non-threatened tunnelers, and 2 threatened and 2 non-threatened dwellers
 153 (Figure 1). For each species, we set up a series of increasing densities, where the number of individuals
 154 varied from 2 to a maximum of 64 individuals, the highest density being set by the local seasonal
 155 abundance of the species (for exact densities used, see Appendix, Table A1).

156 The experiment ran from 14th of August to 4th of October. Fresh dung was collected from a
 157 single herd of Swedish Red cattle grazing on grasslands dominated by graminoids. In order to avoid
 158 any previous colonization of dung pats by insects, we collected fresh dung from inside the milking barn
 159 of the farm. No cow in the herd had been treated with antibiotics or antihelmintics. The dung was
 160 homogenized before being divided into experimental pats of 1kg per mesocosm. Once the dung and

161 beetles had been added to an enclosure, it was covered with nylon mesh cloth in order to prevent the
162 beetles from escaping and others from entering.

163

164 *2.4 Ecological functions investigated*

165 To evaluate the functional efficiency of dung beetles, we focused on three types of ecological
166 functions interconnected in the pasture ecosystem. Of these, the first one reflected impacts on cattle
167 farming as a part of the anthroposphere (dung removal from cattle pasture), the second reflected
168 impacts on greenhouse gas emissions, which are part of the atmosphere, and the third reflected impacts
169 on soil nutrient contents which are part of the lithosphere. Overall, this approach resulted in 7 different
170 response measures as mutually complementary aspects of the three main ecological functions:

171 1) As metrics of **dung removal**, we took repetitive weights of wet dung (g) over the course of
172 the experiment. Changes in this metric are henceforth referred to as dung removal rate. We also
173 recorded the weight of dry dung (g) remaining on the surface at the end of the experiment (henceforth
174 remaining dung mass). By using dry weight, we controlled for any difference in evaporation, thereby
175 isolating the contribution of the insects themselves to dung removal. Importantly, dung removal rate
176 and final remaining dung mass are complementary aspects of the removal function, since one may
177 arrive at the same final weight through steeper or shallower removal trajectories, with a slower removal
178 rate resulting in undecomposed dung remaining on the pasture and retaining nutrients for a longer
179 period. As a combination of dung removal rate and final remaining dung mass, we characterized
180 cumulative wet mass of dung pats by calculating the area under the curve of dung wet weights over
181 time, expressed in gram-days. Quick dung decay will be reflected by low cumulative mass, and slow
182 decay by a high value (cf. Slade et al. 2017). Since cumulative wet mass will per necessity be closely
183 related to other metrics of dung removal, we refrained from analyzing this metric as a separate response
184 (see section EFFECTS OF VARIABLES ON FUNCTIONAL EFFICIENCY) and only evaluated the extent to
185 which it covaried with other metrics (see section CORRELATIONS BETWEEN FUNCTIONS).

186 2) As measures of impacts on **greenhouse gas emissions** from dung pats, we measured fluxes
187 (mg m⁻²h⁻¹) of CO₂ and CH₄ which give an estimate of the GHG emissions per day. Moreover, we
188 evaluated cumulative emissions (mg m⁻²) that give an estimate of total amount of gas emitted at the end
189 of the experiment. Thus, we combined these cumulative emissions of CO₂ and CH₄ in CO₂ equivalents,
190 by converting compound-specific fluxes of CH₄ by using the IPCC 2013 global warming potential
191 (GWP). These metrics are henceforth referred to as GHG emissions. As for the other main functions
192 addressed (above and below), the individual responses targeted reflect complementary aspects of the
193 overall function: Daily compound-specific fluxes may hypothetically combine in multiple ways into the
194 same total (i.e. cumulative emissions of CO₂ equivalents), and analyzing compound-specific patterns
195 will help elucidate overall effects of total GHG fluxes.

196 3) As measures of impacts on **nutrient transfer to the soil**, we measured NH₄⁺ and NO₃⁻
197 concentrations (mg kg⁻¹) underneath the pats at the end of the experiment. These metrics are referred to
198 as soil nutrient content, with compound-specific responses revealing different, complementary aspects
199 of nutrients actually available to plant growth.

200 Individual ecological functions were measured by the following methods and techniques:

201 To measure dung removal rates, we recorded the mass of the dung pats (wet mass) on 6
202 occasions from 14 to 26 of August (i.e. 1, 2, 5, 7, 9, and 12 days from the start of the experiment). To
203 facilitate these measures, we placed a piece of chicken wire (mesh size 2 cm) under each dung pat. At
204 the end of the experiment (4th of October 2016), we dried the remaining dung at 70°C and recorded this
205 final dry mass (i.e. remaining dung mass).

