

Article (refereed) - postprint

Woodcock, Ben A.; Harrower, Colin; Redhead, John; Edwards, Mike;
Vanbergen, Adam J.; Heard, Matthew S.; Roy, David B.; Pywell, Richard F.
2014. **National patterns of functional diversity and redundancy in
predatory ground beetles and bees associated with key UK arable crops.**
Journal of Applied Ecology, 51 (1). 142-151. [10.1111/1365-2664.12171](https://doi.org/10.1111/1365-2664.12171)

© 2013 The Authors. *Journal of Applied Ecology*
© 2013 British Ecological Society

This version available <http://nora.nerc.ac.uk/505206/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. Some differences between this and the publisher's version remain. You are advised to consult the publisher's version if you wish to cite from this article.

Contact CEH NORA team at
noraceh@ceh.ac.uk

1 **Estimating risks to pollination and pest control ecosystem services**
2 **supporting UK crop production**

3

4 Woodcock, B.A.¹, Harrower, C.¹, Redhead, J.¹, Edwards, M.², Vanbergen, A.J.³, Heard,
5 M.S.¹, Roy, D.B.¹, Pywell, R.F.¹.

6

7

8 ¹NERC Centre for Ecology & Hydrology, Maclean Building, Crowmarsh Gifford,
9 Wallingford, Oxfordshire OX10 8BB, UK.

10 ²Leaside Carron Lane, Midhurst, West Sussex GU29 9LB

11 ³NERC Centre for Ecology & Hydrology, BushEstate, Penicuik, Edinburgh EH260QB, UK.

12

13

14

15 Word count: 6,998

16

17 Contact Author B. A. Woodcock (at above address), e-mail:bawood@ceh.ac.uk.

18

19

20 **Summary**

- 21 1. Invertebrates supporting natural pest control and pollination ecosystem services are
22 crucial to worldwide crop production. Understanding national patterns in the spatial
23 structure of natural pest control and pollination can be used to promote effective crop
24 management and contribute to food long-term security.
- 25 2. We mapped the species richness and functional diversity of ground beetles and bees
26 to provide surrogate measures of natural pest control and pollination for Great Britain.
27 Functional diversity represents the value and range of morphological and behavioural
28 traits that support ecosystem services. We modelled the rate with which functional
29 diversity collapsed in response to species extinctions to provide an index of functional
30 redundancy.
- 31 3. Deficits in functional diversity for both pest control and pollination were found in
32 areas of high arable crop production. Ground beetles functional redundancy was
33 positively correlated with the landscape cover of semi-natural habitats where
34 extinctions were ordered by body size and dispersal ability. For bees, functional
35 redundancy showed a weak positive correlation with semi-natural habitat cover where
36 species extinctions were ordered by feeding specialisation.
- 37 4. *Synthesis and applications:* Increasingly evidence suggests that functionally diverse
38 assemblages of ground beetles and bees may be a key element to strategies that aim to
39 support pollination and natural pest control in crops. If deficits in both functional
40 diversity and redundancy in areas of high crop production are to be reversed, then
41 targeted implementation of agri-environmental schemes that establish semi-natural
42 habitat may provide a policy mechanism for supporting these ecosystem services.

43

44 **Keywords:** Arable agriculture, bees, ground beetles, functional diversity, functional
45 redundancy, natural pest control, pollination.

46

47 **Introduction**

48 By 2050 global population size is predicted to increase by 46% necessitating greater
49 agricultural production to achieve food security (FAO, 2006). Historically, increased yields
50 have been achieved by improved agronomy, mechanised farming practices, chemical
51 fertilisers, pesticides and new breeding approaches (Godfray *et al.*, 2010). However, yield
52 increases are increasingly showing evidence of levelling off, and so enhanced production
53 must be achieved using new approaches (Godfray *et al.*, 2010). While the development of
54 new technology and crop varieties is crucial to improved yields, maximising ecosystem
55 services will also contribute to promoting agricultural productivity (Gallai *et al.*, 2009;
56 Godfray *et al.*, 2010; Losey & Vaughan, 2006). Natural pest control and pollination are
57 ecosystem services that support agriculture and are delivered in part by invertebrates (Gallai
58 *et al.*, 2009; Losey & Vaughan, 2006). Invertebrate pests damage 18% of world agricultural
59 production and while their control is achieved principally via chemical methods, the role of
60 predatory and parasitic invertebrates is crucial (Losey & Vaughan, 2006; Straub *et al.*, 2008;
61 Symondson *et al.*, 2002). In the USA invertebrate natural pest control is worth \$4.5 billion
62 *p.a.*, equivalent to 4.2 % of US farm cash receipts (Losey & Vaughan, 2006). Insect
63 pollination is similarly important to agriculture, and is estimated to support 9.5% of world
64 food production (€153 billion) principally in the form of vegetables, fruits and oil producing
65 crops (Gallai *et al.*, 2009). While enhancing natural pest control and pollination could lead to
66 increased crop yields, multiple threats to invertebrate populations are undermining the
67 sustained delivery of these services (Kromp, 1999; Potts *et al.*, 2010; Straub *et al.*, 2008). To

68 properly manage ecosystem services in agricultural landscapes will require an improved
69 understanding of both how they are distributed at policy-relevant (e.g. national) spatial scales
70 and what their likely robustness to environmental change will be.

71 For both natural pest control and pollination, practical limitations mean that direct
72 monitoring of ecosystem services at large spatial scales would be hard to implement.
73 Surrogate metrics derived from invertebrate community structure may provide an alternative
74 to mapping the delivery of ecosystem services. The abundance of invertebrates is one such
75 metric, and is known to be a key determinant of pollination and pest control (Kromp, 1999;
76 Potts *et al.*, 2010; Symondson *et al.*, 2002). However, it is likely to be highly variable across
77 landscapes as a response to local field or farm scale management (Bianchi *et al.*, 2006; Straub
78 *et al.*, 2008; Woodcock *et al.*, 2010). Best practice required to promote the abundance of
79 invertebrates at farm scales are often well understood (e.g. Collins *et al.*, 2002; Woodcock *et*
80 *al.*, 2010), with the limiting factor to their implementation depending on individual farmer
81 management decisions or government policy requirements. However, where there is a
82 limitation in the regional species pool, for example due to wide-scale species loss linked with
83 agricultural intensification, this may place a more fundamental limit on the delivery of
84 pollination and pest control (Potts *et al.*, 2010; Stoate *et al.*, 2009; Straub *et al.*, 2008). For
85 example, direct links between insect pollinator species richness and seed set have been found
86 in many studies (Albrecht *et al.*, 2012; Hoehn *et al.*, 2008). While the effect of species
87 richness on the delivery of natural pest control has been hard to predict in small scale
88 mesocosm studies, there is evidence that species rich assemblages are more likely to deliver
89 improved pest control under real agricultural conditions (Straub *et al.*, 2008). Species
90 richness is a simple descriptor of community structure, and takes no account of the range and
91 value of behavioural or morphological species traits that contribute to ecosystems service
92 delivery. Increased functional diversity of insect pollinators can promote the delivery of

93 pollination services (Albrecht *et al.*, 2012; Hoehn *et al.*, 2008), while dissimilarity in
94 functional traits among invertebrate predators may reduce negative competitive interactions,
95 thereby promoting improved pest control (Schmitz, 2007; Straub *et al.*, 2008; Woodcock &
96 Heard, 2011).

