

# 1 Multi-taxa consequences of management for an avian umbrella species

## 2 Abstract

3 Whether management for so-called umbrella species actually benefits co-occurring biota has rarely  
4 been tested. Here, we studied consequences for multiple invertebrate taxa of two ground-  
5 disturbance treatments designed to support an avian umbrella species (Eurasian stone-curlew,  
6 *Burhinus oediconemus*), and whether analysing ecological requirements across the regional species  
7 pool predicted beneficiaries. Responses were assessed for the abundance of five bird species of  
8 conservation concern, and the abundance, species richness and composition of carabids,  
9 staphylinids, other beetles (non-carabid, non-staphylinid), true bugs and ants, sampling 31258  
10 individuals of 402 species in an extensively-replicated experiment across the UK's largest grass-  
11 heath. Both treatments provided suitable habitat for the umbrella species, in contrast to controls.  
12 Treatment influenced the abundance of only one bird species; but carabid, other beetle and ant  
13 richness increased with one or both treatments, while staphylinid richness and abundance increased  
14 and true bug richness and abundance decreased with both treatments. Richness of 'priority' (rare,  
15 scarce or threatened) invertebrates *a priori* considered to share ecological requirements with the  
16 umbrella species (predicted beneficiaries) increased with both treatments. Resampling and  
17 rarefaction showed landscapes diversified by treatment supported a greater cumulative species  
18 richness of other beetles, ants and true bugs, and importantly priority invertebrates, than a  
19 landscape comprising only untreated controls. Such experiments provide strong evidence to assess  
20 co-benefits of umbrella species management, but are costly and time consuming. The systematic  
21 examination of the autoecological requirements of co-occurring taxa (the 'Biodiversity Audit  
22 Approach') successfully predicted likely beneficiaries. Demonstrating wider biodiversity benefits  
23 strengthens the case for avian conservation management.

24 **Keywords:** Surrogate species, conservation management, Eurasian stone-curlew, *Burhinus*  
25 *oediconemus*, invertebrate conservation, grassland

## 26 1. Introduction

27 Major taxonomic biases exist in conservation (Fazey et al. 2005; Troudet et al. 2017). Thus, whilst  
28 some groups have received considerable attention (e.g. vertebrates, Clark and May 2002), others  
29 have not, with conservation practitioners often lacking information on which species are present  
30 within a region, which ought to be prioritized, and the management interventions each requires  
31 (Dolman et al. 2012). Single-species surrogates (e.g. 'umbrella' species), especially those that garner  
32 public support and funds for conservation ('flagship' species) are often used to drive ecosystem  
33 management (Hunter et al. 2016). However, tests of the wider biodiversity consequences of their  
34 subsequent conservation have rarely been conducted (Branton and Richardson 2011; Roberge and  
35 Angelstam 2004).

36 Traditional tests of the umbrella species concept examine whether the overall richness or  
37 abundance of other species (generally a single taxon or a limited species subset) is higher where the  
38 umbrella species is present (e.g. Suter et al. 2002), or whether they occupy similar habitats (e.g.  
39 Maslo et al. 2016; Sibarani et al. 2019). Whilst such tests may be appropriate for determining where  
40 in the landscape protection should occur (Caro and O'Doherty 1999; Fontaine et al. 2007), they do  
41 not establish whether interventions designed for the umbrella species benefit either wider  
42 biodiversity, or co-occurring species of conservation concern. Within 'semi-natural' habitats, where  
43 conservation requires management interventions that modify vegetation composition and/or  
44 structure (Webb 1998; Wright et al. 2012), experiments that evaluate responses to trial  
45 prescriptions, across multiple taxa, provide the necessary evidence-base to allow the beneficiaries of  
46 umbrella species management to be appraised.

47 Here, we test the consequences of habitat management for Eurasian stone-curlew (*Burhinus*  
48 *oedicnemus*, hereafter 'stone-curlew'), a UK threatened (Stanbury et al. 2017), high-profile species  
49 protected under European legislation (EC 1979) and widely accorded 'flagship' status, not only for a  
50 set of other bird species of conservation concern, but also for multiple invertebrate groups. We  
51 selected stone-curlew because they breed in managed semi-natural landscapes, where their  
52 requirement for bare-open grassland is well-known (Green et al. 2000). Additionally, a systematic  
53 bioregional process that classified species with shared autecological requirements into multi-taxa  
54 'management guilds' (the 'Biodiversity Audit Approach'; Dolman et al. 2012), suggests many  
55 nationally rare, scarce or threatened species (hereafter 'priority' species) should benefit from similar  
56 conditions (see details in Appendix A). However, without validating this experimentally, it is unclear  
57 whether management designed for the umbrella species does indeed improve the status of the  
58 intended beneficiaries, or whether such gains are offset by reductions in other priority species.

59 We thus devised an extensively replicated landscape-scale experiment across the UK's  
60 largest (3850 ha) lowland grass-heath (66 treatment plus 36 control plots, total 204 ha) to examine  
61 outcomes of ground-disturbance interventions designed to benefit stone-curlew. Responses were  
62 examined for priority bird species and five invertebrate groups, each speciose and taxonomically  
63 well-resolved. Although extensive, the assessment of biodiversity is incomplete, as we lacked  
64 expertise (fungi, bryophytes, soil macro-fauna), or personnel (vascular plants) to sample other  
65 important elements. First, we *a priori* predicted that our treatments would create suitable stone-  
66 curlew nesting habitat. Next, we predicted that treatment would increase the abundance of birds  
67 and the abundance and species richness (hereafter 'richness') of some invertebrates groups, while  
68 diversifying invertebrate composition. We specifically hypothesized treatment would increase the  
69 richness of priority invertebrates associated with physically-disturbed and/or heavily-grazed  
70 grassland, but decrease the richness of those associated with lightly-grazed undisturbed grassland.  
71 We further predicted that the entire landscape with treatments and controls would support greater  
72 cumulative richness of each invertebrate group, and of overall priority species, relative to a control-  
73 only landscape.

74

## 75 2. Methods

### 76 2.1. Study area

77 The study was carried out in Breckland, a bio-geographic region (1000 km<sup>2</sup>) of Eastern England  
78 characterised by a semi-continental climate and sandy soils that supports over 2000 priority plant  
79 and invertebrate species (26% of all UK priority species, Dolman et al. 2012). Multi-taxa responses to  
80 ground-disturbance treatments were examined across grass-heath (lightly-grazed undisturbed  
81 grassland) on the Stanford Military Training Area (STANTA) (0°76'E, 52°51'N, 3500 ha), Bridgham  
82 Heath (0°83'E, 52°44'N, 150 ha) and Brettenham Heath (0°83'E, 52°43'N, 200 ha) (see Appendix B for  
83 study area details, and Fig. A.2 for map).

84

### 85 2.2. Experimental treatments

86 Between January and early May 2015, 66 treated plots (33 deep- and 33 shallow-cultivated) and 36  
87 uncultivated controls, each 2 ha (a size advocated for stone-curlew, Appendix A), were located at  
88 least 100 m apart in open grass-heath mostly excluding, but sometimes near, scattered trees or  
89 scrub. Shallow-cultivations were created with a rotovator, which broke up and turned the surface  
90 (10 - 13 cm), and deep-cultivations with an agricultural plough, which inverted soil and vegetation  
91 (25 - 28 cm) bringing up mineral sub-soil. Following usual conservation practice, shallow-cultivated  
92 plots were immediately retreated if the first attempt failed to create sufficient exposed bare  
93 substrate (>50%). Four plots (two shallow-cultivated, two deep-cultivated), located within dense  
94 heather (*Calluna vulgaris*), were topped with a tractor-mounted flail prior to disturbance. Plots with  
95 regenerating thistle (*Cirsium arvense*, *Cirsium vulgare*) or common nettle (*Urtica dioica*) were  
96 topped, also with a flail, in late June and July.

