

1 **Brownfield sites promote biodiversity at a landscape scale**

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18

19 **Abstract**

20 Repurposing of brownfield sites is often promoted, because it is perceived that protecting the  
21 “green belt” limits damage to biodiversity; yet brownfield sites provide scarce habitats with  
22 limited disturbance, so conversely are also perceived to be ecologically valuable. Combining

23 data from three national-scale UK biological monitoring schemes with location data on  
24 historical landfill sites, we show that species richness is positively associated with both the  
25 presence and increasing area of ex-landfill sites for birds, plants and several insect taxa.  
26 Assemblage rarity of birds is also positively associated with presence of ex-landfill sites.  
27 Species richness associated with ex-landfill sites declined over time for birds and insects but  
28 increased over time for plants. These findings suggest that development of brownfield sites  
29 may have unintended negative consequences for biodiversity, and imply that to minimise  
30 loss of biodiversity, brownfield site repurposing could be targeted towards smaller sites, or  
31 sites in areas with a high density of other brownfield sites.

32

### 33 **Keywords**

34 Abandoned land, contaminated land, Lepidoptera, Odonata, post-industrial sites,  
35 repurposing

## 36 **1. Introduction**

37 Brownfield sites (defined as abandoned land that has previously been developed) are often  
38 considered to be good locations for repurposing to a range of uses (e.g. Hard et al., 2019;  
39 Milbrandt et al., 2014). However, brownfield sites can, under some circumstances, have high  
40 ecological value (Beneš et al., 2003; Broughton et al., 2021; Eyre et al., 2003; Gardiner et  
41 al., 2013; Macadam and Bairner, 2012; Mathey et al., 2015; Small et al., 2002; Tropek et al.,  
42 2010; Woods, 2012). This value arises from features which can include low fertility and/or  
43 extreme soil characteristics (Ash et al., 1994) (providing niches for specialist species), early-  
44 successional habitats (Broughton et al., 2021), and low levels of disturbance from both  
45 humans and predators (Kamp et al., 2015), which may otherwise be rare in the landscape.  
46 As a consequence, there are concerns that repurposing of brownfields may have unintended  
47 consequences for biodiversity (Broughton et al., 2021; Fletcher et al., 2011; Meehan et al.,  
48 2010), and so the ecological value of such sites should be a consideration during planning.  
49 However, there is little direct evidence to suggest how ecological communities associated  
50 with brownfield sites compare directly to other land uses, or how brownfield sites contribute  
51 to biological richness at landscape scales.

52 Among brownfield sites, ex-landfill sites are globally relevant, since landfill is one of the most  
53 important forms of solid waste management in countries from all levels of socioeconomic  
54 development (Hoorweg and Bhada-Tata, 2012). In the UK, 24% of all waste was sent to  
55 landfill in 2018 (approx. 50 million tonnes in total), second only to recycling as a form of  
56 waste management (Department for Environment, Food & Rural Affairs, 2021). Ex-landfill  
57 sites are well-suited to landscape-scale studies of brownfield sites (and particularly their  
58 ecology) for both practical and scientific reasons: practically, they represent the only form of  
59 brownfield site for which a national-scale database has been collated (albeit covering only  
60 England, rather than the entire UK; and covering a range of waste types including municipal,  
61 commercial and industrial), whereas data on brownfield sites more generally is collated by  
62 local authorities in a wide and inconsistent range of formats. Scientifically, they may be

63 particularly well suited to repurposing due to the combination of good access to critical  
64 infrastructure (e.g. roads) (Milbrandt et al., 2014) and limited physical structures from past  
65 use (most sites are restored to grassland post-closure (Simmons, 1999)), but restored  
66 grassland on ex-landfill sites can support ecological communities of similar richness to  
67 comparable natural and semi-natural habitat (Tarrant et al., 2013; Rahman et al., 2015).