97 Patterns of species richness and functional diversity may provide a surrogate measure
98 of the current spatial distribution of ecosystem services. However, future land use and
99 environmental change will have consequences for which, and how many, species persist over
100 the long-term (Kotze & O'Hara, 2003; Potts *et al.*, 2010; Williams *et al.*, 2010). If species go
101 locally extinct then the unique traits that they contribute will be lost and overall functional
102 diversity will decline, potentially impacting on ecosystem service delivery (Potts *et al.*, 2010;
103 Straub *et al.*, 2008; Woodcock *et al.*, 2010). The rate of decline in functional diversity with
104 species loss provides an indication of the redundancy of a community in its capacity to
105 deliver ecosystem services. Species are unlikely to go extinct at random, rather ordered
106 patterns of extinctions reflecting sensitivities to environmental change will occur (Bommarco
107 *et al.*, 2010; Kotze & O'Hara, 2003; Williams *et al.*, 2010; Woodcock *et al.*, 2012). For
108 example, in Europe large bodied ground beetles are more prone to population decline than
109 small species (Kotze & O'Hara, 2003). Understanding what the potential consequences of
110 ordered scenarios of species extinctions are on the robustness of pollination and pest control
111 services is crucial to their long-term management.

112 We focus on UK arable farming systems that currently cover 4.4 million ha and has a
113 net value of £ 3.1 billion *p.a.* (Defra, 2010). We map the distribution of species richness and
114 functional diversity for taxa important in the delivery of natural pest control (ground beetles:
115 Coleoptera, Carabidae) and pollination (bees: Hymenoptera, Apidae) (Kromp, 1999; Potts *et*
116 *al.*, 2010). We then model the consequences of ordered species extinctions from these
117 communities to identify how robust their functional diversity will be in response to future

118 environmental change. We predict that: 1) Once corrected for latitudinal differences in
119 species pools, the distribution of species richness and functional diversity across Great
120 Britain will reveal deficits in areas of high agricultural production (Potts *et al.*, 2010; Stoate
121 *et al.*, 2009); 2) The decline in functional diversity with species extinctions (hereafter referred
122 to as functional redundancy) will be affected by the order with which species are lost; 3)
123 Increased availability of semi-natural at a landscape scale will promote functional
124 redundancy and so robustness to future environmental change. Note, most UK habitats are
125 modified and so are assumed to be at best semi-natural.

126

127 **Materials and methods**

128 *Focal taxa for delivering natural pest control and pollination*

129 Generalist predators are abundant and species rich in arable farmland and have been shown to
130 reduce pest populations in 75 % of field studies (Symondson *et al.*, 2002). Their spatial
131 distribution is often well recorded nationally, particularly when compared to specialist pest
132 control agents like hymenopteran parasitoids. We used ground beetles as model taxa for
133 assessing the distribution of these predators. Ground beetles have been used as indicators of
134 anthropogenic disturbance and environmental change (Rainio & Niemela, 2003) and are one
135 of a suite of dominant generalist predators found in arable crops (Symondson *et al.*, 2002;
136 Woodcock *et al.*, 2010). They have been directly shown to reduce population sizes of
137 economically significant agricultural pests, including aphids, slugs, root feeding flies and
138 phytophagous beetles (Bommarco *et al.*, 2007; Collins *et al.*, 2002; Kromp, 1999; Zaller *et*
139 *al.*, 2009). Their abundance can also be actively encouraged through agri-environmental
140 schemes which provide financial incentives for farmer to modify land management
141 (Woodcock *et al.*, 2010). In the case of crop pollination, a variety of insect taxa have been

142 linked with increasing seed set (Albrecht *et al.*, 2012; Hoehn *et al.*, 2008; Potts *et al.*, 2010).
143 However, bees (Apidae) are consistently identified as being primary pollinators for many
144 crops (Potts *et al.*, 2010) and are used here to assess the distribution of pollination services.
145 Bee pollination has been shown to increase the yield and crop quality of oilseed rape, a
146 principal UK arable crops (Bommarco *et al.*, 2012).

147 For both ground beetles and bees a limited set of species are found in association with
148 arable crops, and these are considered to be the key providers of ecosystem services in these
149 systems (see Electronic Appendices S1 & S2). The sub-set of ground beetles found in arable
150 crops was determined using large scale datasets of ground beetles recorded from 250 arable
151 fields and four break crops (Firbank *et al.*, 2003). This sub set was confirmed by comparing
152 it to other published data sets (see Appendix S1). Only predatory (zoophagous) ground
153 beetles were included, limiting the pool to 60 species from 25 genera. As cereal crops do not
154 rely on insect pollination, we consider here bees known to pollinate oilseed rape (*Brasica*
155 *napus* L.: Brassicaceae), which by area is the dominant UK insect-pollinated crop (Defra,
156 2010). Forty-five species of bee from seven genera were determined to be oilseed rape
157 pollinators based on both published (Woodcock *et al.*, 2013) and unpublished non-
158 quantitative surveys (18 UK farms surveyed in 2011; *pers. comm.* S. Faulk, P. Harvey and D.
159 Sheppard).

160

161 *Distribution maps*

162 Distribution maps for ground beetles and bees were derived from records stored in the
163 National Biodiversity Network of the UK Biological Records Centre (BRC). National
164 biodiversity recording is typically carried out by volunteers, and so non-standardised recorder
165 effort is a common problem (Hill, 2012). To correct for variable recorder effort we used the

166 ‘Frescalo’ algorithm to determine the probability of individual species occurrence in 10 km
167 grid squares (Hill, 2012). This method uses a Poisson modelling process incorporating
168 information on benchmark species to correct for sampling effort (Hill, 2012). For each 10
169 km grid square in Great Britain (2,824 squares total) the probability of ground beetle and bee
170 species occurrence was determined. From this the species richness of ground beetles and
171 bees involved in natural pest control and pollination was determined for each grid square.
172 This data was used in all subsequent calculations of functional diversity and redundancy. As
173 semi-natural habitats provide important resources for both ground beetles and bees (Bianchi
174 *et al.*, 2006; Potts *et al.*, 2010; Thiele, 1977; Woodcock *et al.*, 2010) we determined the
175 percentage cover of this resource in each 10 km grid square based on the UK Land Cover
176 Map (Morton *et al.*, 2011). Semi-natural habitat combined the cover of grasslands (rough,
177 acid, neutral and calcareous, but not improved with NPK fertiliser), wetlands (bogs, fen, and
178 marshland), heathland (heather grassland and dwarf shrub heath), woodland (broadleaf and
179 coniferous) and montane habitat.

180

181 *Functional diversity*

182 Traits are defined as physical or behavioural characteristics that evolve in response to
183 competitive interactions and abiotic conditions. They influence survival, fitness and rates of
184 resource processing and so their diversity is linked with ecosystem service delivery (Albrecht
185 *et al.*, 2012; Hoehn *et al.*, 2008; Schmitz, 2007; Straub *et al.*, 2008; Woodcock & Heard,
186 2011). We identified traits based on three broad categories: 1) pollination / hunting
187 efficiency; 2) foraging range / dispersal; 3) key aspects of species ecology and behaviour
188 (Bommarco *et al.*, 2010; Forsythe, 1983; Juliano, 1986; Kotze & O'Hara, 2003; Ribera *et al.*,
189 1999; Wamser *et al.*, 2011; Williams *et al.*, 2010; Woodcock *et al.*, 2010). A full description

190 of the traits and their relevance for the delivery of ecosystem services are given in Table 1.
 191 For each 10 km grid square the functional diversity of ground beetles and bees was
 192 determined using the ‘Functional Dispersion’ index (*FD_{is}*) using the traits described in Table
 193 1 (Laliberté & Legendre, 2010). The *FD_{is}* index represents the average distance of species in
 194 multidimensional space from a centroid defined by a distance matrix weighted by the
 195 probability of individual species occurrence. Species encountered more frequently will have
 196 a greater effect on the value of *FD_{is}*. All traits in the analysis were given equal weighting.
 197 As the traits for both bees and ground beetles (Table 1) were represented by a mixture of
 198 variable types (both continuous and categorical) the Gower method was used to calculate the
 199 distance matrix and all traits scores standardised to have a range of 0 to 1 (Gower, 1971;
 200 Laliberté & Legendre, 2010). This index is not affected by species richness (Laliberté &
 201 Legendre, 2010).