97 The risk posed by unexploded ordnance precluded cultivation treatments in the central  
98 STANTA 'impact area', restricting treatments to outer areas of STANTA, plus Bridgham and  
99 Brettenham Heaths. Thus constrained, treatments and controls were randomly allocated to plots  
100 within four strata, based on soil (NSRI 2014), age since cultivation (Sheail 1979) and plant  
101 composition; these were calcareous grass-heath of any age (hereafter 'calcareous grass-heath'),  
102 young grass-heath ( $\leq 110$  years old), intermediate grass-heath (111-167 years old), and ancient-acid  
103 grass-heath ( $\geq 168$  years old) (see Table A.1 for details). Both treatments and controls were  
104 distributed similarly with respect to Latitude and Longitude (Kruskal-Wallis,  $H = 0.79$ ,  $p = 0.67$ ;  $H =$   
105  $0.46$ ,  $p = 0.79$ , respectively;  $n = 102$ ), but vegetation strata (four groups) were not (Latitude,  $H =$   
106  $19.26$ ,  $p < 0.001$ ; Longitude,  $H = 47.19$ ,  $p < 0.001$ ;  $n = 102$ ) (Fig. A.2).

107

### 108 2.3. Responses to treatment

109 In June 2015, we assessed habitat suitability for stone-curlew within a randomly selected half (1 ha  
110 subplot) of each 2 ha plot. We recorded vegetation height using a sward stick (diameter 90 mm,  
111 weight 250 g; following Green and Griffiths 1994) at 42 points distributed evenly along two parallel  
112 100 m transects (placed 30 - 33 m apart), and also whether bare substrate covered over 50% at each  
113 point (25 mm diameter), giving incidence from 0 to 42. Where an individual height measurement (on  
114 treatment plots) exceeded 2.5 cm due to uneven topography caused by soil disturbance, a new  
115 measurement was taken in a different cardinal direction. Vegetation structure of deep-cultivated,  
116 shallow-cultivated and control plots was related to thresholds of stone-curlew nesting habitat  
117 suitability informed by *a priori* knowledge (see Appendix A) of the species preferences for grass-  
118 heath vegetation height and bare ground cover (here quantified as the proportion of 42 sampled  
119 points in each plot); examining whether modelled 95% CI limits were <2 cm and >40%, respectively.

120 Birds and ground active invertebrates were also sampled in 2015. Bird sampling was  
121 conducted at the scale of the whole 2 ha plot whilst invertebrate sampling was conducted in the  
122 same 1 ha subplot as the vegetation structure sampling. Bird responses were examined across all  
123 plots, whereas invertebrate responses were examined across 20 deep-cultivated, 20 shallow-  
124 cultivated and 16 control plots located outside the impact area, to limit risks from unexploded  
125 ordnance.

126 Bird abundance was sampled for five species of UK conservation concern, defined as 'Red' or  
127 'Amber' listed (Eaton et al. 2015); woodlark (*Lullula arborea*), yellowhammer (*Emberiza citronella*),  
128 common linnet (*Linaria cannabina*), Northern lapwing (*Vanellus vanellus*), and Eurasian curlew  
129 (*Numenius arquata*). Abundant, ubiquitous breeding species (e.g. skylark, *Alauda arvensis*), were not  
130 considered. Analyses considered the maximum number of individuals detected on any one of three,  
131 40-minute visits, made to each plot between 1 April and 31 May (mean visit interval: 13.8 days  $\pm$  6.5  
132 SD) between dawn and 11:00 during dry, still mornings (Beaufort wind force <4), with at least one  
133 week between plot establishment and the first survey to allow territory settlement. During visits, we  
134 recorded individuals on, or singing directly above, the plot; initially from a vehicle, followed by  
135 walking through the plot edge and center. Observations were restricted to vehicles for three of 306  
136 plot-visits (affecting three deep-cultivated treatments) to minimize disturbance to breeding stone-  
137 curlew; for these vehicles were repositioned to maximize coverage.

138 Invertebrates on each plot were sampled using six pitfall traps (11 cm depth, 8 cm diameter,  
139 covered with 12 mm wire mesh, with 50 ml of a saturated salt solution, NaCl), set 15 m apart in a 15  
140 m x 30 m grid, opened for seven consecutive days, separately in each of June, August and October.  
141 Samples were pooled across pitfalls and months giving one composite sample per plot. Subsequent  
142 analyses controlled for cumulative 'trap-days' arising from partially-successful (considered inactive  
143 for half the exposure period) or failed traps (considered inactive for the whole exposure period), and  
144 unavoidable, though slight, variation in exposure (traps on two deep-cultivated, one shallow-  
145 cultivated, and one control plot were deployed two days longer in August due to military  
146 restrictions, affecting 2.4% of all seven-day plot deployments).

147 Invertebrates within five groups were identified to species: carabid, staphylinid, all other  
148 beetles, true bugs (but excluding aphids), and ants. Following Dolman *et al.* (2012), priority species  
149 were identified as those designated as: (i) threatened (critically endangered, endangered and  
150 vulnerable) or near-threatened based upon red list guidelines developed by the International Union  
151 for Conservation of Nature; or (ii) Nationally Rare (NR) and Nationally Scarce (NS), or the older  
152 designations of Red Data Book (RDB) and Nationally Notable (Na, Nb). A few beetles (1.2%) and true  
153 bugs (1.9%) were only identifiable to genus, or a group of species (Table A.2).

154 Following Dolman *et al.* (2012), priority invertebrate species with similar autecological  
155 requirements were grouped into 'management guilds', which allowed us to classify those species  
156 associated with dry-open terrestrial habitats (excluding other habitats) as either requiring physical  
157 disturbance or heavy grazing to create bare ground or short-open turf (hereafter 'disturbed-  
158 grassland' species), or associated with lightly-grazed and physically undisturbed to only lightly-  
159 disturbed conditions (hereafter 'undisturbed-grassland' species) (Table A.2).

160

## 161 **2.4. Data analysis**

162 Separate analyses considered: vegetation structure (height and bare ground cover, to examine  
163 suitability for the umbrella species); bird abundance (five analyses, one per species); richness and  
164 abundance of each invertebrate group and of priority invertebrates; and richness of disturbed-  
165 grassland and undisturbed-grassland priority invertebrates. Using Generalised Linear Models (GLMs),  
166 we examined fixed effects of treatment (three levels), vegetation strata (initially four levels, see  
167 below), and for invertebrates the cumulative number of trap-days per sample. Ants were omitted

168 from abundance analyses as coloniality can locally inflate abundance. All models were run in R (R  
169 Core Team 2015).

