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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).

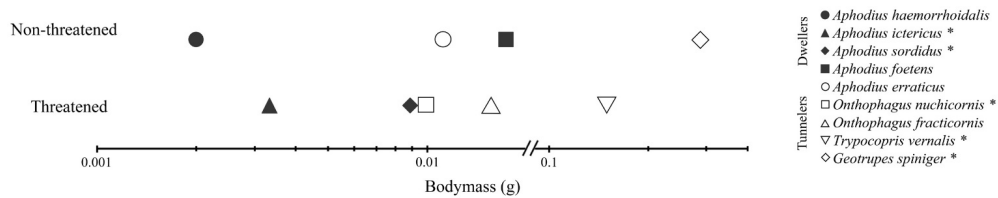
116 Dung beetles were collected manually and using pitfall traps baited with cattle dung. The  
117 collections were made in August 2016 at five localities within an overall area of ca 55 km<sup>2</sup>. We placed  
118 15 pitfall traps for 24 hours at the localities identified in the Appendix (Table 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 14<sup>th</sup> of August to 4<sup>th</sup> 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<sup>-2</sup>h<sup>-1</sup>) of CO<sub>2</sub> and CH<sub>4</sub> which give an estimate of the GHG emissions per day. Moreover, we  
188 evaluated cumulative emissions (mg m<sup>-2</sup>) that give an estimate of total amount of gas emitted at the end  
189 of the experiment. Thus, we combined these cumulative emissions of CO<sub>2</sub> and CH<sub>4</sub> in CO<sub>2</sub> equivalents,  
190 by converting compound-specific fluxes of CH<sub>4</sub> 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 CO<sub>2</sub> 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 NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>  
197 concentrations (mg kg<sup>-1</sup>) 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 (4<sup>th</sup> 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 15<sup>th</sup> and 26<sup>th</sup> of August (i.e. 15<sup>th</sup>, 16<sup>th</sup>, 19<sup>th</sup>, 21<sup>st</sup>, 23<sup>rd</sup>, and 26<sup>th</sup> of August). Gas  
218 contents of CO<sub>2</sub> and CH<sub>4</sub> measured from the chamber headspace (in ppm) were converted into mg m<sup>-2</sup>  
219 h<sup>-1</sup>. Cumulative fluxes of CO<sub>2</sub> and CH<sub>4</sub> 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 19<sup>th</sup> and 16<sup>th</sup> 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 CO<sub>2</sub> and CH<sub>4</sub> by converting to CO<sub>2</sub> 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 NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>) 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 NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> 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,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , and cumulative emissions of  $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{CO}_2$ -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,  $\text{CO}_2$  and  $\text{CH}_4$  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  $\text{CH}_4$  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 ( $\text{mg m}^{-2}$ ) observed during the course of the  
291 experiment (of  $\text{CO}_2$ ,  $\text{CH}_4$  and combined emissions of  $\text{CO}_2$  and  $\text{CH}_4$ , in  $\text{CO}_2$  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**