202 As the pool of species found in northern latitudes is limited by fundamental climate
 203 requirements (e.g. Thiele, 1977), both the species richness (*SR*) and functional diversity (*FD*)
 204 of ground beetles and bees was characterised by a negative latitudinal cline. Without
 205 correcting for latitudinal gradients in species richness any management intended to support
 206 ecosystem service providing taxa (e.g. agri-environment schemes) might be biased to
 207 northern clines based on the misconception that there was a local ecosystem service deficit.
 208 To account for this we calculated a derived index of species richness (*SR_{Lat}*) and functional
 209 diversity (*FD_{Lat}*) represented by the residuals from a linear regression of species richness or
 210 functional diversity with latitude (ground beetles: $SR=63.52 - 3.91 \times 10^{-5} \times \text{latitude (m)}$; $FD =$
 211 $0.24 - 1.217 \times 10^{-8} \times \text{latitude}$; bees: $SR=44.25 - 3.80 \times 10^{-5} \times \text{latitude}$). For bee functional
 212 diversity, *FD_{Lat}* was based on the residuals from a third order polynomial response to latitude
 213 ($FD = 0.24 + 1.13 \times 10^{-7} \times \text{latitude} - 3.36 \times 10^{-14} \times \text{latitude}^2 - 2.50 \times 10^{-19} \times \text{latitude}^3$)

214

215 *Functional redundancy*

216 Functional redundancy has been defined in many different ways, but is considered here to be
217 a measure of the rate of decline in functional diversity with species extinctions. This is
218 defined by the slope parameter (β) of a linear regression between the number of species that
219 have gone extinct and the change in functional diversity (*FDis*) after each species is lost.
220 High rates of decline in functional diversity in response to species loss indicate a community
221 with low functional redundancy. Such a community would be limited in its capacity to
222 maintain ecosystem services where environmental change resulted in local species
223 extinctions. While biologically unlikely, a null model of random species extinction was used
224 to assess the relative rates of decline in functional diversity compared to species extinctions
225 ordered in a biologically realistic manner (see below) (Bommarco *et al.*, 2010; Kotze &
226 O'Hara, 2003; Williams *et al.*, 2010). For each 10 km grid square species were deleted until
227 only one remained. Following each species deletion the functional diversity of the remaining
228 assemblage was calculated based on their combined traits (Table 1). The deletion process
229 was repeated 500 times and a mean slope parameter (β_{Random}) defining the null model of
230 functional redundancy was calculated for each 10 km grid square.

231 The slope parameters for this null model were compared to an equivalent slope (β
232 *Ordered*) defined by species extinctions ordered by traits known to affect population sizes and
233 local extinction rates in both ground beetles and bees. These were:

234 1) body size: For ground beetles, species loss was ordered so that the largest species (body
235 mass) went extinct first, reflecting observed declines in European ground beetles linked to
236 their reduced dispersal and lower reproductive rates (Kotze & O'Hara, 2003). For the bees,
237 smaller species (based on inter-tegular distance) were assumed to go extinct first. Although it
238 has been suggested that smaller bees may be better suited to surviving in small habitat

239 patches (Williams *et al.*, 2010), larger bees have greater foraging ranges and so are better able
 240 to utilise widely distributed resources in fragmented agricultural landscapes (Bommarco *et*
 241 *al.*, 2010; Greenleaf *et al.*, 2007).

242 2) Diet specialisation: Species with specialist niches, such as a limited diet breadth, are more
 243 likely to undergo population declines in both ground beetles (Kotze & O'Hara, 2003) and
 244 bees (Bommarco *et al.*, 2010). For ground beetles, extinctions were in order of collembola
 245 specialist, obligate predators and then omnivores. For bees, oligophagous flower foraging
 246 species were deleted before polyphagous species.

247 3a) Ground beetle flight: ground beetles with wing dimorphism can colonise fragmented and
 248 isolated habitat, then once established flightless morphs of the same species are superior
 249 competitors (Kotze & O'Hara, 2003). In contrast, obligate flightless species are ill suited to
 250 persist in highly fragmented landscapes, while obligate fully winged species tend to be
 251 comparatively poor competitors once colonised (Kotze & O'Hara, 2003). We modelled
 252 species extinctions in order of flightless, full winged and then wing dimorphic species.

253 3b) Sociality: social bees are more sensitive to pesticides and isolation from semi-natural
 254 habitats than solitary species (Bommarco *et al.*, 2010; Williams *et al.*, 2010) and so were
 255 modelled to go extinct first.

256 Following the same procedure as described above the slope parameter ($\beta_{Ordered}$) was
 257 calculated following sequential extinctions from each 10 km grid square. Where traits used
 258 to describe the order of species loss were categorical (e.g. solitary vs. social bees) species
 259 were deleted at random within a particular trait level before moving onto the next. As for the
 260 null model, this process was repeated 500 times and an average slope parameter calculated.
 261 A relative index of functional redundancy ($FR_{Relative}$) was then calculated as the percentage
 262 difference between these decline slopes for random and ordered species extinctions ($FR_{Relative}$
 263 $index = (\beta_{Random} - \beta_{Ordered}) / \beta_{Random} \times 100$). Positive values of $FR_{Relative}$ indicate a rate of

264 decline in functional diversity that is lower than would be expected if species extinctions had
265 been entirely at random, with the converse of this being true for negative values.

266

267 *Analyses*

268 The response of the latitude corrected species richness (SR_{lat}), latitude corrected
269 functional diversity (FD_{lat}) and all functional redundancy indexes ($FR_{Relative}$) to the
270 percentage cover of semi-natural habitat in 10 km grid squares was assessed using general
271 linear models in SAS v9.1. Following Borcard and Legendre (2002) we used principal
272 coordinates of neighbour matrices (PCNM) to account for spatial autocorrelation in these
273 models. Geographic distances among sampling points (taken to be the south east corner of
274 each 10 km grid square) were used to obtain eigenvectors that describe the spatial structure of
275 the data at a wide variety of scales. These eigenvectors were subsequently included as
276 covariates in GLM models. As the PCNM method calculates a large number of eigenvectors
277 describing a complex range of spatial structures underpinning the data (equivalent to c. 50%
278 of all the 2,824 sampling points) we tested the first 200 of these as univariate correlations
279 against each response variable. Only those shown to be significantly ($p < 0.05$) correlated with
280 a response variable were included in final models with semi-natural habitat cover. Note, that
281 as the PCNM eigenvectors have only been included as covariates to account for underlying
282 spatial structure they are not be reported in the results section. While the percentage cover of
283 arable crop in each 10 km grid square was considered as a potential covariate describing land
284 use intensity, its strong negative correlation with the percentage cover of semi-natural habitat
285 ($F_{1,2562}=280.3$, $p < 0.001$, $\beta = -0.95$) and resulting lack of independence made its inclusion
286 inappropriate. Paired t tests were also used to determine if there was an overall difference in

287 the slope of decline in functional diversity resulting from random (β_{Random}) or ordered (β_{Ordered}) species extinctions.