206 To evaluate gas emissions from the mesocosms, we used a non-steady-state closed chamber
207 technique (Aim et al. 2007; Livingston and Hutchinson 1995). Gas fluxes were measured using a
208 portable gas analyser Gasmeter™ DX4015 (Gasmeter Technologies Oy, Helsinki, Finland) in a closed-
209 loop system in which the gas sample was circulated through the analyzer and back to the chamber.
210 During the measurements, the chamber was fitted in a slit cut in the ground around the dung pat, and

211 the chamber headspace was constantly mixed with a fan. (Since the volume of the dung pat accounted
212 for less than 1/20 of the chamber head space, this volume was not considered in further calculations.)
213 Once the chamber was placed into the soil, the concentration of gases per chamber was measured over
214 a minimum period of 5 minutes. The temperature inside the chamber was recorded during each
215 measurement and later used to correct flux estimates (for details see Appendix, Text 1). Between
216 measurements, the chamber was removed and the mesh replaced. Gas emissions were measured on 6
217 occasions between 15th and 26th of August (i.e. 15th, 16th, 19th, 21st, 23rd, and 26th of August). Gas
218 contents of CO₂ and CH₄ measured from the chamber headspace (in ppm) were converted into mg m⁻²
219 h⁻¹. Cumulative fluxes of CO₂ and CH₄ over the course of the experiment were calculated for each
220 enclosure and expressed as areas under the curve of the gas flux over time (for equations, see
221 Appendix, Text 2). Two data points on methane fluxes from mesocosms with *Geotrupes spiniger* (with
222 2 and 8 individuals, respectively, as recorded on 19th and 16th August) proved completely out of range
223 compared to all other data. These outliers were assumed to be technical errors and were omitted from
224 all GHG analyses. To evaluate the warming potential of GHGs from dung pats, we combined the
225 cumulative fluxes of CO₂ and CH₄ by converting to CO₂ equivalents, based on 100 year warming
226 potential (IPCC 2013).

227 To estimate the effect of dung beetles on nutrient transfer from the dung into the soil, we
228 collected 5 cm soil cores beneath the center of each dung pat. After removing the remaining visible
229 plant parts, fresh soil samples were sieved at 2 mm. Inorganic N (total NH₄⁺ and NO₃⁻) was extracted
230 from the moist soil samples (10 g) with 1 mol/L KCl (1:5 soil:solution ratio), suspensions were
231 centrifuged at 1,200×g for 10 min, and the supernatant filtered first through Whatman No. 42 filter
232 paper and subsequently through a 0.45-µm membrane filter. Moisture content was also determined on a
233 separate aliquot of soil to allow all concentrations to be expressed as dry soil weight. The concentration
234 of total NH₄⁺ and NO₃⁻ was determined spectrophotometrically as described in Cucu et al. (2014).

235

236 2.5 Statistical analysis

237 SPECIES-SPECIFIC BODY MASS – Since we used several endangered species in the experiment, we
238 refrained from estimating the species-specific body mass from any extensive, purpose-collected and
239 dried material. Instead, we estimated the species dry weight from a regression model described below.
240 Thus, to estimate the body mass of all dung beetle species present in Scandinavia, we used size data
241 (i.e. body-mass and length) available for *Aphodius haemorrhoidalis*, *Aphodius erraticus*, *Onthophagus*
242 *fracticornis*, *Anoplotrupes stercorosus* and *Geotrupes stercorarius*. For these species, \log_e -transformed
243 dry body mass (Nervo et al. 2014, and Piccini unpublished data) was regressed against the \log_e -
244 transformed mean length of the species ($R^2=0.98$, with length data extracted from Roslin et al. 2014).
245 Following Radtke and Williamson (2005), we then interpolated the body mass of remaining species
246 using the resultant regression line and the typical length of species (as adopted from Roslin et al. 2014).

247 IDENTIFICATION OF RESPONSE TRAITS – In order to identify which traits make species more
248 sensitive to extinction, we examined whether species threatened in Scandinavia shared some specific
249 traits. More specifically, to evaluate the effect of traits (nesting strategy and body mass) on species'
250 response, we built a generalized linear model (GLM) threat status of all Scandinavian species
251 (threatened versus non-threatened; 0/1), as a function of nesting strategy and body mass, assuming a
252 logit link function and binomially distributed errors. This model was fitted using the 'stats' package in
253 the R (v3.2.1) statistical and programming environment (R Development Core Team 2005). To check
254 for overdispersion of residuals from the final model, we divided the residual deviance by the degrees of
255 freedom. Since the result was 1.2 and thus close to unity, and closely adhered to both binomial and
256 quasi-binomial distribution families ($P>0.32$), we inferred no signs of overdispersion.