170 For each analysis the appropriate error term (normal, binomial, Poisson, or negative  
171 binomial) was selected by examining the ratio of deviance / residual degrees of freedom of full  
172 (global) models; with normal error, response variables were log or square-root transformed where  
173 appropriate. For parsimony, vegetation strata were combined if parameter estimates were similar  
174 and their merger did not reduce model performance (change in Akaike's Information Criterion  
175 corrected for small sample size,  $\Delta AICc$ , on combination  $\leq 2$ ; Burnham and Anderson 2002); where all  
176 vegetation strata were similar then levels were not combined and subsequent model selection  
177 removed this variable. Next, candidate models comprising all possible variable combinations were  
178 examined using the package 'lme4' (Bates et al. 2017); the top ranked model was considered 'best' if  
179  $\Delta AICc > 2$  relative to the next-ranked model; where competing models were within 2  $\Delta AICc$  the most  
180 parsimonious was selected, as additional variables lacked strong support (Burnham and Anderson,  
181 2002). Where treatment was retained, category means were compared by Tukey's pairwise  
182 comparison. For analyses of vegetation structure and bird abundance, separate models were  
183 examined that considered either all control plots, including those within the central impact area  
184 (where there are no ground-disturbance plots); or that excluded ten 'impact area controls' located  
185  $> 200$  m inside the impact area boundary. Spatial autocorrelation of model residuals was examined  
186 by Moran's  $I$  in the package 'Ape' (Paradis et al. 2004).

187 For each invertebrate group, sampling efficiency of treatments and controls was assessed by  
188 comparing sample-based rarefaction (re-scaled to the number of individuals, using the Mao Tau  
189 function) extrapolated to the predicted asymptote, using the package iNEXT (Hsieh et al. 2018).

190 Assemblage composition of treatments and controls was examined separately for each  
191 invertebrate group by Non-Metric Multidimensional Scaling (NMDS) performed using a Bray-Curtis  
192 dissimilarity-matrix of abundance data (square root transformed with Wisconsin double  
193 standardization, following Clarke and Warwick 2001) using the 'Vegan' package (Oksanen et al.  
194 2018). Invertebrate records not resolved to species, and plots with fewer than three observations for  
195 that group, were omitted. Model performance was assessed by examining stress ( $< 0.05$  excellent;  
196  $< 0.1$  good;  $< 0.2$  potentially useful;  $> 0.3$  close to arbitrary, Clarke and Warwick 2001) and NMDS axis  
197 one and two scores were compared between treatment and control (three levels) using Kruskal  
198 Wallis tests with Dunn-Bonferroni pairwise comparisons ( $p < 0.05$ ).

199 To determine whether diversifying the landscape through umbrella species management,  
200 would support a higher cumulative richness of each invertebrate group and of (multi-taxa) priority  
201 species, we used rarefaction (resampling among plots). Five scenarios were examined: resampling  
202 control plots only ('control-only' landscape); the existing landscape diversified by management for  
203 the umbrella species ('treatment-control' landscapes, resampling either from: control and shallow-  
204 cultivated plots; control and deep-cultivated plots; or control, deep-cultivated, and shallow-  
205 cultivated plots); and a 'treatment-only' landscape (resampling both deep- and shallow-cultivated  
206 plots, but without control plots). For each scenario, sample-based rarefaction was extrapolated to  
207 the sampling intensity (number of individuals) of the full set, examining the overlap in 95% CIs.  
208

## 209 **3. Results**

### 210 **3.1. Stone-curlew habitat suitability**

211 Vegetation height decreased progressively from control to shallow- then deep-cultivation (Fig. 1)  
212 and was lower on pooled young and calcareous than on pooled intermediate and ancient-acid grass-  
213 heath. Conversely, bare ground cover increased from control to shallow then deep cultivation and  
214 was not influenced by vegetation strata (Table A.5). Both treatments, but not controls, provided  
215 habitat suitable for nesting stone-curlew (Fig. 1).

216 Residuals from the bare ground cover model (but not the vegetation height model) were  
217 weakly spatially autocorrelated (Moran's  $I = 0.05$ ), suggesting some variation attributable to a  
218 spatially correlated factor(s) not considered in the modeling. Nevertheless, we consider inference for  
219 treatment effects to be robust, as treatments and controls were distributed randomly and were  
220 balanced across vegetation strata (Table A.1). Impact-area controls were retained in both analyses,  
221 as their inclusion did not affect model inference.

222

### 223 **3.2.1. Management consequences for wider biodiversity**

224 Sampling gave 187 bird registrations, comprising 52 woodlark, 41 Northern lapwing, 49 Eurasian  
225 curlew, 12 yellowhammer, and 33 common linnet; and 31258 invertebrates from 402 species (Table  
226 A.2), including: 4740 carabids from 57 species; 5580 staphylinids from 116 species; 1617 other  
227 beetles from 139 species (largely from 4 families; 498 Curculionidae, 31%; 243 Elateridae, 15%; 216  
228 Chrysomelidae, 13%; 192 Scarabaeidae, 12%); 1874 true bugs from 72 species; and 17447 ants from  
229 18 species. Of the 402 invertebrates, 52 were priority species, including eleven carabids, ten  
230 staphylinids, twenty other beetles, nine true bugs, and two ants. For carabids, staphylinids, other  
231 beetles, and ants, sample-based rarefaction approached the asymptote in treatments and controls  
232 (Fig. A.1) indicating sampling had effectively captured the composition of these assemblages.  
233 However, true bugs were uncommon on, and therefore insufficiently sampled from, deep-cultivated  
234 treatments (but approached the asymptote on controls and shallow-cultivated treatments).

235 Although residuals of the carabid, staphylinid, other beetle, true bug and ant richness and  
236 abundance models (both all species and priority species models) were not spatially autocorrelated,  
237 residuals from two of the five models considering bird abundance (Northern lapwing and Eurasian  
238 curlew) and the priority disturbed-grassland species model (but not the priority undisturbed-  
239 grassland species model) were significantly, though again weakly, autocorrelated (Moran's  $I = 0.05$ ,  
240  $0.04$ , and  $0.09$ , respectively). However, for each affected model, we consider inference of treatment  
241 effects to be robust for the reasons explained above. For the priority disturbed-grassland species  
242 model, where Moran's  $I$  was greatest, removing one particularly abundant species (*Philonthus*  
243 *lepidus*, that comprised 48% of the 471 individuals in this group), removed autocorrelation and gave  
244 similar interpretation.

245

### 246 **3.2.2. Birds**

247 Of the five species considered, treatment only influenced Northern lapwing abundance (Table A.4),  
248 with more recorded on shallow-cultivated treatments than controls (with abundance intermediate  
249 on deep-cultivated treatments, Fig. 2). Vegetation strata influenced woodlark and yellowhammer  
250 abundance (but was not important in other models), with fewer woodlarks on young than pooled  
251 intermediate, calcareous and ancient-acid grass-heath, and more yellowhammers on ancient-acid  
252 than on pooled young, intermediate and calcareous grass-heath (Table A.3 and Table A.5). Impact-  
253 area controls were retained in all analyses, as their inclusion did not affect model inference.