289

290 **Results**

291 *Species richness and functional diversity*

292 The spatial distribution of ground beetle and bee species richness (SR_{Lat}) showed deficits in
293 both the South-West and North-West regions of Great Britain (Fig. 1). In contrast, central
294 and eastern parts of England associated with high levels of arable crop production supported
295 high levels of SR_{Lat} for both ground beetles and bees, with this trend extending to eastern
296 parts of Scotland for the bees. However, this was somewhat reversed for the companion
297 measure of ecosystem service delivery, functional diversity (FD_{Lat}). In contrast to SR_{Lat} ,
298 central and eastern England had deficits in FD_{Lat} for both the ground beetles and bees (Fig.
299 1). For the ground beetles, functional diversity was highest in the West of the UK, although
300 this distribution was somewhat patchy. For the bees, FD_{Lat} was highest in Scotland, Wales,
301 Northern and South-West England.

302 For both the ground beetles ($F_{1,2699}=64.9$, $p<0.001$) and bees ($F_{1,2691}=237.7$, $p<0.001$)
303 SR_{Lat} was negatively correlated with the percentage cover of semi-natural habitat in 10km
304 grid squares (Fig. 2). In contrast, FD_{Lat} was positively correlated with the availability of semi-
305 natural habitat for both the ground beetles ($F_{1,2693}=133.3$, $p<0.001$) and bees ($F_{1,2695}=79.9$,
306 $p<0.001$), although the slope was greater for the ground beetles (Fig 2).

307

308 *Functional redundancy*

309 The rate of decline in ground beetle functional diversity in response to species extinctions (β_{Ordered})
310 was found to be significantly different from that predicted by the null model of

311 random species extinction (β_{Random}). However, the direction of this difference varied with
 312 species trait. Where beetle species extinctions were ordered by diet specialisation ($t_{2823} =$
 313 55.98, $p < 0.001$) the rate of decline in functional diversity with species loss was lower than
 314 was predicted by the null model. Whereas the rate of decline in functional diversity was
 315 higher than what was predicted by the null model when beetle extinctions were ordered by
 316 body size ($t_{2823} = -52.5$, $p < 0.001$) and ability to fly ($t_{2823} = -117.6$, $p < 0.001$). For bees, species
 317 extinctions ordered by body size led to greater rates of decline in functional diversity with
 318 species loss compared to the null model ($t_{2823} = -60.0$, $p < 0.001$). Where social bees were
 319 modelled as going extinct before solitary bees, there was conversely an increase in the rate of
 320 decline in functional diversity with species loss ($t_{2823} = -57.6$, $p < 0.001$). However, for bees
 321 the loss of dietary specialists before generalists resulted in a lower rate of decline in
 322 functional diversity, compared to the null model ($t_{2823} = 54.6$, $p < 0.001$).

323 Functional redundancy ($FR_{Relative}$), describing the percentage difference in the decline
 324 slopes for random and ordered species extinctions, was correlated with the percentage cover
 325 of semi-natural habitat for both the ground beetles and bees. For the ground beetles, $FR_{Relative}$
 326 was positively correlated with semi-natural habitat cover where species extinctions
 327 were ordered by both body size ($F_{1,2708} = 30.8$, $p < 0.001$; Fig.3a) and ability to fly ($F_{1,2697} = 21.2$,
 328 $p < 0.001$, Fig.3c), although not by diet specialisation ($F_{1,2703} = 0.18$, $p > 0.05$). For the bees $FR_{Relative}$
 329 was positively correlated with the percentage cover of semi-natural habitat where
 330 species extinctions were ordered by diet specialisation ($F_{1,2648} = 7.09$, $p < 0.01$, Fig. 3b),
 331 although this correlation was not significant where extinctions were ordered by social
 332 structure ($F_{1,2665} = 2.30$, $p > 0.05$) or body size ($F_{1,2662} = 0.98$, $p > 0.05$). The slope coefficients for
 333 the response of $FR_{Relative}$ to the cover of semi-natural habitat resulting from bee extinctions
 334 ordered by diet specialisation were small ($\beta = 0.02$) compared to those reported for the
 335 ground beetles (body size: $\beta = 0.75$; ability to fly: $\beta = 0.51$). This suggests that over the range

336 of semi-natural habitat covers encountered the change in $FR_{Relative}$ for the bees would be
337 largely inconsequential (Fig. 3).

338

339 **Discussion**

340 *Species richness and functional diversity*

341 By mapping national scale patterns of species richness and functional diversity we
342 provide crucial information for the development of targeted mitigation measures intended to
343 support ecosystem services (Bianchi *et al.*, 2006; Woodcock *et al.*, 2010). Contrary to our
344 prediction, low levels of species richness (once corrected for latitude) were not spatially
345 linked with regions of high crop production; in particular the intensively managed arable
346 landscapes of central and eastern England (Defra, 2010). Similarly species richness was
347 negatively correlated with the cover of semi-natural habitats. This may on the surface appear
348 to contradict evidence that habitat loss and degradation driven by intensive agriculture has led
349 to declining ground beetle and bee species richness (e.g. Bommarco *et al.*, 2010; Kotze &
350 O'Hara, 2003; Kromp, 1999; Potts *et al.*, 2010; Williams *et al.*, 2010). However, it is
351 important to take into account that we focused not on overall species richness, but instead on
352 a subset of species known to be linked with arable agriculture and so likely to deliver
353 ecosystem services. Species most likely to suffer from the effects of intensive agriculture are
354 likely to be non-crop habitat specialists (Bommarco *et al.*, 2010; Kotze & O'Hara, 2003; Potts
355 *et al.*, 2010), however, such species were excluded from our analysis. Species found in
356 arable crops are likely to possess adaptations that predispose them to colonisation and
357 survival in agricultural habitats (Thiele, 1977). Thus it is not unexpected that such species
358 would at least be associated with areas of agricultural production, although their densities
359 may well be relatively low in many such areas (Kotze & O'Hara, 2003; Potts *et al.*, 2010;
360 Williams *et al.*, 2010). This highlights a failing of using species richness as an indicator of

361 ecosystem services. Specifically, it is an un-weighted measure of invertebrate community
362 structure that makes no distinction between rare and ubiquitous species; consequently it may
363 lack the resolution of information on rarity to be an inadequate indicator of ecosystem service
364 provision.

365 In contrast, functional diversity, while dictated by species composition, has the
366 advantage of being weighted by the probability of species occurrence. As species become
367 rarer in landscapes denuded of semi-natural habitat, their contribution to overall functional
368 diversity and so ecosystem service provision is reduced (Laliberté & Legendre, 2010;
369 Woodcock *et al.*, 2010). This in part explains why species richness and functional diversity
370 are respectively negatively and positively correlated with the percentage cover of semi-
371 natural habitat. Enhancement of semi-natural habitat cover will promote functional diversity
372 of ecosystem service providers in crops by increasing the probability of species occurrence.
373 The implementation of agri-environmental schemes may therefore be more valuable in
374 diversifying the trait structure of ground beetles and bees than necessarily promoting
375 increased species richness (Woodcock *et al.*, 2010).