257 EFFECTS OF VARIABLES ON FUNCTIONAL EFFICIENCY – To identify how body mass and/or nesting
258 strategy affect the functional efficiency of the species, we applied the framework of generalized linear
259 mixed effects models to our hierarchical, partly repeated data structure (e.g. Zuur et al. 2009).
260 Remaining dung mass (pat-specific dry weight), dung removal rates (pat-specific wet weight trends

261 over time), nutrient content in the soil and GHG emissions, were first adopted as metrics of ecological
262 functioning. Since plots of dung mass over time were generally indicative of exponential decline, we
263 linearized the relation by applying a natural logarithmic transformation (\log_e). Each response (dry dung
264 weight, NH_4^+ , NO_3^- , and cumulative emissions of CO_2 , CH_4 and CO_2 -equivalents) was then modelled
265 as a separate linear function of \log_e -transformed species body mass (Body_mass) and densities
266 (Density) as continuous variables, and nesting strategy (Nesting_Strategy) and threat status
267 (Threat_Status) as categorical variables. Here, the density will capture the change in functioning with
268 the addition of individuals of the focal species, and the effect of body mass will reflect the change in
269 functioning with increasing species size. Thus, our focal interest concerns the interactions Body_mass
270 \times Density; Nesting_Strategy \times Density; Threat_Status \times Density and Body_mass \times Nesting_Strategy \times
271 Density, which capture the extent to which these effects vary with the body mass and nesting strategy
272 of the species. To adjust for variation between species, species identity was included as a random
273 intercept. Data from beetle-free control mesocosms were excluded from these analyses.

274 For dung removal rates and GHG emissions, our data consisted of repetitive measures over time
275 (of wet weight, CO_2 and CH_4 fluxes, respectively). Hence, to adjust for multiple observations of the
276 same units (i.e. for the separate variation arising from the fact that we repeatedly inspected particular
277 mesocosms and particular species, rather than repeatedly randomized units), we included species and
278 mesocosms as a random intercept and measurement day as a random slope term. For dung removal
279 rates and CH_4 emissions, where daily emissions varied in a highly non-linear pattern, we modelled
280 measurement day as a fixed categorical effect.

281 Following the principle of model reduction, we removed the three-way interaction from models
282 when non-significant (i.e. from the models of GHG emissions and soil nutrient content). Each model
283 was fitted using the 'lmerTest' package in the R (v3.2.1) statistical and programming environment (R
284 Development Core Team 2005), assuming an identity link and normally distributed errors. P-values

285 were estimated using type III *F*-tests with the Satterthwaite approximation of the relevant degrees of
286 freedom (Satterthwaite 1946).

287 CORRELATIONS BETWEEN FUNCTIONS –To establish whether a species that was particularly
288 efficient in promoting one ecological function was also efficient in promoting others, we analyzed the
289 pairwise relationships between the mesocosm-specific rates of each ecological function (n=36 per
290 function). For gas fluxes, we used the cumulative emissions (mg m⁻²) observed during the course of the
291 experiment (of CO₂, CH₄ and combined emissions of CO₂ and CH₄, in CO₂ equivalents, respectively).
292 In a logically equivalent vein, we characterized dung decomposition rates by the cumulative wet mass
293 of dung pats (called ‘Cumulative wet dung’ in Figure 6).

294

295 **3. Results**

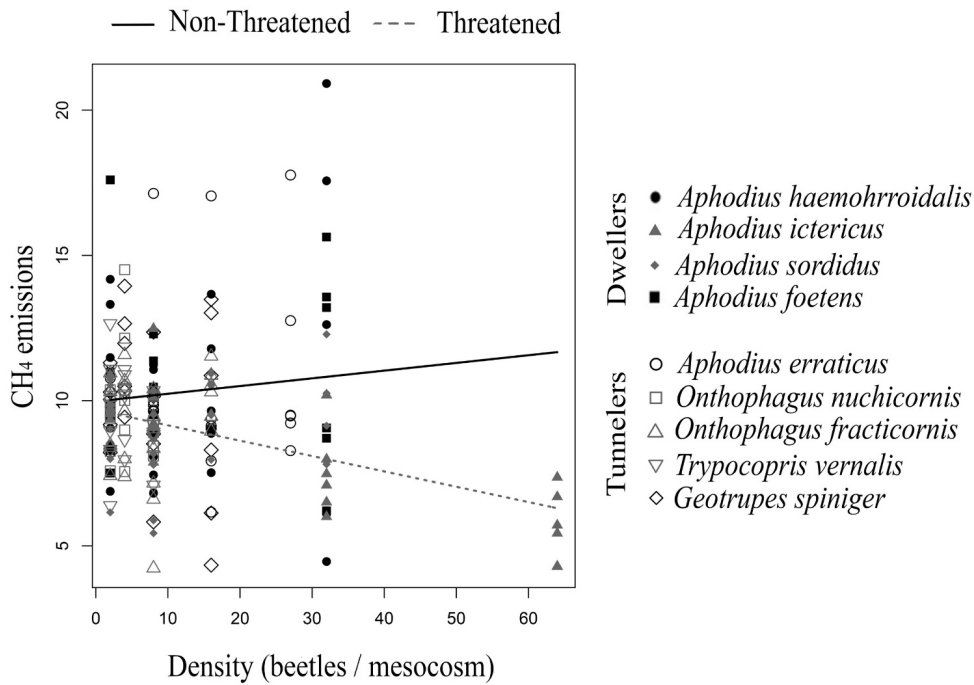
296 *3.1 Identification of response traits*

297 Among 61 dung beetle species encountered in Sweden, 45 are dwellers and 16 are tunnelers. Of
298 these, 13 out of 45 dweller species and 12 out of 16 tunneler species are currently regarded as
299 threatened in Sweden or in at least three Scandinavian countries (Table 3 from Roslin et al. 2014).
300 Indeed, nesting strategy is significantly related to threat status ($Z=2.19$, $p=0.03$), whereas neither
301 biomass ($Z=-0.47$; $p=0.64$), nor the interaction between nesting strategy and biomass ($Z=0.42$, $p=0.67$),
302 has a detectable impact on threat status.