254

255 **3.2.3. Carabids**

256 For all carabids, richness was greater on shallow-cultivated treatments than deep-cultivated  
257 treatments or controls (Fig. 3) and was not influenced by vegetation strata (Table A.4), while  
258 abundance was lower on ancient-acid than pooled young, intermediate and calcareous grass-heath,  
259 but was not influenced by treatment (Table A.3 and Table A.5). For priority carabids, richness and  
260 abundance were greater on the controls than deep-cultivated treatments (while shallow-cultivated  
261 treatments did not differ from controls, they held a greater abundance than deep-cultivated  
262 treatments), and on pooled young, intermediate and calcareous than ancient-acid grass-heath.  
263 Assemblage composition of treatments and controls differed along NMDS axis one (but not axis two,  
264 Fig. 4), with composition contrast relative to controls increasing from shallow to deep-cultivation.

265

266 **3.2.4. Staphylinids**

267 For all staphylinids, richness and abundance were greater on both treatments than controls (Fig. 3),  
268 and for abundance only, on young than pooled intermediate, calcareous and ancient-acid grass-  
269 heath (Table A.5) (though retaining both young and calcareous grass-heath as distinct gave similar  
270 models, Table A.3). For priority staphylinids, neither treatment nor vegetation strata influenced  
271 richness (Table A.4), but abundance was again greater on young grass-heath (again retaining young  
272 and calcareous grass-heath as distinct gave similar models). Composition of treatments and controls  
273 differed along NMDS axis one (but not axis two, Fig. 4), with contrast relative to controls again  
274 increasing from shallow- to deep-cultivation.

275

276 **3.2.5. Other beetles**

277 For all other beetles, richness was greater on shallow-cultivated than deep-cultivated treatments or  
278 controls (Fig. 3), and on pooled young and intermediate than pooled ancient-acid or calcareous  
279 grass-heath (Table A.3 and Table A.5). Abundance was greater on shallow-cultivated than deep-  
280 cultivated treatments, but with controls similar to both and no effect of vegetation strata (Table  
281 A.4). For priority other beetles, richness and abundance were greater on both treatments than  
282 controls (vegetation strata were not important). Composition of shallow- and deep-cultivated  
283 treatments were similar, but differed from controls along both axes (Fig. 4).

284

285 **3.2.6. True bugs**

286 Richness and abundance of true bugs declined from control to shallow- then deep-cultivation (Fig. 3)  
287 and was greater on intermediate than pooled young, calcareous, and ancient-acid grass-heath (Table  
288 A.3 and Table A.5). Neither treatment nor vegetation strata influenced the richness or abundance of  
289 priority true bugs (Table A.4). Composition of treatments differed from controls along NMDS axis  
290 one (Fig. 4), while on axis two controls and shallow-cultivation differed from deep-cultivation.

291

292 **3.2.7. Ants**

293 For all ants, richness was greater on both treatments than on controls (Fig. 3, Table A.5) (vegetation  
294 strata were not important, Table A.4). Neither treatment nor vegetation strata influenced the  
295 richness of priority ants. Composition of shallow- and deep-cultivated treatments were similar, but  
296 differed from controls along NMDS axis two (but not axis one, Fig. 4).

297

298 **3.2.8. Disturbed-grassland and undisturbed-grassland priority invertebrates**

299 Of the 52 priority invertebrate species, 22 (471 individuals) and 19 (287 individuals) were classified  
300 as disturbed-grassland and undisturbed-grassland species, respectively (ten were not principally  
301 associated with dry-open terrestrial habitats, and for one, insufficient autecological information  
302 prohibited classification, see Table A.2). Richness of disturbed-grassland species was greater on both  
303 treatments than controls, whilst the richness of undisturbed-grassland species was not influenced by  
304 treatment (Fig. 5). Pooled young, intermediate and calcareous grass-heath held a greater richness of  
305 disturbed-grassland and undisturbed-grassland species than ancient-acid grass-heath (Table A.5);  
306 though disturbed-grassland models which retained intermediate and ancient-acid grass-heath as  
307 distinct, or all vegetation strata categories as distinct, were similar (Table A.3).

308

### 309 **3.3. Landscape-scale management consequences**

310 Extrapolated rarefaction curves showed that the cumulative richness of other beetles, true bugs,  
311 ants, and priority invertebrates (but not of carabids or staphylinids) increased when both treatments  
312 were combined with controls (treatment-control landscape), relative to the control-only landscape  
313 (Fig. 6). Scenarios that re-sampled controls plus only one treatment, or both treatments but not  
314 controls (the treatment-only landscape), gave greater cumulative richness of other beetles, ants and  
315 priority invertebrates, compared to the control-only landscape, but did not differ from resampling  
316 controls plus both treatments. For true bugs, resampling either deep-cultivated and control plots, or  
317 a treatment-only landscape, increased cumulative richness relative to the control-only landscape;  
318 however resampling shallow-cultivated plus control plots did not. For staphylinids, a treatment-only  
319 landscape gave lower cumulative richness than any treatment-control landscape, but not than the  
320 control-only landscape.



## 321 4. Discussion

322 We quantified the multi-taxa consequences of stone-curlew management through a well-replicated  
323 landscape-scale experiment making over 200 bird observations and obtaining 30000 invertebrate  
324 records. Both treatments, unlike controls, supported suitable stone-curlew nesting habitat, and five  
325 treatment plots (four deep-cultivated, one shallow-cultivated, but not controls) were colonized by  
326 breeding pairs during this study (2015) (confirmed during avian surveys or additional follow up  
327 visits). Whilst staphylinid richness / abundance and ant richness increased with both treatments, and  
328 carabid richness, other beetle richness, and Northern lapwing abundance increased with shallow-  
329 cultivated treatments (but not deep-cultivated), the richness / abundance of one group (true bugs)  
330 declined with both treatments. However, the richness of disturbed-grassland priority invertebrate  
331 species (predicted beneficiaries) increased with both treatments, invertebrate assemblage  
332 composition differed between treatments and controls for every group, and diversified landscapes  
333 with treatments and control plots supported a higher cumulative richness of ants, other beetles,  
334 true bugs, and priority invertebrates, than a control-only landscape.

335

### 336 4.1. Contrasting taxonomic responses

337 Treatment only influenced Northern lapwing abundance from the five bird species studied  
338 (increased with shallow-cultivation); though woodlark subsequently increased when management  
339 was re-applied annually, and was then greater on both treatments than controls (Hawkes et al.  
340 2018). Either shallow-cultivation, or both shallow- and deep-cultivation, were associated with  
341 increased staphylinid, carabid, other beetle and ant richness, as well as staphylinid abundance, but  
342 lower true bug richness and abundance. Consistent with evidence from Swedish semi-natural  
343 grasslands, where different taxa have contrasting habitat-process requirements (Vessby et al. 2002),  
344 our results demonstrated that whilst stone-curlew management benefitted some groups, others  
345 were disadvantaged. When only priority species were considered, only the richness and abundance  
346 of priority carabids (that declined with deep- but not shallow-cultivation) and other beetles (that  
347 increased with both treatments) were influenced by treatment. Importantly, just four of the 52  
348 priority species were found exclusively on controls, of which two, *Harpalus pumilus* and *Leiodes*  
349 *longipes*, are regarded as NR / RDB. Thus, although the richness / abundance of priority species was  
350 similar among treatment and control plots for most groups, few species were lost entirely though  
351 treatment.