376

377 *Functional redundancy and the order of species extinctions*

378 Functional redundancy was typically lowest where extinctions were ordered
379 according to traits known to affect species sensitivity to environmental change (Bommarco *et*
380 *al.*, 2010; Kotze & O'Hara, 2003; Williams *et al.*, 2010). Where species extinctions were
381 ordered by body size (bees and ground beetles), flight ability (beetles) and sociality (bees) the
382 decline in functional diversity with species loss was higher than occur under random
383 extinction scenarios. Body size is strongly inter-correlated with a wide variety of traits,
384 including dispersal, reproductive capacity and diet breadth (Bommarco *et al.*, 2010; Greenleaf
385 *et al.*, 2007; Kotze & O'Hara, 2003). These other trait characteristics will be systematically

386 lost from the community with size-dependent extinctions, leading to an increased rate of
387 collapse in functional diversity with species loss for both ground beetles and bees. Other
388 species characteristics, not considered here, may also exacerbate the consequences of
389 collapse in functional diversity with ordered species loss. For example, social bees have been
390 found to be responsible for four times as many visitations to flowers as solitary bees
391 (Albrecht *et al.*, 2012). An increased likelihood of their local extinction may therefore have
392 greater than predicted consequences for the delivery of pollination services (Williams *et al.*,
393 2010). Land management could be adapted to preferentially support populations of species at
394 the sensitive ends of a particular trait spectrum. For example, reducing levels of pesticide
395 application or isolation from semi natural habitat will benefit population stability of social
396 bees, thus reducing the rate at which they go extinct (Williams *et al.*, 2010). Such targeted
397 management could therefore be used to promote functional redundancy in arable systems.

398 Where species extinctions were ordered by diet specialisation, functional redundancy
399 was consistently higher than predicted by the random model for both the ground beetles and
400 bees. For the bees it may be the case that, while diet specialisation is a predictor of responses
401 to environmental change (e.g. sensitivity to habitat fragmentation), its consequences on
402 ordered extinction rates do not occur independently of interactions with other traits. For
403 instance, Bommarco *et al.* (2010) demonstrated that body size can be important in predicting
404 the response of bees to habitat loss, but only when considered in the context of the dietary
405 specialisation of individual species. For dietary generalists, species of small size were more
406 affected by habitat loss than larger bodied species, with the reverse true for dietary
407 specialists. It should be noted that Bommarco *et al.* (2010) considered this finding to be a
408 potential artefact resulting from the possibility that the majority of small diet specialist bees
409 had already gone extinct from the landscapes investigated. It is quite possible, however, that
410 a similar mechanism is in operation with ground beetles, where the importance of diet

411 specialisation as a predictor of extinction rates is moderated by other as yet unconsidered
412 species traits.

413

414 *Semi-natural habitats to promote functional redundancy.*

415 For the ground beetles, correlative relationships suggested that their functional
416 redundancy could be promoted by increasing the availability of semi-natural habitat at
417 landscape scales, but only where extinctions are ordered by body size and flight ability.
418 While there was some evidence that bee functional redundancy also increased with semi-
419 natural habitat cover, the strength of this trend was too weak to make inferences that would
420 be biologically relevant to applied management. For the bees, the spatial structure of semi-
421 natural habitat may be more important in predicting the occurrence of individual species and
422 their associated traits than simply its overall percentage cover in a 10 km grid square
423 (Bommarco *et al.*, 2010; Potts *et al.*, 2010). Bees may also be more specific in what elements
424 of semi-natural habitats represent viable alternative resources in an agricultural landscape
425 (Potts *et al.*, 2010) (i.e. those rich in flowers), particularly when contrasted with ground
426 beetles that may be more plastic in their habitat associations (Thiele, 1977). For this reason,
427 the importance of semi-natural habitat as a key landscape element supporting robustness to
428 environmental change may have been underestimated for the bees due to a limited capacity to
429 define exactly which habitats were important. The existence of positive, albeit sometimes
430 weak, correlations between functional redundancy and semi-natural habitat does emphasise
431 the role that landscape scale conservation could play in supporting ecosystem service
432 robustness by creating new semi-natural habitat (Bianchi *et al.*, 2006; Lawton *et al.*, 2010;
433 Potts *et al.*, 2010; Woodcock *et al.*, 2012). As agri-environment schemes are implemented in
434 association with arable agriculture they represent a policy mechanism that can be used in
435 promoting robustness of pest control and pollination by establishing new semi-natural habitat

436 (Bianchi *et al.*, 2006; Pywell *et al.*, 2011; Woodcock *et al.*, 2010). However, as the utility of
437 different agri-environment scheme for pollinators and natural pest control agents differs,
438 research effort is still required to assess best management practices to support these taxa
439 (Pywell *et al.*, 2011; Woodcock *et al.*, 2010).

440 *Conclusions*

441 For invertebrates our ability to predict large scale patterns in ecosystem service
442 provision have been limited by our understanding of the mechanistic relationship between
443 community composition, functional diversity and ecosystem service provision rates.
444 Although not considered in the current study, management at local scales that promotes
445 abundances of these taxa will also be important in the delivery of ecosystems services. While
446 research is increasingly focusing on interactions that underpin these relationships for both
447 pest control and pollination, current predictions of service delivery must be based on
448 assumptions that would be likely in time to be refined (Albrecht *et al.*, 2012; Hoehn *et al.*,
449 2008; Straub *et al.*, 2008; Woodcock & Heard, 2011). Independent of this, there remains a
450 pressing need to develop new approaches to determine the distribution of ecosystem services,
451 particularly where this allows responses to future environmental change to be predicted.
452 Without such methodologies we will be unable to manage agricultural landscapes in a pre-
453 emptive manner and be limited to reactionary approaches that attempt to prop up failing
454 levels of pollination and pest control as a reaction to falling yields. This is clearly a serious
455 long-term issue, as while there are many methods to establish semi-natural habitats to benefit
456 pest control and pollination supporting invertebrates, they all take time to implement (Lawton
457 *et al.*, 2010; Pywell *et al.*, 2011; Woodcock *et al.*, 2010). The identification of landscapes
458 that may be vulnerable to deficits in ecosystem services delivery, now or in the future, allows

459 interventions to be devised that will secure their value and function in the long-term (Lawton
460 *et al.*, 2010).

461

462 **Acknowledgements**

463 This work was partly supported by the PRESS2 project of the PEER research
464 consortium. Thanks to James Bullock for his valuable comments on the manuscript and the
465 Biological Records Centre and all individuals involved in the recording of these taxa for
466 access to long term data sets. Species distribution data used in this paper are accessible via
467 the National Biodiversity Network's Gateway (<http://data.nbn.org.uk/>).

468

469

470

471 **References**

472 Albrecht, M., Schmid, B., Hautier, Y., & Müller, C.B. (2012) Diverse pollinator communities enhance
473 plant reproductive success. *Proceedings of the Royal Society, Series B*, **279**, 4845-4852.

474 Bauer, T., Desender, K., Morwinsky, T., & Betz, O. (1998) Eye morphology reflects habitat demands in
475 three closely related ground beetle species (Coleoptera : Carabidae). *Journal of Zoology*, **245**,
476 467-472.

477 Bianchi, F.J.J.A., Booij, C.J.H., & Tscharntke, T. (2006) Sustainable pest regulation in agricultural
478 landscapes: a review on landscape composition, biodiversity and natural pest control.
479 *Proceedings of The Royal Society of London, Series B.*, **273**, 1715-1724.