303

304 *3.2 Species threat status versus functional efficiency*

305 Overall, threat status influenced neither dung removal nor nutrient content in the soil. However,
306 threat status had a significant impact on GHG emissions from dung pats – more specifically, on CH₄
307 emissions. Significantly less methane was released into the atmosphere with an increase in the density
308 of threatened species than with an equivalent increase of non-threatened species (interaction Density ×
309 Threat_Status: $F_{1;182,4}=5.31$, $p=0.022$; Figure 2; Appendix, Table A5).



310

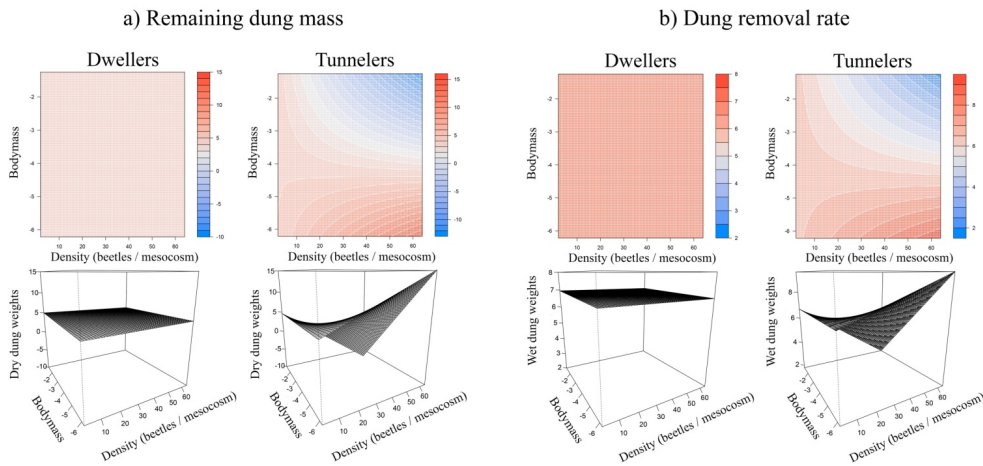
311 **Figure 2: Threat status versus functional efficiency in terms of methane emissions.** Shown is the
 312 interaction between threat status (black line for non-threatened and grey dashed line for threatened
 313 species) and the number of individuals per mesocosm (density) for methane emissions ($\text{mg m}^{-2} \text{h}^{-1}$).
 314 The data points show partial residuals, with the lines derived from the linear regression described in
 315 Materials and Methods. Symbols identify species, where black corresponds to non-threatened species
 316 and grey to threatened species; filled symbols identify dwellers and open symbols tunnelers.

317

318 3.2 Species traits versus functional efficiency

319 REMAINING DUNG MASS – Density had a general, significant effect on the amount of remaining
 320 dung (Density: $F_{1;19,31} = 34.36$, $p < 0.001$; Appendix, Table A3). Nonetheless, there was a strong
 321 interaction between density, body mass and nesting strategy (interaction Density \times Body_mass \times

322 Nesting_Strategy: $F_{1;19.52}=33.80$, $p<0.001$), with large tunneling species proving the most effective in
 323 removing dung per individual (Figure 3a; Appendix, Table A3).



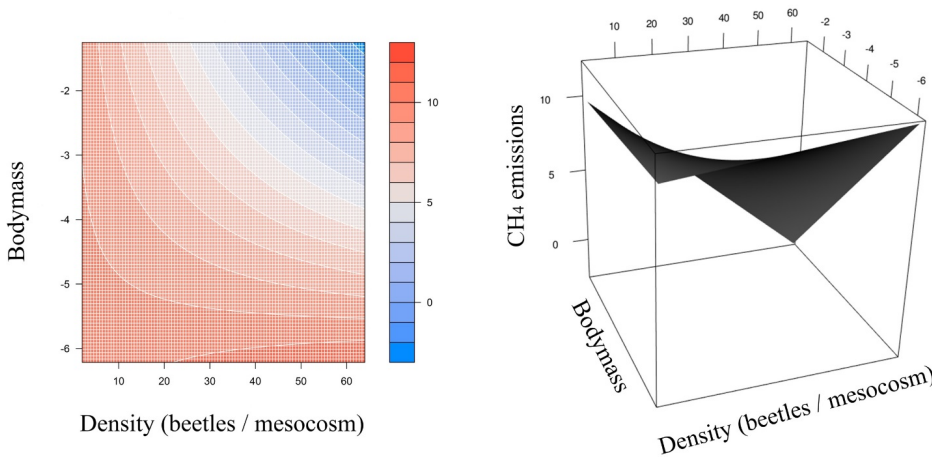
324

325 **Figure 3: Interaction between body mass and nesting strategy in determining ecological**
 326 **functioning.** Shown is the significant interaction between the species body mass, nesting strategy and
 327 the number of individuals per mesocosm for dung removal, measured as: (a) remaining dung mass (g)
 328 and (b) dung removal rate (g). The two rows of graphs represent the same interactions from different
 329 perspectives; the top row shows two-dimensional heat maps of the three-dimensional surfaces
 330 represented on the lower row. In the heat maps, a redder color represents more dung remaining on the
 331 surface whereas a bluer color represents less dung remaining.