352 Invertebrate assemblage composition differed between treatments and controls for all five  
353 groups, probably because the open sparsely-vegetated structure created by treatments promoted  
354 the warmer micro-climate (Krämer et al. 2012) required by thermophilous species (Cameron and  
355 Leather 2011; Pedley et al. 2013), whilst controls retained the taller vegetation and plant  
356 assemblage required by many herbivores (Woodcock and Pywell 2010). Interestingly, this difference  
357 increased progressively from control to shallow- then deep-cultivation for carabids, staphylinids and  
358 true bugs, consistent with the observed increase in extent of bare ground from controls (largely  
359 closed swards), through shallow-cultivation then greatest in deep-cultivation (almost entirely bare)  
360 (Fig. 1).

361 Our knowledge that stone-curlew and large numbers of priority species share similar  
362 management requirements (informed by Biodiversity Auditing, Dolman et al. 2012) provides us with  
363 an important justification for regarding the bird as an umbrella species, but establishing whether  
364 these species respond as expected is important. In agreement with our *a priori* prediction, the  
365 richness of disturbed-grassland priority invertebrates, the predicted beneficiaries, increased with  
366 both treatments. It is noteworthy that sampling revealed 22 priority disturbed-grassland species  
367 within eight months of treatment establishment, as many of the most range-restricted species  
368 within this region are often absent from isolated suitable habitat (Bertoncelj and Dolman 2013; Lin  
369 et al. 2006). We anticipate more disturbed-grassland associated priority species will gradually

370 accrue, as reported for specialist carabids and plants in response to similar ground-disturbance  
371 management (Pedley et al. 2013).

372

#### 373 **4.2. Consequences of landscape diversification and transformation**

374 Thus far we have examined how birds and invertebrates differed in richness (alpha diversity),  
375 abundance and composition between treatments and controls. Whilst this demonstrates the  
376 consequences of management, focal-species conservation is rarely implemented across entire  
377 landscapes. We were therefore particularly interested in the effects management might have on  
378 total species-richness (beta diversity) by diversifying the landscape.

379 Resampling a hypothetical landscape comprising treatments plus controls, gave greater  
380 cumulative richness of ants, other beetles, true bugs and priority invertebrates compared to a  
381 control-only landscape. However, the decision to implement either one, or both, treatments did  
382 little to influence this outcome in all but one instance (true bug richness did not increase with the  
383 addition of shallow-cultivations). This reflects that, although invertebrate assemblage composition  
384 tended to be distinctly different between treatments and controls (Fig. 4), the two treatments  
385 tended to show at least some (carabids) or considerable (other beetles, ants) overlap in  
386 composition. Differences between our hypothetical intervention (treatment-only or treatment-  
387 control) and non-intervention (control-only) landscapes are consistent with other studies, which  
388 show a positive relationship between richness or abundance and landscape heterogeneity (Smith et  
389 al. 2010; Weibull et al. 2000). Considering a hypothetical treatment-only landscape lacking any  
390 undisturbed grassland gave a greater cumulative richness of ants, other beetles, true bugs and  
391 priority invertebrates, than a control-only landscape, but fewer staphylinids than any control-  
392 treatment landscape. This suggests that conservation scenarios that diversify but do not entirely  
393 replace grasslands through stone-curlew management, would support the most species.

394

#### 395 **4.3. Consequences for Biodiversity conservation of grassland and heath**

396 Lowland heath and dry (chalk, acid or dune) grasslands have distinct assemblages but similar  
397 ecological processes (Rodwell 1991, 1992); and biodiversity response to management (Dolman et al.  
398 2012). In this mosaic of soils (podsol to rendzina) and grass-heath age, vegetation strata influenced  
399 woodlark and yellowhammer abundance; carabids, staphylinids, other beetles, and true bugs  
400 richness / abundance; and cross-taxa richness of both disturbed and undisturbed-grassland priority  
401 species. Crucially, no stratum was consistently better than others, which is unsurprising given  
402 grassland invertebrates differ in their habitat preference (Woodcock and Pywell 2010).

403 Invertebrate assemblage composition consistently differed between treatments and  
404 controls, though richness / abundance (alpha diversity, per plot) did not increase for all groups.  
405 Focusing on priority invertebrates, just two groups (carabids and other beetles) were influenced by  
406 treatment, while for those priority species associated with disturbed-grassland (i.e. predicted  
407 beneficiaries) cross-taxa richness increased with both treatments, consistent with our *a priori*  
408 prediction. Combining ground-disturbance management with controls increased the cumulative  
409 landscape-wide richness (beta-diversity) of most invertebrate groups, and importantly of priority  
410 invertebrates across groups. It is on this basis that we conclude that stone-curlew represent a  
411 suitable management surrogate within this landscape, and recommend strategies that promote  
412 heterogeneity by implementing stone-curlew management, across vegetation strata, whilst also  
413 maintaining undisturbed grassland. Further work will investigate whether the immediate benefits  
414 observed by this study are retained with follow-up management (e.g. repeat disturbance to maintain  
415 open habitats), or whether retaining some plots fallow beyond their suitability for stone-curlew  
416 offers different outcomes to broader biodiversity

## 417 **5. Conclusion**

418 Because the requirements of single species rarely embrace the requirements of all co-occurring  
419 biota, the appropriateness of the umbrella species concept has been questioned (e.g. Roberge and  
420 Angelstam 2004). However, most tests of efficacy fail to consider the consequences of umbrella  
421 species management on other biota; the appropriate appraisal within semi-natural landscapes,  
422 where adoption of umbrella species drives interventions beyond site protection (e.g. Thornton et al.  
423 2016). Our study demonstrated that appropriate experiments can provide strong evidence to assess  
424 both co-beneficiaries and the disadvantaged from umbrella species management. Importantly,  
425 responses differed strongly between taxa suggesting that experimental tests of surrogacy must be  
426 broad in taxonomic scope. A precautionary approach, to retain areas untreated, is also advised given  
427 uncertain responses of unsampled taxonomic groups.

428         Whilst experiments such as ours provide the best means of assessing umbrella species  
429 management efficacy, they are costly and time consuming. Systematically examining autoecological  
430 requirements across multiple co-occurring taxa (the 'Biodiversity Audit Approach') successfully  
431 predicted the beneficiaries of umbrella management in our study and may offer a feasible  
432 alternative. Here, we were able to test these *a priori* expectations with an experiment, with both our  
433 results and existing autoecological knowledge providing important justification for the widespread  
434 adoption of avian conservation management. Similar approaches would be valuable in regions with  
435 high concentrations of priority species, especially where management interventions currently focus  
436 on a limited, unrepresentative and biased subset of species.