68 In this study, we investigated whether landscapes (here, meaning 1 x 1 km grid squares  
69 surveyed as part of biodiversity recording schemes) containing ex-landfill sites differed from  
70 surrounding landscapes in terms of their biodiversity richness and assemblage rarity. To  
71 achieve this, we combined data on the locations of former landfill sites in England  
72 (Environment Agency, 2020) with landscape-scale citizen science data from three UK  
73 biodiversity recording schemes, covering multiple taxonomic groups: the Breeding Bird  
74 Survey (BBS; birds), the National Plant Monitoring Scheme (Pescott et al., 2015: NPMS;  
75 plants) and the Wider Countryside Butterfly Survey (Brereton et al., 2011a: WCBS;  
76 Lepidoptera (butterflies and moths) and Odonata (dragonflies and damselflies)).

77 Specifically, we tested the following questions for each taxon: (i) whether species richness  
78 and assemblage rarity differ between grid squares containing ex-landfill sites and those  
79 without; (ii) whether the area covered by ex-landfill sites within a grid square relates to its  
80 species richness and assemblage rarity; and (iii) whether the time since landfill site closure  
81 (i.e. site age) relates to its species richness and assemblage rarity. Because there is a  
82 perception that brownfield sites can have high ecological value due to the presence of early-  
83 successional habitats, we formed a general hypothesis that biodiversity richness and  
84 assemblage rarity would show a positive relationship with brownfield presence and size, but  
85 a negative relationship with brownfield age. However, we tested each taxon separately,  
86 because some taxa might respond differently to others as ecological succession proceeds  
87 on brownfield sites.

88

## 89 **2. Material and methods**

### 90 *2.1. Datasets*

91 We used data obtained by three recording schemes (with similar designs) to investigate the  
92 influence of brownfield sites on biodiversity at landscape-scales. Specifically, we used data  
93 from the Breeding Bird Survey (BBS) (Harris et al., 2020); the National Plant Monitoring  
94 Scheme (NPMS) (Pescott et al., 2015); and the Wider Countryside Butterfly Survey (WCBS)  
95 (Brereton et al., 2011a), in which recorders can optionally record moths (Lepidoptera),  
96 dragonflies (Odonata: Epiprocta) and damselflies (Odonata: Zygoptera) as well as the target  
97 taxon, butterflies (also Lepidoptera).

98 In each scheme, participants record target taxa within a 1 x 1 km grid square on at least two  
99 occasions per year. Grid squares are selected for recording using a stratified-random  
100 approach, ensuring that coverage of recorded squares is representative of the wider  
101 countryside rather than biased towards high-quality or protected habitats (c.f. the UK  
102 Butterfly Monitoring Scheme (Brereton et al., 2011b)). In both the BBS and the WCBS,  
103 participants record target taxa along two roughly parallel transects of 1km each across the  
104 survey square (Brereton et al., 2011a). In the NPMS, participants record at least five plots  
105 within the survey square (preferably from a shortlist of up to 25 plots distributed in a grid  
106 within the square), using a mixture of 5 x 5 m square plots and 1 x 25 m linear plots.  
107 Records are made to species level wherever possible, and abundance (as percentage  
108 cover, in the NPMS) recorded as appropriate. All three datasets were up-to-date to 2019 at  
109 the point of analysis, and recording in each scheme began in 1994 (BBS), 2006 (WCBS) and  
110 2015 (NPMS) respectively.

111 Birds, plants and butterflies were the main target taxon of their respective recording  
112 schemes, so we assumed that all recorders made an attempt to record these groups and  
113 therefore included all squares in our initial dataset for these taxa. By contrast, recorders in  
114 the WCBS had the option to record any moths, dragonflies and damselflies encountered

115 during their surveys, but were not obliged to do so. For these groups, we only included  
116 squares with non-zero species richness in our initial dataset, since it was impossible to know  
117 whether zero species richness indicated that no species were present, or that recorders had  
118 declined to record these optional taxa. We found that moths had been recorded in  
119 approximately half of WCBS squares in our final dataset (Supplementary Table 1), so we  
120 treated these separately from butterflies, even though the two groups form paraphyletic taxa  
121 within the order Lepidoptera. Similarly, we decided to treat dragonflies and damselflies  
122 separately even though they collectively form the order Odonata, because dragonflies are  
123 generally more familiar to the majority of recorders in the UK and therefore may have been  
124 recorded in some squares where damselflies were not (indeed, we found that dragonflies  
125 had been recorded in slightly more WCBS squares in our final dataset than damselflies).