332

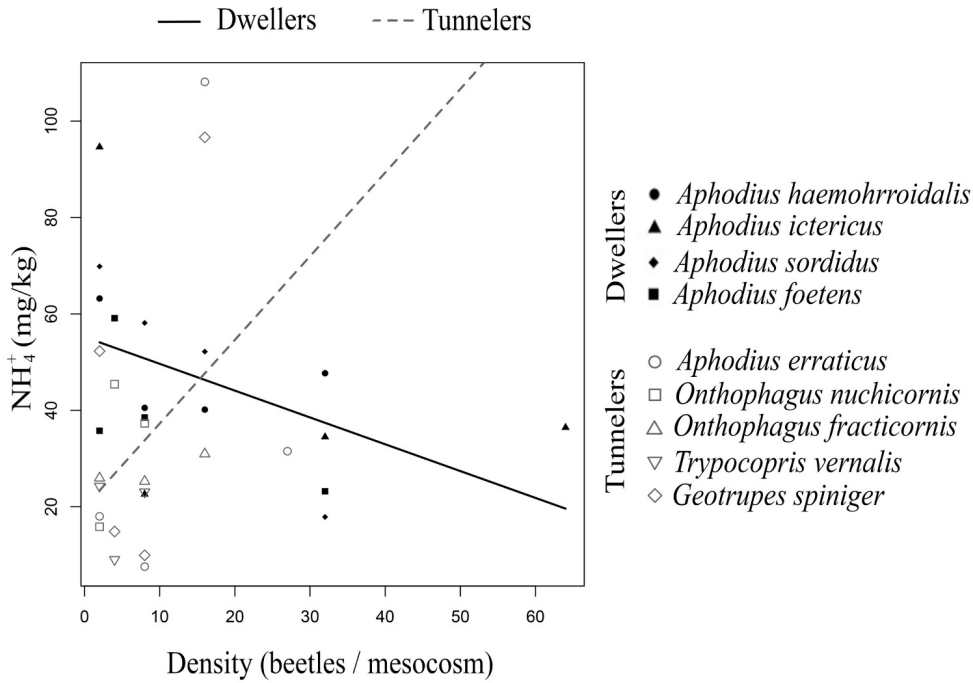
333 DUNG REMOVAL RATE – Dung wet weight progressively decreased over the course of the
 334 experiment (Measurement days: $F_{1;183.21}=125.83$, $p<0.001$; Appendix, Table A4), with a significant
 335 effect of density ($F_{1;186.84}=27.86$, $p<0.001$; Appendix, Table A4). However, both nesting strategy and
 336 body mass affected the density-specific dung removal rates per individual (interaction Density \times
 337 Nesting_Strategy \times Body_mass: $F_{1;186.16}=26.93$, $p<0.001$), with larger tunnelers removing more dung
 338 per individual than small dwellers (Figure 3b; Appendix, Table A4).

339 GHG EMISSIONS – Overall, the amount of GHG emissions decreased with time (Measurement
 340 days: $F_{1;177.97}=43.22$, $p<0.001$; Appendix, Table A5) and density (Density: $F_{1;181.93}=5.34$, $p=0.02$;
 341 Appendix, Table A5). However, the per capita effect of dung beetles on CH₄ emissions drastically
 342 increased with an increase in individual body mass (interaction Density \times Body_mass: $F_{1;181.74}=65.20$,
 343 $p=0.024$; Figure 4; Appendix, Table A5). Neither nesting strategy nor body mass had any detectable
 344 effect on fluxes of CO₂ or CO₂-equivalents, or on cumulative emissions of any of the three responses
 345 (CO₂, CH₄ and CO₂-equivalents).



346
 347 **Figure 4: The effect of species body mass on methane emissions.** Shown is the significant
 348 interaction between species body mass and the number of individuals per mesocosm in determining
 349 methane emissions from dung pats ($\text{mg m}^{-2} \text{h}^{-1}$). The two graphs represent the same interactions from
 350 different perspectives; the left-hand panel shows a two-dimensional heat map of the three-dimensional
 351 surface represented on the right. In the heat maps, a redder color represents more dung remaining on
 352 the surface whereas a bluer color represents less dung remaining.
 353

354 NUTRIENT CONTENT OF THE SOIL – Dwellers affected ammonium concentration in soil more than
 355 tunnelers (Nesting strategy: $F_{1,24,99} = 4.11$, $p=0.053$; Appendix, Table A6). However, NH_4^+
 356 concentration in the soil underneath dung pats showed a tendency towards higher values with higher
 357 densities of tunnelers in the pat, whereas there was a decrease in NH_4^+ concentration with increasing
 358 dweller density (interaction Density \times Body_mass: $F_{1,24,99}=3.28$, $p=0.082$; Figure 5; Appendix, Table
 359 A6). NO_3^- concentration showed no detectable change with either nesting strategy or biomass.