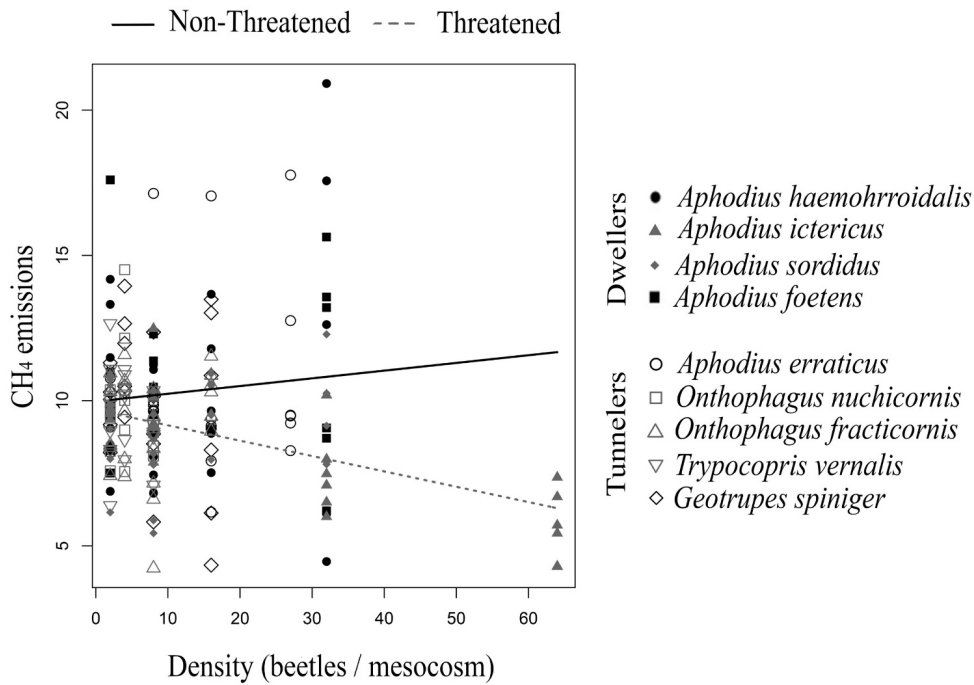
#### 296 *3.1 Identification of response traits*

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  $\text{CH}_4$   
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  $\times$   
309 Threat\_Status:  $F_{1;182,4}=5.31$ ,  $p=0.022$ ; Figure 2; Appendix, Table A5).



310

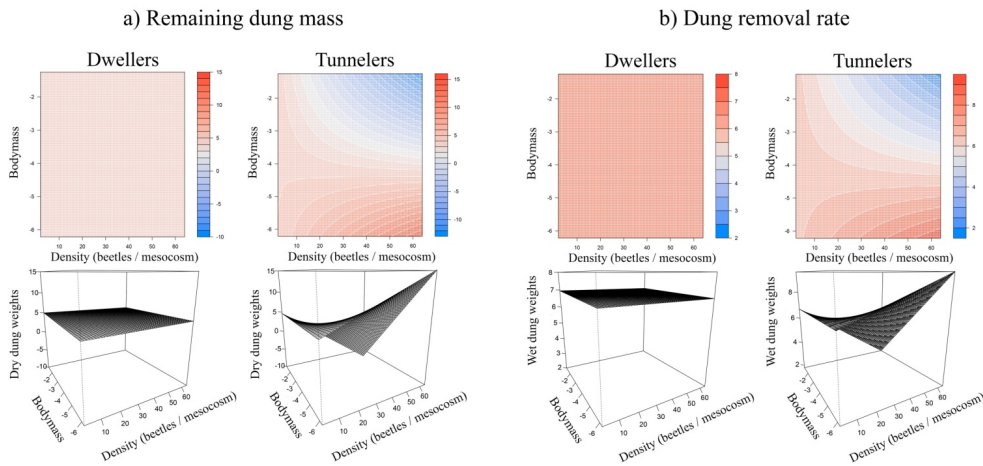
311 **Figure 2: Threat status versus functional efficiency in terms of methane emissions.** Shown is the  
 312 interaction between threat status (black line for non-threatened and grey dashed line for threatened  
 313 species) and the number of individuals per mesocosm (density) for methane emissions ( $\text{mg m}^{-2} \text{h}^{-1}$ ).  
 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