437

438

439 **Supplementary data**

440 Supplementary data to this article can be found online at:

441 **Literature cited**

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## Figures

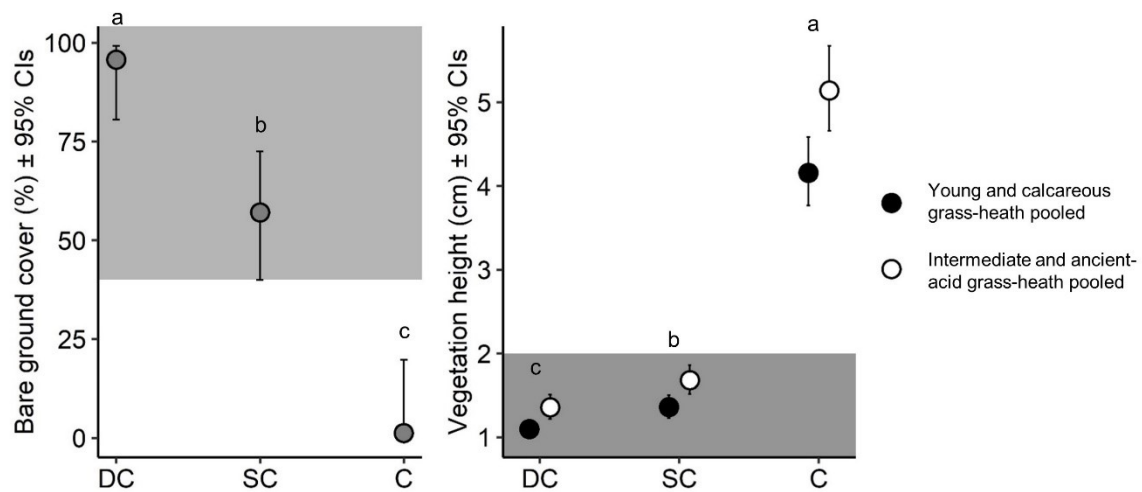


Figure 1. Bare ground cover and vegetation height across deep-cultivated (DC), shallow-cultivated (SC) and control (C) grass-heath plots ( $n = 102$ ). Showing means and 95% CI (bars) from Generalized Linear Models that included the fixed effect of treatment (three levels, both models), and vegetation strata in the bare ground cover model (two categories, see legend); means that share a superscript (homogenous sub-sets, a – c) do not differ significantly (Tukey pairwise comparisons  $p > 0.05$ ). Shading denotes limits of suitable Eurasian stone-curlew *Burhinus oedicnemus* nesting habitat. See Table A.5 for selected models.



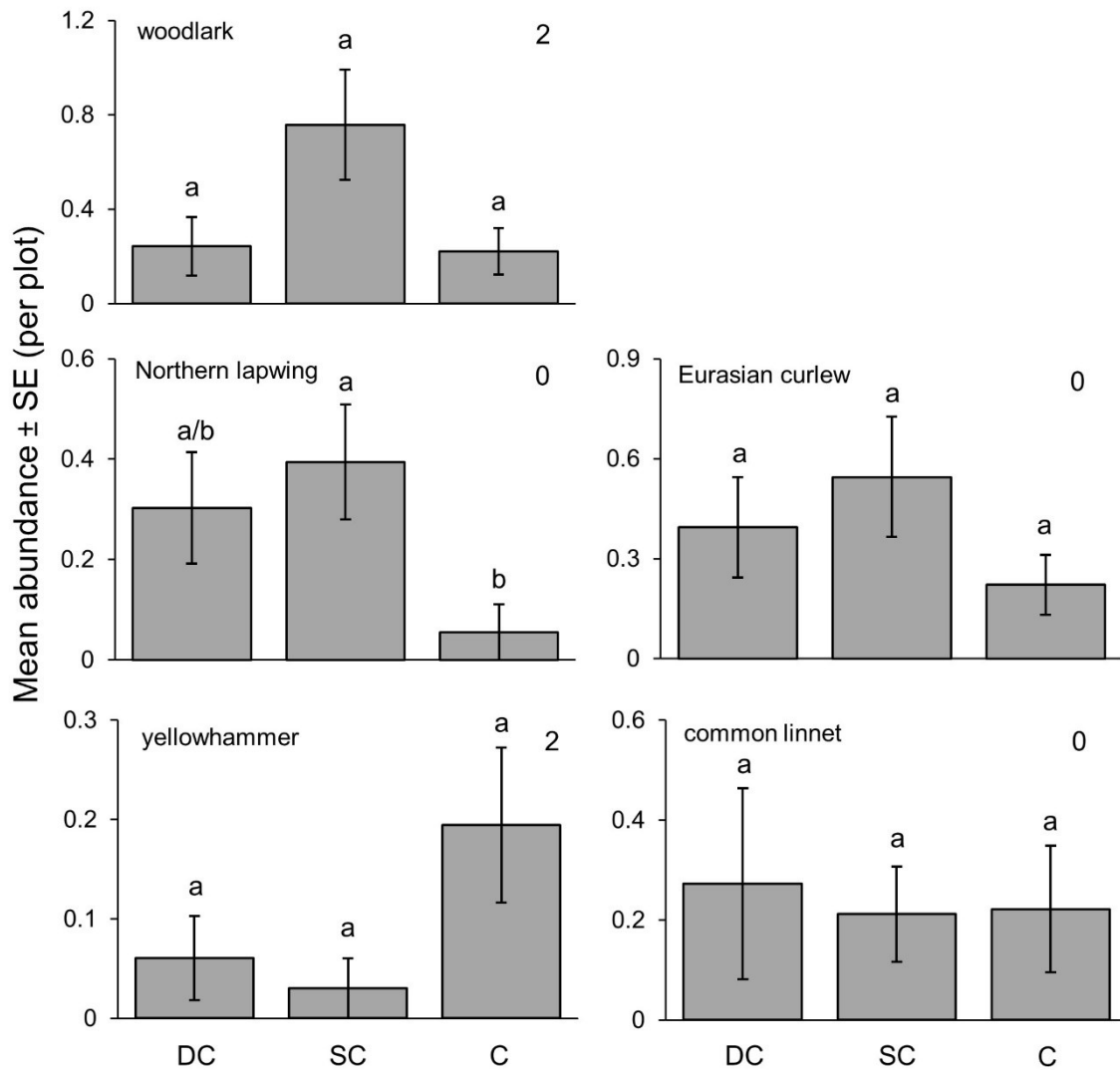


Figure 2. Observed mean ( $\pm$  S.E.) abundance of five bird species of conservation concern across deep-cultivated (DC), shallow-cultivated (SC), and control (C) grass-heath plots ( $n = 102$ ). Treatments and controls were compared by Generalized Linear Models, controlling for vegetation strata (panels show the number of categories in each analysis, see Table A.3 for identities; '0' indicates vegetation strata is excluded from the model); means that share a superscript (homogenous sub-sets, a – b) did not differ significantly (Tukey pairwise comparisons  $p > 0.05$ ). See Table A.5 for selected models.