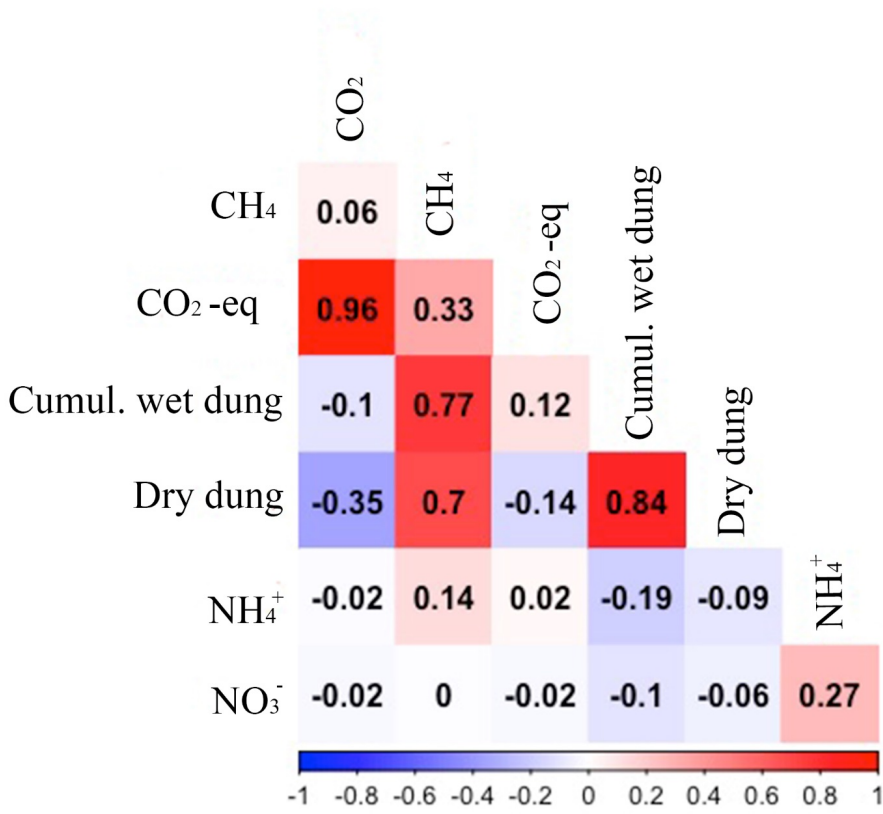


360
 361 **Figure 5: The effect of nesting strategy on nutrient cycling.** Shown is the marginally significant
 362 interaction between density and nesting strategy (black line for dwellers and grey dashed line for
 363 tunnelers) in determining ammonium concentration in the soil (mg kg^{-1}). The data points show partial
 364 residuals, with the lines derived from the linear regression described in Materials and Methods.
 365 Symbols identify species, filled symbols identify dwellers and open symbols tunnelers.

366

367 3.3. *Comparison of different functions*

368 In terms of the multiple ecological functions investigated in this experiment, we found highly
369 variable relationships between individual pairs of functions (Figure 6). Overall, several functions were
370 only weakly related to each other (as illustrated by light colors in Fig. 6). In terms of the stronger
371 associations observed, some were self-evident. For example, since more wet dung at an early stage will
372 result in more dry dung at the end of the experiment, these two metrics were naturally highly correlated
373 (Figure 6). Likewise, since overall CO₂ equivalents are composed of CO₂ and CH₄, all three quantities
374 were correlated, but this correlation was stronger for CO₂ as it accounts for the main part of the
375 combined fluxes (Fig. 6). However, a higher dung mass was primarily correlated with higher CH₄
376 fluxes, whereas higher emissions of CO₂ were associated with a lower mass of remaining dung. Higher
377 transfer of NH₄⁺ to the soil was also associated with higher transfer NO₃, and with less dung remaining
378 at the soil surface (Figure 6).