126 We additionally made use of a well-established divide within British butterfly species  
127 between wider countryside (WC) generalists and habitat specialists (HS) (Asher et al., 2001)  
128 to examine whether the value of brownfield sites in the landscape varied according to  
129 species' ecological specialization. Like moths and odonates, habitat specialist butterflies  
130 were also only recorded in a proportion of all WCBS squares (Supplementary Table 1), but  
131 in this case, we decided that absence of records was more likely to indicate absence of  
132 species, since recorders were explicitly instructed to record all butterfly species observed  
133 (not just WC species). Therefore, we included all squares (including those with zero records  
134 of HS species) in our initial dataset for this taxon.

135 These schemes collectively provide high resolution species occupancy data for six  
136 taxonomic groups: birds, plants, butterflies (collectively, and split into generalists and  
137 specialists), moths, dragonflies, and damselflies. Across all three schemes, we assessed  
138 almost 10,000 1 x 1 km grid squares in our initial dataset (Supplementary Table 1).

139 To identify the location of historical landfill sites, we used the Environment Agency's Historic  
140 Landfill Sites database (Environment Agency, 2020). This provides the location of all sites

141 for which there has previously been a Pollution Prevention and Control permit or waste  
142 management licence issued, but no permit or licence is currently in force, along with known  
143 landfill sites that existed before the current waste licensing regime commenced. The  
144 database contains information on a range of waste types including municipal, commercial  
145 and industrial; many commercial and industrial sites are classed as “inert” and are  
146 particularly well-suited to repurposing. Data were provided as vector-format shapefiles. This  
147 dataset covers England only, and therefore our study was restricted to England, even though  
148 our initial dataset for all three recording schemes included recorded squares in the other  
149 nations that comprise the UK.

150 To assess land use within recorded squares, we used raster data from the Land Cover Map  
151 2015 (Rowland et al., 2017) to identify the dominant (modal) land use classification within  
152 each recorded square (i.e. that with the most 25 x 25 m pixels within the grid square).

## 153 *2.2. Data curation and indicators*

154 From our initial dataset, we used the Historic Landfill Sites data to quantify the area of  
155 historical landfill within each recorded square. From these, we identified all recorded squares  
156 with > 5 % landfill by area; these formed the focus of our study and were termed “target  
157 squares”. Among target squares, percentage cover by landfill ranged between 5.03–69.04  
158 %, with the majority of squares falling between 5 and 20 % (Supplementary Fig. 1). Date of  
159 landfill site closure is documented in the Historic Landfill Sites database via two metrics, date  
160 of last input and date on which the relevant permit/licence was surrendered, with both  
161 variables available for some sites and neither for others. We used these metrics to estimate  
162 the date on which each landfill site was closed (giving preference to the date of last input for  
163 sites where both metrics had been recorded), and used this to calculate the time in years  
164 since each landfill site closed (Supplementary Fig. 2). Where a target square contained  
165 multiple ex-landfill sites, we used the minimum value of time since closure (i.e. the most  
166 recently-closed site) in analyses.