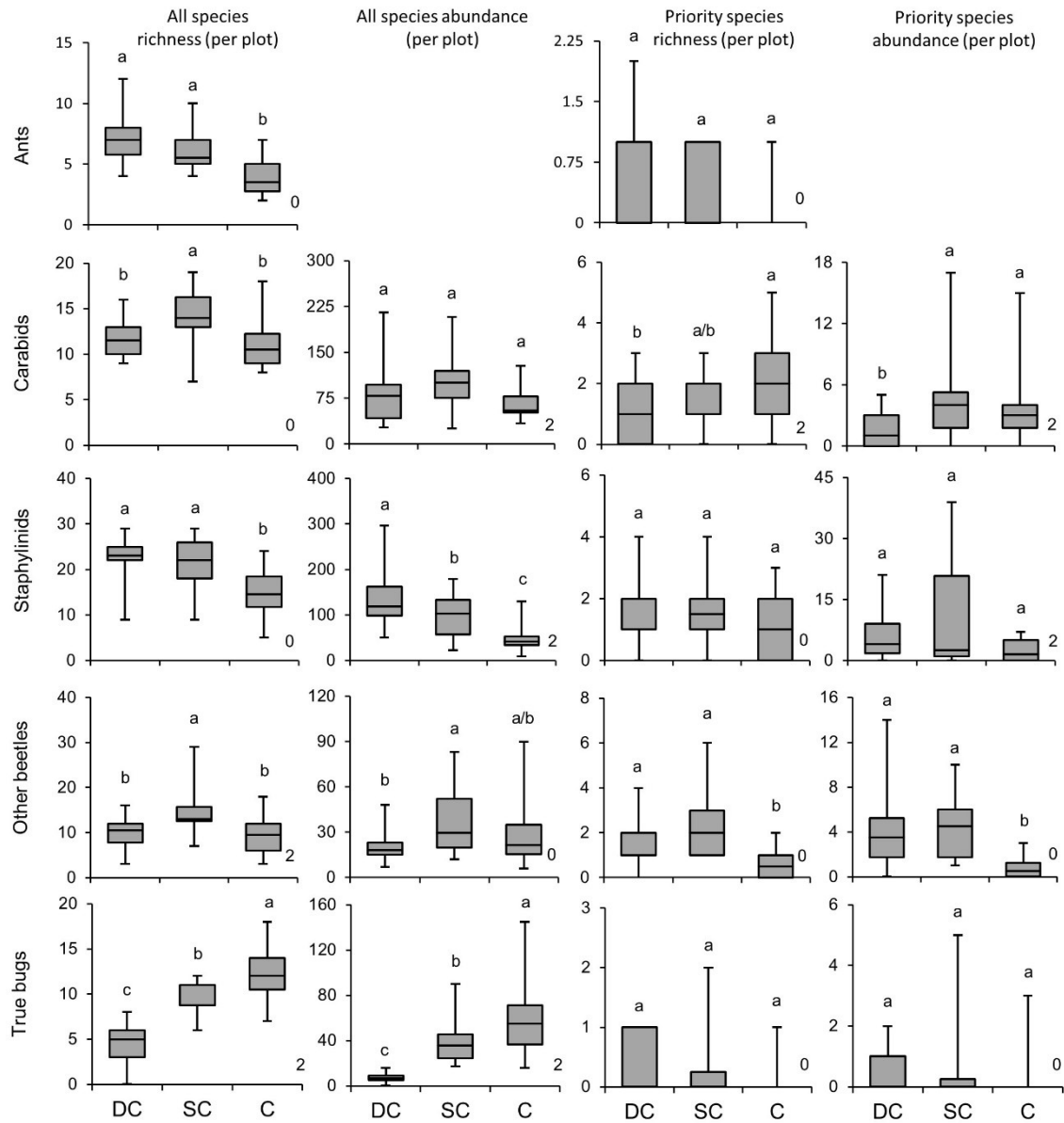


Figure 3. Observed richness and abundance of all species or just priority (rare, scarce or threatened) species, separately for each of five invertebrate groups, across deep-cultivated (DC), shallow-cultivated (SC) and control (C) grass-heath plots ( $n = 56$ ). Treatments and controls were compared by Generalized Linear Models controlling for vegetation strata (panels show the number of categories in each analysis, see Table A.3 for identities; '0' indicates vegetation strata is excluded from the model); means that share a superscript (homogenous sub-sets, a – c) did not differ significantly (Tukey pairwise comparisons  $p > 0.05$ ). Box plots show the median (central line), 25<sup>th</sup> and 75<sup>th</sup> percentiles (box) and range (whiskers).

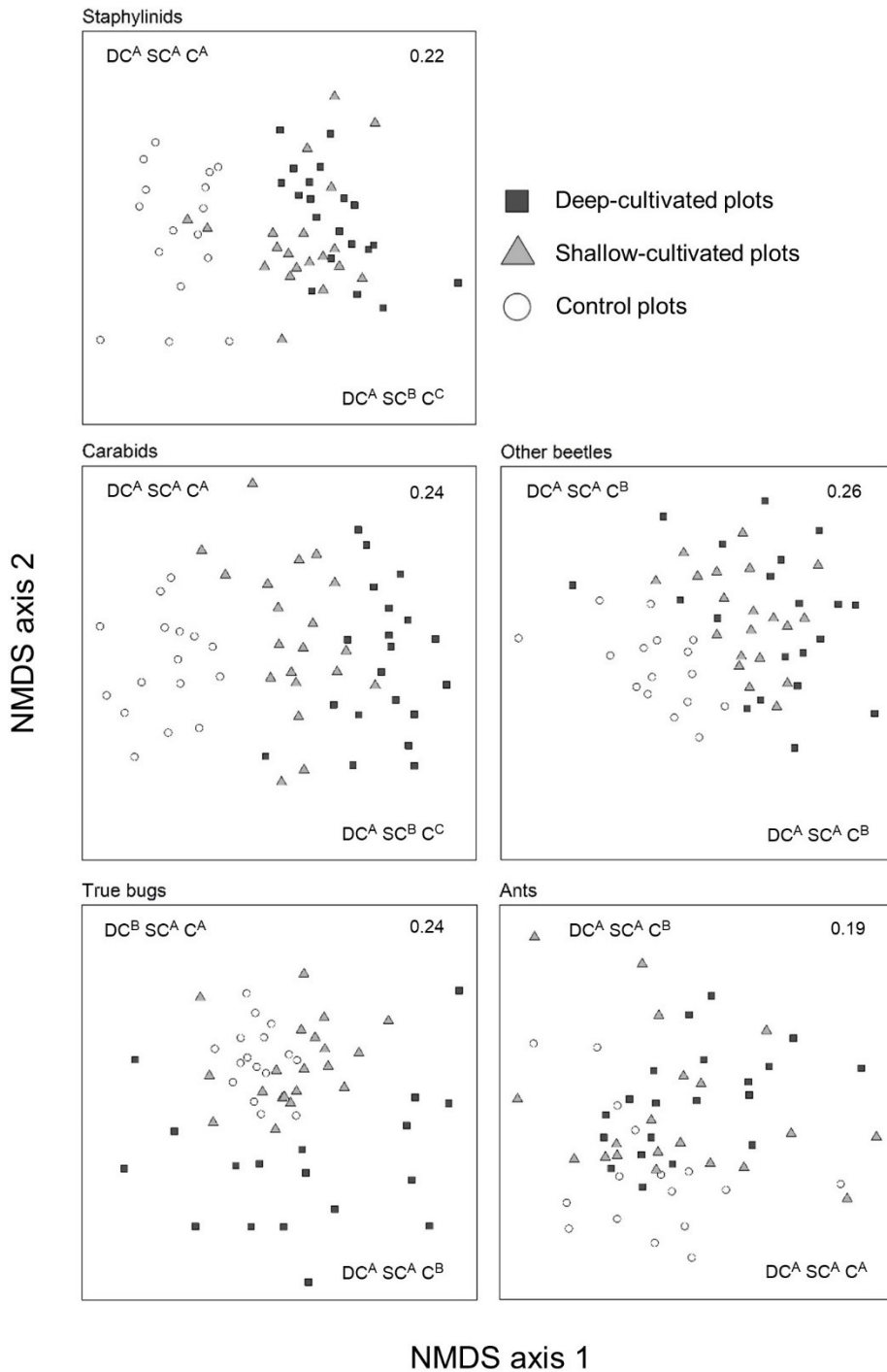


Figure 4. Non-metric Multidimensional Scaling (NMDS) ordination for each of five invertebrate groups across deep-cultivated (DC), shallow-cultivated (SC), and control (C) plots ( $n = 56$ ; except for true bugs  $n = 54$  as two deep-cultivated plots with fewer than three observations were omitted). Differences between axis scores of treatment and control plots were compared through Kruskal Wallis tests; categories that share a superscript (homogeneous subset, a-c ranked highest to lowest) do not differ significantly (Dunn-Bonferroni pairwise comparisons  $p < 0.05$ ), reported separately for axis 1 (bottom right) and axis 2 (top left) on each. Stress values are shown on each (top right).