379
 380 **Figure 6. Associations between pairs of ecological functions.** Shown are Pearson's correlation
 381 coefficients between different aspects of ecosystem functioning (cumulative fluxes of carbon dioxide
 382 (CO₂), methane (CH₄) and both gases (CO₂+CH₄) combined into CO₂ equivalents, cumulative weight
 383 of wet dung remaining on the ground over time (Cumul. wet dung), total dry dung remaining at the end
 384 of the experiment, ammonium and nitrate concentration found in soil beneath dung pats). Red reflects
 385 positive correlations, blue corresponds to negative correlations, with the darkness of the color reflecting
 386 the strength of association.
 387

388

389 **4. Discussion**

390 Species extinction is a non-random process (Purvis et al. 2000a, b; Ives and Cardinale 2004;
391 Vamossi and Wilson et al. 2008), with some species being more sensitive than others to joint
392 environmental stressors. Of particular concern is the extinction of functionally important species
393 linking multiple parts of the environment. The strength of the link between traits rendering species
394 more extinction-prone and those that determine the functional contribution of a species will depend on
395 how they are jointly filtered by the environment (Lavorel and Garnier 2002). In our study, we sought
396 for traits affecting the efficiency of dung beetle species in determining the functioning of different parts
397 of the pasture environment. We also compared the functional efficiency of non-threatened versus
398 threatened dung beetle species across this range of ecological functions. In doing so, we asked whether
399 traits which make species sensitive to disturbance also make these species functionally efficient.
400 Overall, we found that nesting strategy has a strong impact on the probability with which a species is
401 threatened. In terms of functional efficiency, the impact of specific traits depends on the exact
402 ecological functions investigated. However, the key trait associated with threat status (nesting strategy)
403 was also associated with functional efficiency across a range of functions, as was body mass. Within
404 threat categories, non-threatened species differed from threatened ones in terms of functional efficiency
405 only for methane emissions. Below, we will discuss each of these findings in turn.

406

407 *4.1 Nesting strategy is a response trait*

408 Among dung beetles, large species have been proposed as being more prone to extinction than
409 small species (Larsen et al. 2005, Larsen et al. 2008). Yet, in the set of Scandinavian dung beetle
410 species, individual size appeared to have little effect, whereas nesting strategy left a consistent imprint
411 on threat status. This feature in the life history of species is closely associated with phylogeny.
412 Tunnelers belonging to the subfamily Scarabaeinae (of which 100% are threatened) seem more

413 sensitive to environment change than species in Geotrupinae (of which 40% are threatened) and
414 Aphodiinae (of which 30% are threatened). In fact, all Scandinavian species of Scarabaeinae are either
415 currently classified as threatened, or have been so in previous, national red lists (Roslin et al. 2014). As
416 a consequence, a much larger proportion of tunnelers (75%) than dwellers are currently threatened
417 (30%), with taxonomy as good a predictor of threat status as nesting habit *per se*, since the two are
418 intimately related.

419 As a potential explanation for this *status quo*, Roslin et al. (2014) have proposed that tunnelers
420 have suffered disproportionately from the decline in cattle farming and thus grazing pressure across
421 Scandinavia. Being characterized by a long larval period spent under the soil surface, these taxa may be
422 particularly sensitive to the amount of sunlight reaching the soil surface, and thus prone to the adverse
423 effect of decreased grazing pressure coupled with increased vegetation height and decreased insolation.
424 This is particularly valid for Scarabaeinae, since species belonging to this subfamily have limited
425 fecundity (a single ovary) and a general lack of adaptation to cool climates. Contrary to the patterns
426 found by Larsen et al. (2005), extinction sensitivity for Swedish species is not detectably related to the
427 biomass of the species. Thus, biomass itself does not explain a species' vulnerability to extinction (an
428 observation supported by Fofopoulos and Ives 1999). Naturally, threat status could also be related to
429 some other traits not investigated here, making the species more resistant to stressors (e.g.
430 physiological traits such as temperature tolerance and metabolic capacity; Moretti et al. 2016).

431

432 *4.2 Nesting strategy and body mass are sometimes effect traits*

433 The trait that makes a species functionally efficient depends on the ecological function
434 investigated. More specifically, both body mass and nesting strategy affect dung removal rates, as
435 equally reflected by the decline in wet weight over time and the dung mass remaining at the end of the
436 experiment. Large tunnelers have been previously shown to have the largest effect on dung removal
437 (Slade et al. 2007; Amézquita and Favila 2010; Kaartinen et al. 2013; Nervo et al. 2014, 2017).

438 Moreover, we identified body mass as a pivotal trait affecting methane fluxes from dung pats, with
439 larger species reducing methane emissions more per individual than smaller ones. This finding is likely
440 due to the fact that large beetles excavate larger holes and galleries inside and below the dung mass,
441 consequently aerating the dung and reducing methane formation by anaerobic archaea (cf. Piccini et al.
442 2017).

443 Nesting strategy also affected the nutrient content of the soil. Tunneling species transport more
444 dung into the soil, and are therefore more efficient than dwellers in soil fertilization (Yamada et al.
445 2007). Indeed, the concentration of ammonium in the soil increased with an increase in tunneler
446 density. On the other hand, soil ammonium concentration decreased when dweller density increased.
447 This pattern was probably related to a greater consumption of nutrients in the dung by dweller adults
448 and larvae, thus tying up nitrogen as protein rather than releasing it. Overall, increasing the number of
449 small-bodied dwellers in the mesocosms did not markedly change the provisioning of ecological
450 functions. In contrast, when large-bodied tunnelers were added, increased functioning was generally
451 observed. In Sweden, small-sized dwellers typically make up the main part of the dung-inhabiting
452 beetle community, whereas large tunnelers are scarcer but have proven to be the most functionally
453 efficient (Kaartinen et al. 2013). This suggests that the loss of such larger species may have particularly
454 important consequences for the functioning of the overall ecosystem.