167 For each target square, we additionally identified the nearest recorded square with the same  
168 dominant habitat type (“matched land-use squares”), and the nearest three recorded  
169 squares with different dominant habitat types (“different land-use squares”), to provide  
170 comparison. In theory, this was intended to facilitate comparison between brownfield sites  
171 and other sites with both similar and different habitat types, since the biodiversity value of  
172 brownfield sites could be shaped by two non-mutually exclusive factors: first, the presence of  
173 early-successional habitats that often form on such sites as ecological succession proceeds  
174 post-abandonment or restoration (Tarrant et al., 2013) (but which do not *exclusively* form on  
175 brownfield sites), and second, characteristics unique to brownfield sites themselves (e.g.  
176 potentially polluted soils and low disturbance) (Ash et al., 1994). If the target square has  
177 similar biodiversity to its matched land-use square, but differs from the different land-use  
178 squares, then the effect is more likely to be driven by the dominant land use associated with  
179 squares containing ex-landfill sites, whereas effects associated with the ex-landfill sites  
180 themselves should present even in comparisons with matched land-use squares. However, it  
181 should be noted that the land use of the brownfield site itself may not be dominant within the  
182 target square (especially for target squares closer to the 5 % cover threshold for inclusion),  
183 and that other confounding factors might be present in target squares but not captured by  
184 this analysis. Similarly, within target squares, the intersection between ex-landfill sites and  
185 actual recording locations (where available) was often minimal or non-existent; therefore,  
186 data from these squares should not be considered to represent a census of the biodiversity  
187 of brownfield sites themselves, but rather of landscapes that contain brownfield sites (and  
188 likewise, data from matched land-use and different land-use squares represents censuses of  
189 the biodiversity of various landscapes that do not contain brownfield sites).

190 For all target, matched and neighbouring squares, we calculated four biodiversity indices: (i)  
191 observed species richness (simply the total number of species observed across all surveys  
192 of the square per taxon); (ii) estimated species richness, extrapolated using the Chao2  
193 incidence-based estimator (Chao, 1987; we used Chao2 rather than the Chao1 abundance-

194 based estimator because most squares had data from repeated visits across multiple years,  
195 and under such circumstances this approach is more robust than abundance-based  
196 estimation (Colwell and Coddington, 1994)); (iii) sampling completeness (a function of the  
197 relationship between observed and estimated species richness, allowing the consistency of  
198 sampling effort across sites in different treatments to be examined); and (iv) an index of  
199 species rarity which varied from 0 (when a square contained only species recorded in every  
200 single square nationally) to 1 (when a square contained only species recorded in no other  
201 square nationally). To calculate this index, we assigned each species a rarity weight  
202 according to the proportion of recorded squares in which it had been observed; e.g. among  
203 butterflies, Small Blue *Cupido minimus* (recorded in 32 squares; 1.5 %) and Meadow Brown  
204 *Maniola jurtina* (recorded in 1832 squares; 87.4 %) were assigned weights of 0.985 and  
205 0.136 respectively. We calculated the square-level rarity index based on these species-level  
206 rarity weights, following the approach of Leroy *et al.* (2013; who used a different method to  
207 calculate species-level rarity weights).

### 208 2.3. Statistical analysis

209 We used two related approaches to assess the effect of historical landfill sites in the  
210 landscape on biodiversity richness and rarity.

211 First, we tested whether target squares (those containing ex-landfill sites) differed in their  
212 biodiversity richness and rarity from their corresponding matched land-use and different  
213 land-use squares. To this end, we fitted generalised linear mixed-effects models to data from  
214 all squares, with 'square type' (i.e. target, matched land-use, or different land-use) as the  
215 fixed effect and a grouping factor as a random effect (to allow the model to pair each target  
216 site with its own counterparts). Models were fitted with a Poisson error distribution for  
217 species richness (except in one case, estimated species richness of moths, where a  
218 Quasipoisson distribution was fitted to address under-dispersion), and a binomial error  
219 distribution for sampling completeness and rarity index. We tested significance of the full

220 model using a Likelihood Ratio Test. We then refitted each model twice, to separately test  
221 for differences between target squares and matched land-use and different land-use  
222 counterparts respectively.