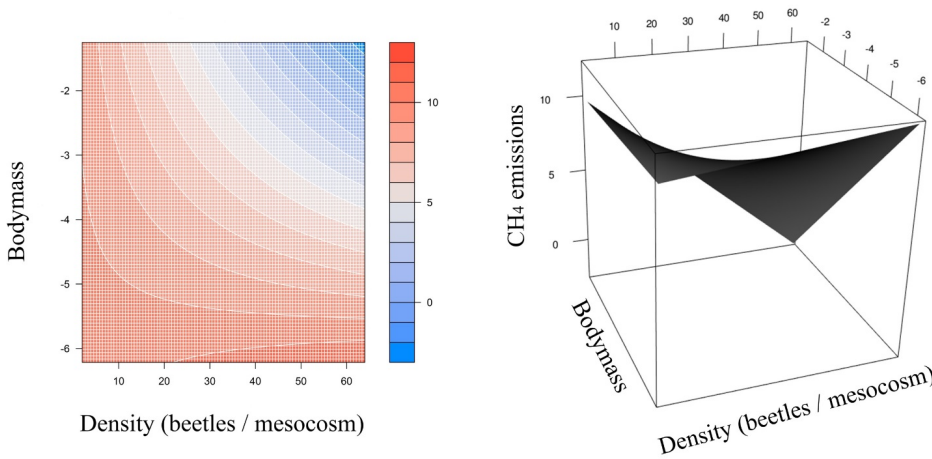
325 **Figure 3: Interaction between body mass and nesting strategy in determining ecological**  
 326 **functioning.** Shown is the significant interaction between the species body mass, nesting strategy and  
 327 the number of individuals per mesocosm for dung removal, measured as: (a) remaining dung 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).

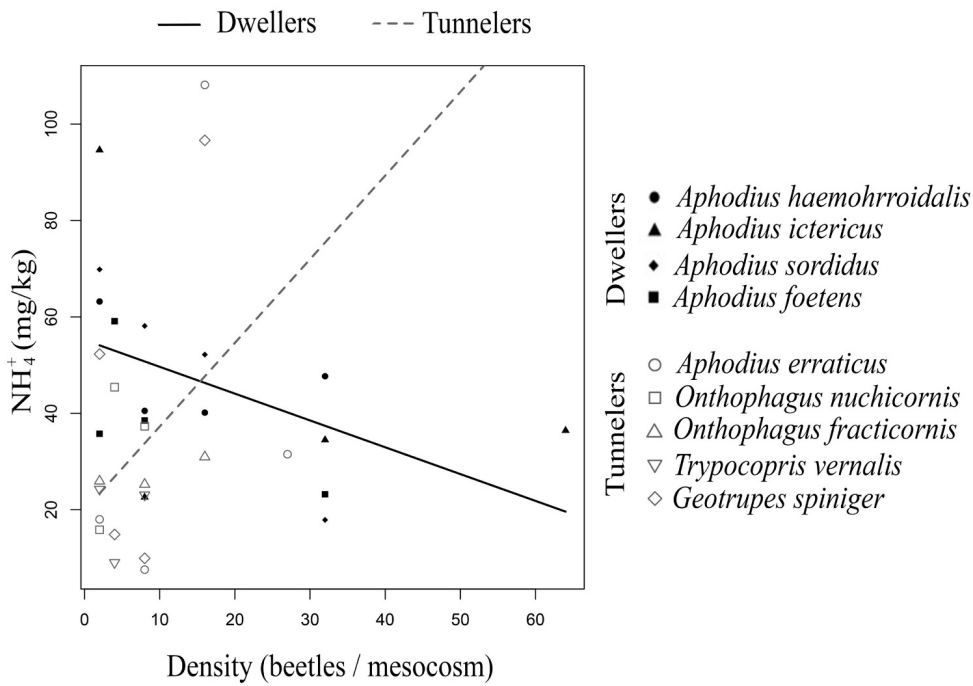


339 GHG EMISSIONS – Overall, the amount of GHG emissions decreased with time (Measurement  
340 days:  $F_{1;177.97}=43.22$ ,  $p<0.001$ ; Appendix, Table A5) and density (Density:  $F_{1;181.93}=5.34$ ,  $p=0.02$ ;  
341 Appendix, Table A5). However, the per capita effect of dung beetles on CH<sub>4</sub> 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 CO<sub>2</sub> or CO<sub>2</sub>-equivalents, or on cumulative emissions of any of the three responses  
345 (CO<sub>2</sub>, CH<sub>4</sub> and CO<sub>2</sub>-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,  $\text{NH}_4^+$   
 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  $\text{NH}_4^+$  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).  $\text{NO}_3^-$  concentration showed no detectable change with either nesting strategy or biomass.