455

456 *4.3 Effect and response traits are linked*

457 Among dung beetles, large species have been proposed to be both more prone to extinction and
458 more functionally efficient than small ones (Larsen et al. 2005). In our experiment, non-threatened
459 species did not detectably differ from threatened ones in terms of efficiency, except for methane
460 emissions from dung pats, where threatened species proved more efficient than non-threatened species.
461 This difference could not be specifically attributed to any of the traits that we measured.

462 Overall, our study identifies nesting strategy as a key response trait, with a major impact on
463 species' threat status in Scandinavia. At the same time, the sensitive, tunneling species are also efficient
464 providers of ecosystem functioning, especially in terms of dung removal and increasing nutrient
465 content in the soil. Thus, our study identifies nesting strategy as both a response and an effect trait.
466 Links between response and effect traits have also been observed in several other studies (reviewed in
467 Hevia et al. 2017), including some plants (Lavorel and Garnier 2002; Violle et al. 2007; Suding et al.
468 2008) and among plants and grasshoppers (Moretti et al. 2013). Among the current set of dung beetles,
469 the link can be attributed to the relocation of dung into the soil for breeding, which simultaneously
470 makes tunnelers more functionally efficient (by increasing dung removal rates, promoting nutrient
471 transfer and decreasing dung mass remaining on the surface) and more sensitive to environmental
472 stressor. By breeding in the soil, they become sensitive to current changes in the Scandinavian
473 landscape, including increased vegetation height, less insolation and thus lower soil temperatures.
474 These effects may prolong critically larval development in the cool climate of higher latitudes (Roslin
475 et al. 2014).

476

477 *4.4 Dung beetle traits influence the overall pasture environment*

478 Recent research has focused on the complex relations between species richness and ecosystem multi-
479 functionality (Wagg et al. 2014; Maestre et al. 2012; Hector and Bagchi 2007). Instead of using a single
480 function as a proxy for overall ecosystem functioning (cf. the critique by Rosenfeld 2002, Nervo et al.
481 2017), we estimated the influence of dung beetles on a range of functions linking the different spheres
482 of the pasture ecosystem: the amount of soil nutrients (lithosphere) and GHG emissions (atmosphere)
483 through transfer and decomposition of dung (i.e. dung removal rate and remaining dung mass). While
484 we were only able to address a few selected responses per sphere, we found different functions to vary
485 in discord rather than in concert: beyond obvious relations between wholes and their parts (see
486 Results), individual functions were mostly weakly correlated (Fig. 6). Fluxes of different GHGs were,

487 in fact, negatively related: greater dung mass on the soil surface was associated with higher CH₄ fluxes,
488 but lower emissions of CO₂. This difference is likely related to their different modes of emergence.
489 CO₂ is mostly a product of aerobic respiration, resulting in higher dung decomposition. CH₄ is
490 primarily generated under anaerobic conditions (Penttilä et al. 2011), as favored by higher and wetter
491 dung mass. Overall, different dung beetle species with different impacts on dung aeration and dung
492 removal will thus have different impacts on GHG fluxes (Piccini et al. 2017). These findings illustrate
493 the general importance of maintaining diverse dung beetle communities to provide multiple ecosystem
494 services (Benyon et al. 2012; Manning et al. 2016; Piccini et al. 2017; Slade et al. 2017).

495

496 *5. Conclusions*

497 The results presented here identify dung beetles as key engineers of the pasture environment,
498 influencing GHG emissions to the atmosphere, nutrient cycling between dung and soil and the amount
499 of dung and the time it remains on the surface of pastures. Our findings suggest that some of the same
500 traits which make Scandinavian dung beetle species sensitive to environmental change will also render
501 them functionally efficient, and thus they fit squarely with the paradigm that functional and response
502 traits are linked. This is a worrying scenario, since it implies both that some of the most functionally
503 important species are already threatened, and that further species, although not threatened to date, are
504 likely to become so in the near future. To conserve the functional integrity of pasture ecosystems, we
505 should therefore conserve species of the highest functional efficiency, with the highest risk of suffering
506 decline. Among dung beetles, large tunnelers should be the first priority. Yet, two observations add
507 nuances to this simplistic rule of thumb: first, the observation that different ecosystem functions vary in
508 discord rather than unison, and second, that several functions were only weakly related to any of the
509 traits examined here. Both considerations highlight the importance of maintaining diverse communities
510 rather than dung beetles of a single type. Given the paramount impact of pasture processes on global
511 change (Slade et al. 2016a), maintaining their functional integrity emerges as a key concern – a task

512 which we can only achieve by understanding how their functioning hinges on the composition of local
513 communities.

514
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