- 480 Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I.,
481 & Öckinger, E. (2010) Dispersal capacity and diet breadth modify the response of wild bees
482 to habitat loss. *Proceedings of The Royal Society of London, Series B.*, **277**, 2075-2082.
- 483 Bommarco, R., Firle, S.O., & Ekbom, B. (2007) Outbreak suppression by predators depends on spatial
484 distribution of prey. *Ecological Modelling*, **201**, 163-170.
- 485 Bommarco, R., Marini, L., & Vaissière, B.E. (2012) Insect pollination enhances seed yield, quality, and
486 market value in oilseed rape. *Oecologia*, **169**, 1025-1032.
- 487 Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal
488 coordinates of neighbour matrices. *Ecological Modelling*, **153**, 51-68.
- 489 Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M., & Chaney, K. (2002) Influence of beetle banks
490 on cereal, aphid predation in winter wheat. *Agriculture Ecosystems & Environment*, **93**, 337-
491 350.
- 492 Defra (2010) *Agriculture in the United Kingdom 2010*. Defra, London.
- 493 FAO (2006) *World agriculture: towards 2030/2050. Prospects for food, nutrition, and major*
494 *commodity groups*. Food and Agricultural Organisation, Global Perspectives Study Unit,
495 Rome.
- 496 Firbank, L.G., Heard, M.S., Woiwod, I.P., Hawes, C., Houghton, A.J., Champion, G.T., Scott, R.J., Hill,
497 M.O., Dewar, A.M., Squire, G.R., May, M.J., Brooks, D.R., Bohan, D.A., Daniels, R.E., Osborne,
498 J.L., Roy, D.B., Black, H.I.J., Rothery, P., & Perry, J.N. (2003) An introduction to the Farm-Scale
499 Evaluations of genetically modified herbicide-tolerant crops. *Journal of Applied Ecology*, **40**,
500 2-16.
- 501 Forsythe, T.G. (1983) Locomotion in ground beetles (Coleoptera carabidae): An interpretation of leg
502 structure in functional terms. *Journal of Zoology*, **200**, 493-507.
- 503 Gallai, N., Salles, J., Settele, J., & Vaissière, B.E. (2009) Economic valuation of the vulnerability of
504 world agriculture confronted to pollinator decline. *Ecological Economics*, **68**, 810-821.

- 505 Godfray, H.C.J., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Nisbett, N., Pretty, J., Robinson, S.,
506 Toulmin, C., & Whiteley, R. (2010) The future of the global food system. *Philosophical*
507 *Transactions of the Royal Society B-Biological Sciences*, **365**, 2769-2777.
- 508 Gower, J.C. (1971) A general coefficient of similarity and some of its properties. *Biometrics*, **27**, 857-
509 871.
- 510 Greenleaf, S.G., Williams, N.M., Winfree, R., & Kremen, C. (2007) Bee foraging ranges and their
511 relationship to body size. *Oecologia*, **153**, 589-596.
- 512 Hill, M.O. (2012) Local frequency as a key to interpreting species occurrence data when recording
513 effort is not known. *Methods in Ecology and Evolution*, **3**, 195-205.
- 514 Hoehn, P., Tschardtke, T., Tylianakis, J.M., & Steffan-Dewenter, I. (2008) Functional group diversity of
515 bee pollinators increases crop yield. *Proceedings of The Royal Society of London, Series B.*,
516 **275**, 2283-2291.
- 517 Juliano, S.A. (1986) Food limitation of reproduction and survival for populations of *Brachinus*
518 (Coleoptera: Carabidae). *Ecology*, **67**, 1036-1045.
- 519 Kotze, D.J. & O'Hara, R.B. (2003) Species decline - but why? Explanations of carabid beetle
520 (Coleoptera, Carabidae) declines in Europe. *Oecologia*, **135**, 138-148.
- 521 Kromp, B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy,
522 cultivation impacts and enhancement. *Agriculture, Ecosystems & Environment*, **74**, 187-228.
- 523 Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity
524 from multiple traits. *Ecology*, **91**, 299–305.
- 525 Lawton, J.H., Brotherton, P.N.M., Brown, V.K., Elphick, C., Fitter, A.H., Forshaw, J., Haddow, R.W.,
526 Hilborne, S., Leafe, R.N., Mace, G.M., Southgate, M.P., Sutherland, W.J., Tew, T.E., Varley, J.,
527 & Wynne, G.R. (2010) *Making Space for Nature: a review of England's wildlife sites and*
528 *ecological network. Report to Defra.* Defra, Peterborough.
- 529 Losey, J.E. & Vaughan, M. (2006) The economic value of ecological services provided by insects.
530 *Bioscience*, **54**, 311-323.

- 531 Luff, M.L. (1978) Diel activity patterns of some field Carabidae. *Ecological Entomology*, **3**, 53-62.
- 532 Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R., & Simpson, I.C.
533 (2011) *Final Report for LCM2007 - the new UK Land Cover Map*. Centre for Ecology &
534 Hydrology, Lancaster.
- 535 Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W.E. (2010) Global
536 pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, **25**, 345-353.
- 537 Pywell, R.F., Meek, B.R., Loxton, R.G., Nowakowski, M., Carvell, C., & Woodcock, B.A. (2011)
538 Ecological restoration on farmland can drive beneficial functional responses in plant and
539 invertebrate communities *Agriculture Ecosystems & Environment*, **140**, 62-67.
- 540 Radloff, F.T. & DuToit, J.T. (2004) Large predators and their prey in a southern African savanna: a
541 predator's size determines its prey size range. *Journal of Animal Ecology*, **73**, 410-423.
- 542 Rainio, J. & Niemela, J. (2003) Ground beetles (Coleoptera : Carabidae) as bioindicators. *Biodiversity
543 and Conservation*, **12**, 487-506.
- 544 Ribera, I., Foster, G.N., Downie, I.S., McCracken, D.I., & Abernethy, V.J. (1999) A comparative study
545 of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae). *Annales
546 Zoologici Fennici*, **36**, 21-37.
- 547 Schmitz, O.J. (2007) Predator diversity and trophic interactions. *Ecology*, **88**, 2415-2426.
- 548 Stoate, C., Baldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L., &
549 Ramwell, C. (2009) Ecological impacts of early 21st century agricultural change in Europe - A
550 review. *Journal of Environmental Management*, **91**, 22-46.
- 551 Straub, C.S., Finke, D.L., & Snyder, W.E. (2008) Are the conservation of natural enemy biodiversity
552 and biological control compatible goals? *Biological Control*, **45**, 225-237.
- 553 Symondson, W.O.C., Sunderland, K.D., & Greenstone, M.H. (2002) Can generalist predators be
554 effective biocontrol agents? *Annual Review of Entomology*, **47**, 561-594.
- 555 Thiele, H.-U. (1977) *Carabid Beetles in their Environment. A Study on Habitat Selection by
556 Adaptation in Physiology and Behaviour*. Springer-Verlag, New York.

- 557 Wamser, S., Dauber, J., Birkhofer, K., & Wolters, V. (2011) Delayed colonisation of arable fields by
558 spring breeding ground beetles (Coleoptera: Carabidae) in landscapes with a high availability
559 of hibernation sites. *Agriculture Ecosystems & Environment*, **144**, 235-240.
- 560 Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L., & Potts, S.G. (2010) Ecological
561 and life-history traits predict bee species responses to environmental disturbances.
562 *Biological Conservation*, **143**, 2280–2291.
- 563 Woodcock, B.A., Bullock, J.M., Nowakowski, M., Orr, R., Tallowin, J.R.B., & Pywell, R.F. (2012)
564 Enhancing floral diversity to increase the robustness of grassland beetle assemblages to
565 environmental change. *Conservation Letters*, **5**, 459-469.
- 566 Woodcock, B.A., Edwards, M., Redhead, J., Meek, W.R., Nuttall, P., Falk, S., Nowakowski, M., &
567 Pywell, R.F. (2013) Crop flower visitation by honeybees, bumblebees and solitary bees:
568 small scale behavioural differences linked to landscape scale responses. *Agriculture,*
569 *Ecosystems & Environment*, **171**, 1-8.
- 570 Woodcock, B.A. & Heard, M.S. (2011) Disentangling the effects of predator hunting mode and
571 habitat domain on the top-down control of insect herbivores. *Journal of Animal Ecology*, **80**,
572 495–503.
- 573 Woodcock, B.A., Redhead, J., Vanbergen, A.J., Hulmes, L., Hulmes, S., Peyton, J., Nowakowski, M.,
574 Pywell, R.F., & Heard, M.S. (2010) Impact of habitat type and landscape structure on
575 biomass, species richness and functional diversity of ground beetles. *Agriculture Ecosystems*
576 *& Environment*, **139**, 181-186
- 577 Zaller, J., Moser, D., Drapela, T., & Frank, T. (2009) Ground-dwelling predators can affect within-field
578 pest insect emergence in winter oilseed rape fields. *Biocontrol*, **54**, 247-253.
- 579
580
- 581 **Appendix S1.** Species list of predatory ground beetles identified as occurring in association with UK
582 arable agriculture.