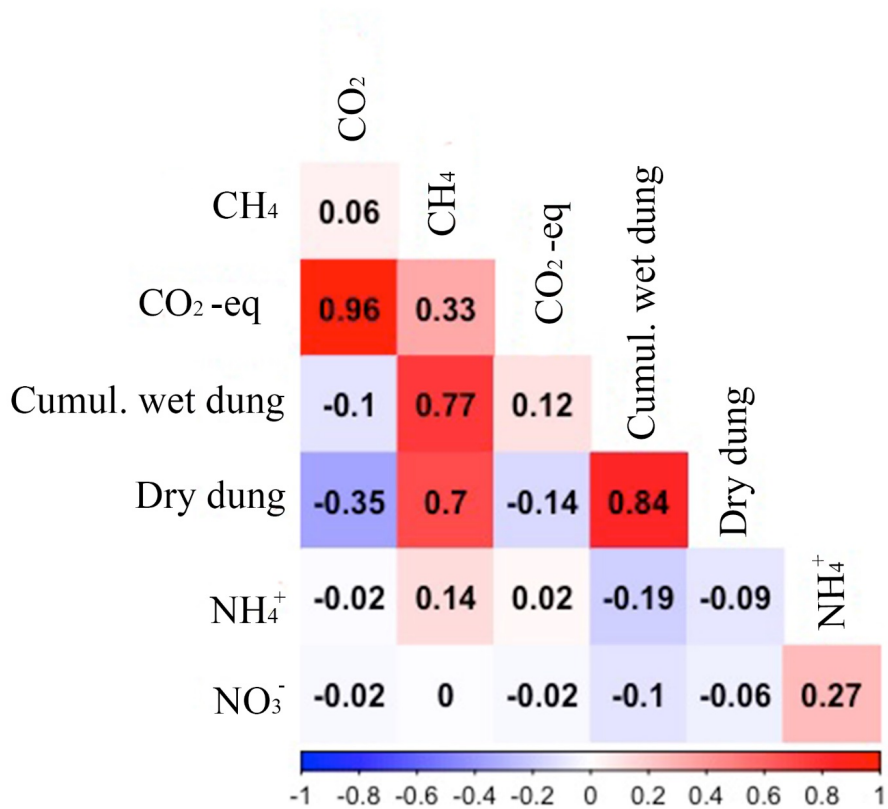


360  
 361 **Figure 5: The effect of nesting strategy on nutrient cycling.** Shown is the marginally significant  
 362 interaction between density and nesting strategy (black line for dwellers and grey dashed line for  
 363 tunnelers) in determining ammonium concentration in the soil ( $\text{mg kg}^{-1}$ ). 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 CO<sub>2</sub> equivalents are composed of CO<sub>2</sub> and CH<sub>4</sub>, all three quantities  
374 were correlated, but this correlation was stronger for CO<sub>2</sub> as it accounts for the main part of the  
375 combined fluxes (Fig. 6). However, a higher dung mass was primarily correlated with higher CH<sub>4</sub>  
376 fluxes, whereas higher emissions of CO<sub>2</sub> were associated with a lower mass of remaining dung. Higher  
377 transfer of NH<sub>4</sub><sup>+</sup> to the soil was also associated with higher transfer NO<sub>3</sub>, 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 (CO<sub>2</sub>), methane (CH<sub>4</sub>) and both gases (CO<sub>2</sub>+CH<sub>4</sub>) combined into CO<sub>2</sub> 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 CH<sub>4</sub> fluxes,  
488 but lower emissions of CO<sub>2</sub>. This difference is likely related to their different modes of emergence.  
489 CO<sub>2</sub> is mostly a product of aerobic respiration, resulting in higher dung decomposition. CH<sub>4</sub> 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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**Formattato:** Allineato a sinistra, Nessuna, Rientro:  
Sinistro: 0 cm, Sporgente 1.25 cm