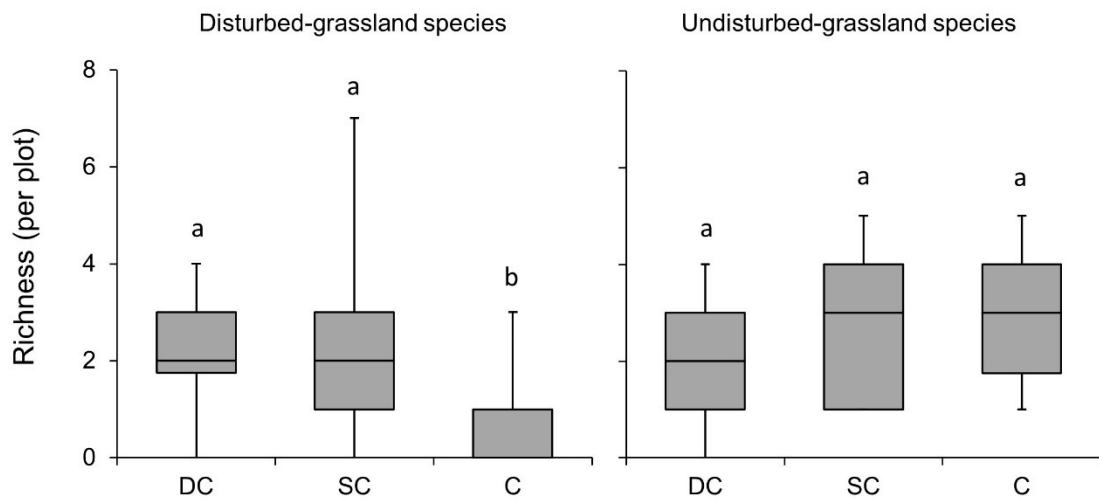


Figure 5. Observed cross-taxa richness of priority (rare, scarce or threatened) invertebrate species, shown separately for those associated with disturbed (i.e. physically-disturbed and/or heavily-grazed) grassland or with undisturbed grassland, across deep-cultivated (DC), shallow-cultivated (SC) and control (C) grass-heath plots ( $n = 56$ ). Treatments and controls were compared by Generalized Linear Models controlling for vegetation strata (ancient-acid grass-heath vs pooled young, intermediate and calcareous grassland); means that share a superscript (homogenous sub-sets, a – b) do not differ significantly (Tukey pairwise comparisons  $p > 0.05$ ). Box plots show the median (central line), 25<sup>th</sup> and 75<sup>th</sup> percentiles (box) and range (whiskers).

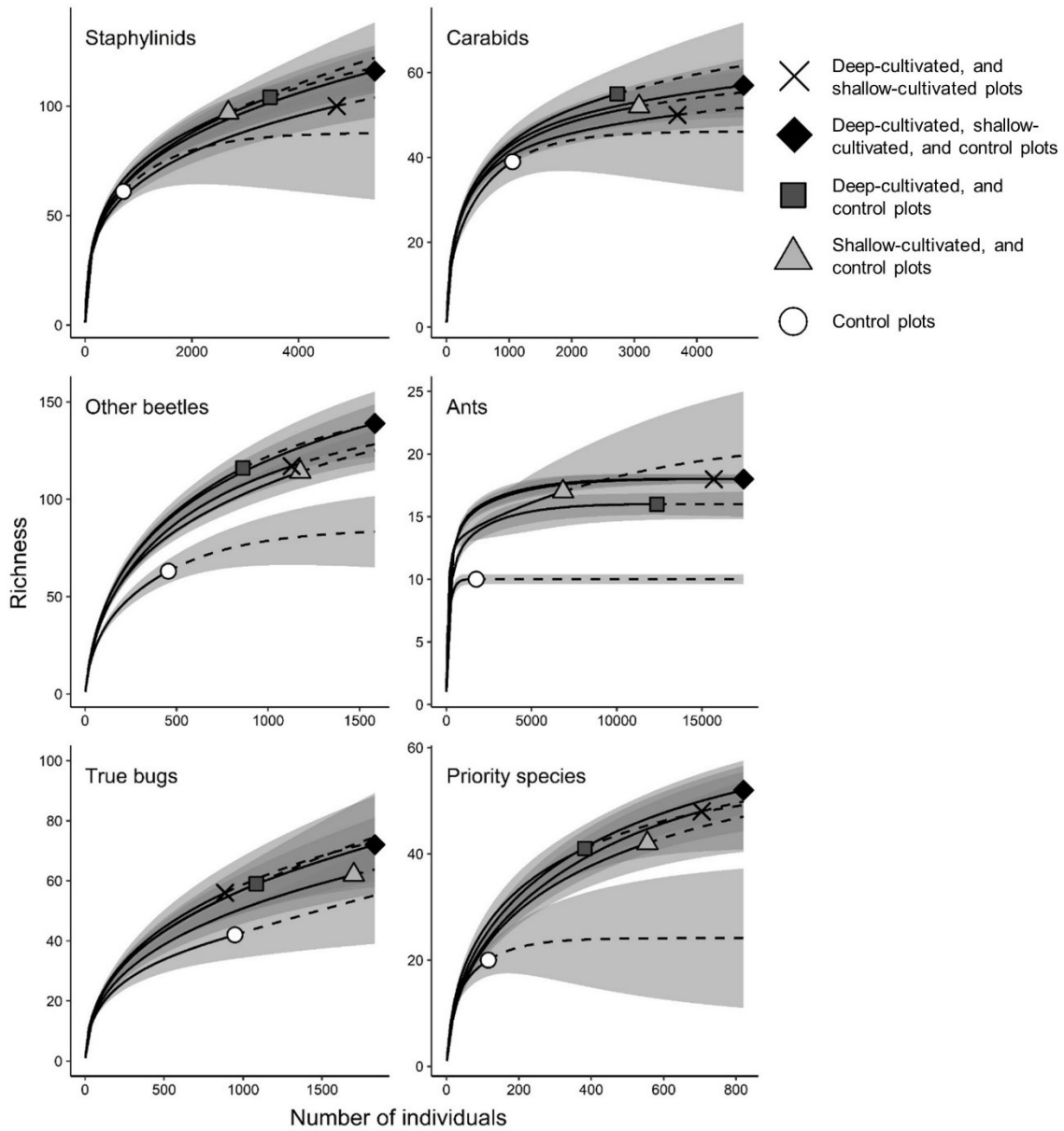


Figure 6. Extrapolated rarefaction curves and 95% CI limits for each of five invertebrate groups, and for all priority (rare, scarce or threatened) invertebrate species, for five hypothetical landscapes comprising different combinations of control and treatment plots (see key). Symbols denote observed richness; solid and dashed lines interpolated and extrapolated richness respectively; shading represents 95% CI bounds. Sample-based rarefactions are rescaled to numbers of sampled individuals.