583 **Appendix S2.** Species list of bees found in association with UK oilseed rape crops.

584 **Figure captions**

585

586 **Fig. 1.** Maps of species richness (SR_{Lat}) and functional diversity (FD_{Lat}) for ground beetles
587 and bees in England, Wales and Scotland. All values presented represent latitude corrected
588 species richness and functional diversity (see methods).

589

590 **Fig. 2.** The relationship between the percentage cover of semi-natural vegetation in 10 km
591 grid squares and species richness (SR_{Lat}) and functional diversity (FD_{Lat}) for ground beetles
592 and bees.

593

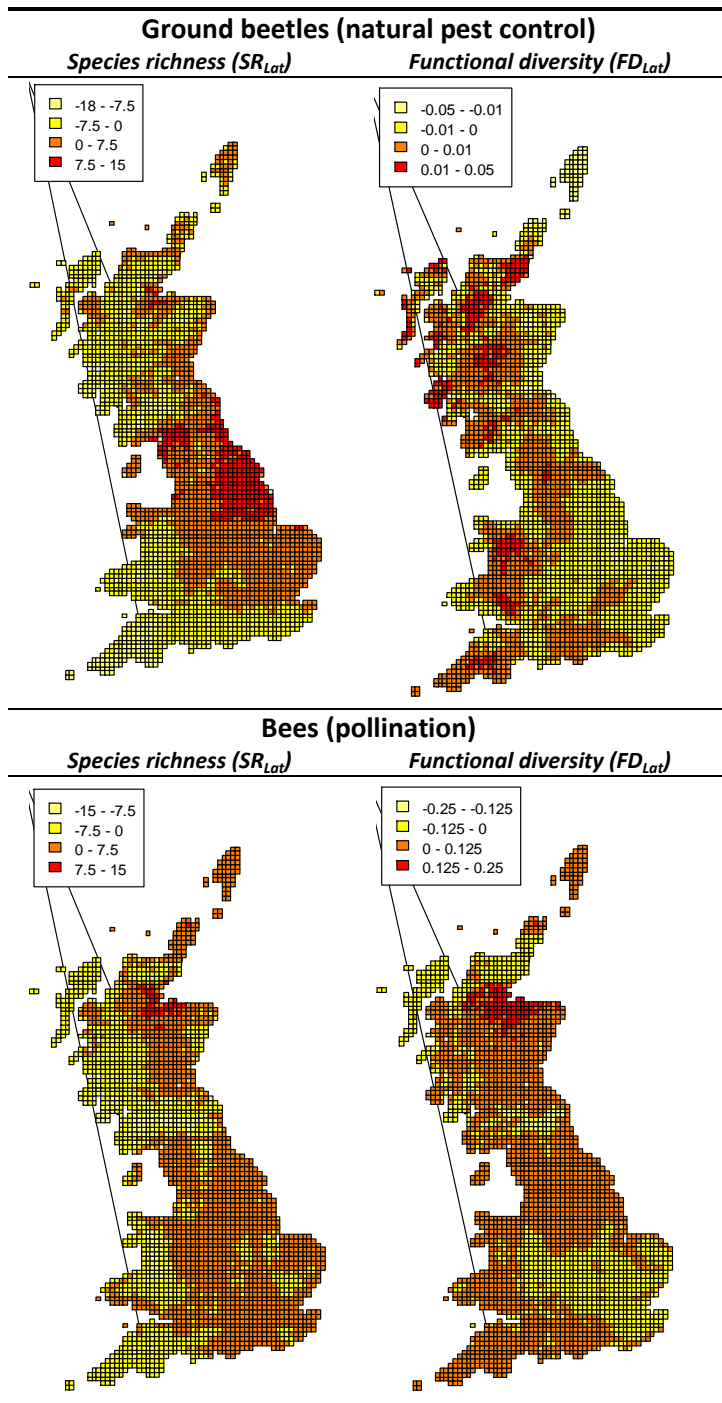
594 **Fig. 3.** The relationship between the percentage cover of semi-natural vegetation in 10 km
595 grid squares and functional redundancy. Functional redundancy is given as the percentage
596 difference in slopes describing the rate of decline in functional diversity between random and
597 ordered species extinctions ($FR_{Relative}$). Positive values of $FR_{Relative}$ show increased levels of
598 functional redundancy, and so robustness to possible future environmental change. The
599 converse is true for negative values.

600

601

602

603 **Fig.1**

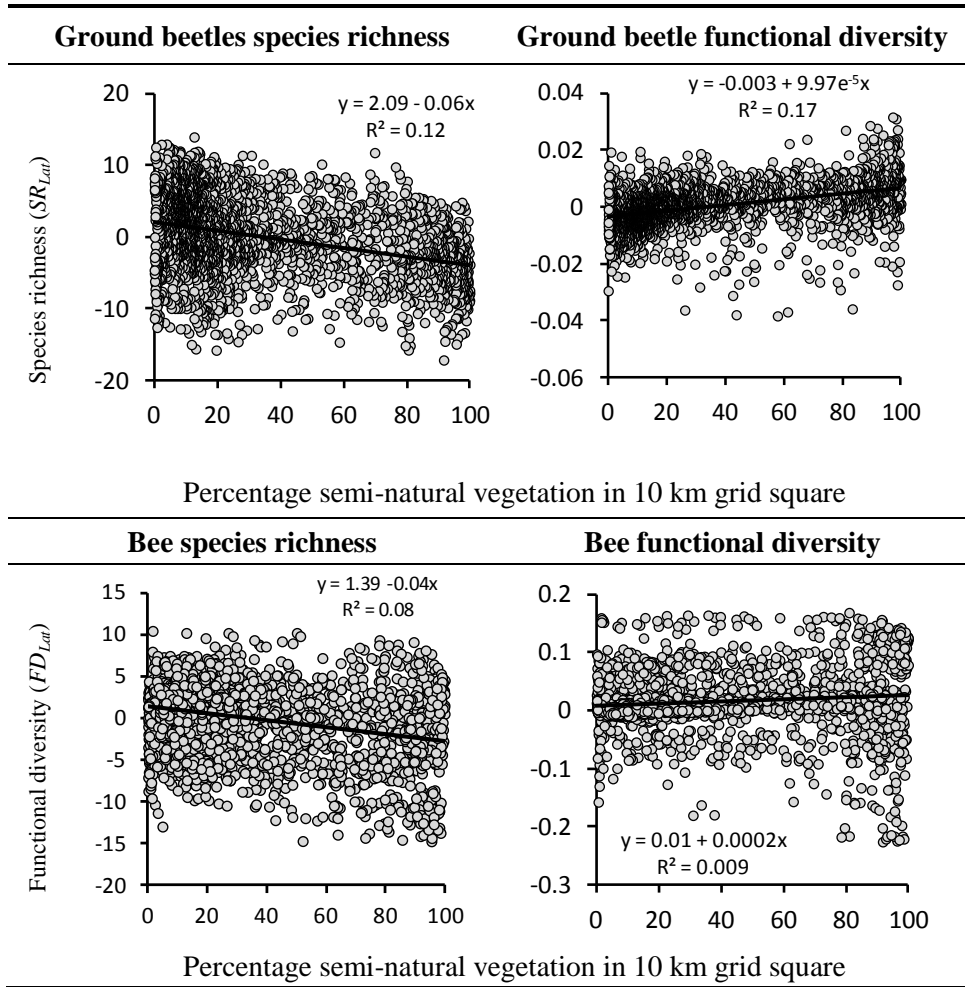


604

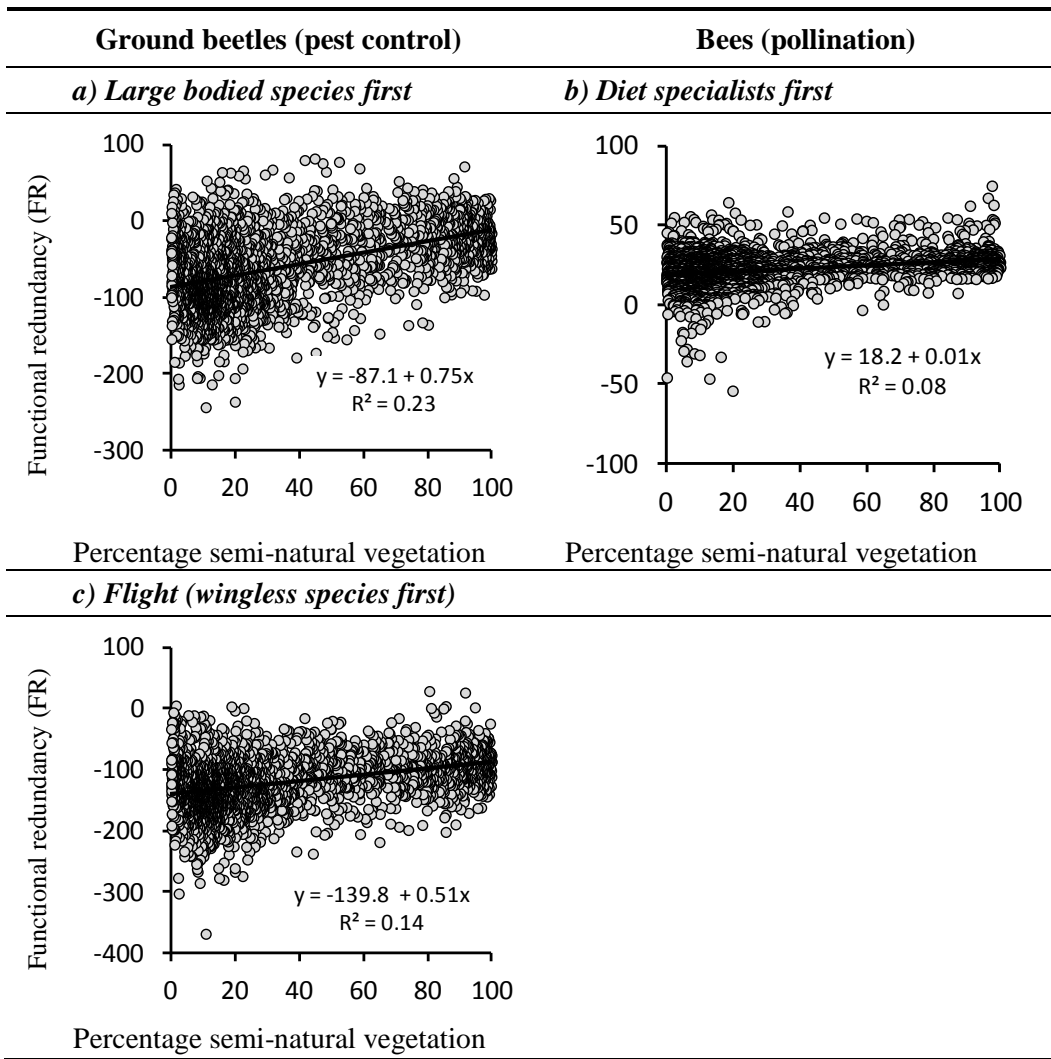
605

606 Fig. 2

607



608 **Fig 3**



609

610

611 **Tables 1**
612

Ground beetles (pest control)	Bees (pollination)
Efficiency in delivering pest control / pollination	
<p>Diet specialisation (<i>Collembola</i> specialists, obligate predators and omnivores): The range of potential pest species eaten will affect natural pest control.</p> <p>Visual and sensory acuity (<i>ratios of Eye: head width and Antennae: body length</i>): Defines the relative size of key sensory organs used during hunting and foraging (Bauer <i>et al.</i>, 1998; Ribera <i>et al.</i>, 1999; Woodcock <i>et al.</i>, 2010).</p> <p>Feeding rate (body mass): Body size (mg) affects partitioning of prey types between species (Radloff & DuToit, 2004), is positively related to feeding rates (Juliano, 1986) and negatively related to reproductive output (Kotze & O'Hara, 2003).</p>	<p>Diet specialisation (<i>polylectic vs. oligolectic</i>): The range of plants foraged upon will affect specificity to the crop and ability to persist on secondary resources across complex landscapes (Williams <i>et al.</i>, 2010).</p> <p>Temporal range of pollinating activity: These are defined by i) the start month of the flight period, and ii) the total duration of flight period (months). This will influence the likelihood on congruence of bees with flowering crops.</p>
Mobility and utilisation of complex landscape structure	
<p>Foraging range (<i>Femora width: length ratio</i>): Used as an index of walking speed and so potential area covered foraging (Forsythe, 1983; Ribera <i>et al.</i>, 1999).</p> <p>Flight (<i>Wings full, absent or dimorphic</i>): Presence of wings affect dispersal ability and utilisation of fragmented landscapes (Kotze & O'Hara, 2003)</p>	<p>Foraging range (<i>Intertegular distance categorised as 1-3mm, 3-4, 4-6mm and > 6mm</i>): Intertegular distance is correlated with bee foraging ranges (Greenleaf <i>et al.</i>, 2007) and so affect resource utilisation across complex landscapes (Bommarco <i>et al.</i>, 2010). As intra-specific range in ITD can be large it was treated as categorical.</p>
Biology and behaviour	
<p>Diurnal activity (<i>nocturnal, diel or both</i>): Activity period will influence what pests are likely to be encountered, their activity rates on an off plants and so inter-specific resource partitioning (Luff, 1978).</p> <p>Breeding period (<i>autumn/winter or spring/summer</i>): Breeding periods affect activity rates and so encounter with prey throughout the year, and can influence rates of colonisation of arable fields after winter (Wamser <i>et al.</i>, 2011).</p>	<p>Social behaviour (<i>social or solitary</i>): As social bees are more sensitive to pesticides increased diversity in this trait will promote pollination under typical agricultural management (Williams <i>et al.</i>, 2010).</p> <p>Nesting behaviour (<i>mining, cavity nesting or other</i>): Affects sensitivity to tillage regimes and so persistence under different agricultural management (Williams <i>et al.</i>, 2010).</p> <p>Brood number (<i>single, double or continuous</i>): May influence population recovery rates after agricultural management.</p>

613
614 **Table 1.** Traits used to define functional diversity and redundancy of natural pest control and
615 pollination services delivered by ground beetles and bees.

616
617