223 Second, we tested whether the area of ex-landfill within target squares, and the time since  
224 landfill site closure, were correlated with biodiversity richness and rarity. To this end, we  
225 fitted generalised linear models to data from target squares only, with either the logarithm of  
226 the percentage of the square's area which was ex-landfill (the logarithm was taken to  
227 normalize this variable's distribution) or the time in years since closure as the fixed effect.  
228 Error distributions and significance testing were as above.

229 For both sets of analyses (those comparing target squares to counterparts, and those  
230 assessing linear or log-linear effects within target squares), we conducted false discovery  
231 rate (FDR) correction using the Benjamini-Hochberg procedure (Benjamini and Hochberg,  
232 1995), because we effectively tested the same hypothesis (that biodiversity would be  
233 different in squares containing ex-landfill sites than other squares) multiple times, both by  
234 comparing separately within the same datasets to matched and different land-use squares,  
235 and by testing with data for multiple taxa.

236 All analyses were conducted in R version 4.0.3 (R Core Team, 2020), except initial  
237 assessment of the intersection between landfill sites and recorded grid squares, which was  
238 conducted in QGIS (QGIS Development Team, 2021). R scripts are archived on Zenodo  
239 (doi: [10.5281/zenodo.4580297](https://doi.org/10.5281/zenodo.4580297)).

240

### 241 **3. Results**

242 Overall, we found that estimated species richness was significantly higher in target squares  
243 than their counterparts in matched and different land-uses for birds, plants and moths (Fig.  
244 1, Supplementary Table 2). Observed species richness was similarly higher in target

245 squares for birds and moths, but significantly lower in target squares for plants (a clear  
246 discrepancy with the results for estimated species richness). However, analysis of sampling  
247 completeness revealed that it was highly variable between squares for all taxa, and in some  
248 cases showed evidence of systematic differences between squares in different categories  
249 (with a significant effect detected for butterflies (Supplementary Table 2), though not for  
250 other taxa recorded in the same WCBS surveys). Given this finding, we ascribe greater  
251 confidence to the results for estimated species richness, which indicate a consistent positive  
252 effect of brownfield sites across birds, plants and moths. A trend towards this same positive  
253 effect was also evident in both groups of Odonata, but was non-significant after Benjamini-  
254 Hochberg correction (Benjamini and Hochberg, 1995) for false discovery rate (FDR) in both  
255 instances (Supplementary Table 3). By contrast, no such effect was present among  
256 butterflies; indeed, among habitat specialist butterflies, observed and estimated species  
257 richness were lower in target squares than different land-use squares, with no difference to  
258 matched land-use squares (Supplementary Table 2). For birds only, assemblage rarity was  
259 also higher in target squares containing brownfield; this effect was absent in all other taxa  
260 after FDR correction (Fig. 1).

261 We found a consistent, positive relationship between the area of brownfield within a target  
262 square and estimated species richness across birds, plants, dragonflies and damselflies, but  
263 not any group of Lepidoptera (Fig. 2, Supplementary Table 4). However, only the effects on  
264 birds and dragonflies retained significance after FDR correction (Supplementary Table 5).  
265 The same outcomes were found for observed species richness across all groups except  
266 damselflies. In other words, target squares containing larger ex-landfill sites tended to have  
267 richer ecological communities. We found a consistent, negative relationship between the age  
268 of brownfield within a target square and estimated species richness across birds, moths,  
269 dragonflies and damselflies (Fig. 2, Supplementary Table 6; although the latter was not  
270 significant after FDR correction: Supplementary Table 7), with a converse significant positive  
271 relationship for plants and no relationship for butterflies. In other words, species richness of

272 birds and insects in target squares containing ex-landfill sites tended to decline over time,  
273 whereas species richness of plants tended to increase over time. However, we found no  
274 effects of brownfield site area or age on assemblage rarity for any taxon.

275

#### 276 **4. Discussion**

277 Overall, our results indicate a positive effect of ex-landfill sites on landscape-scale  
278 biodiversity. Grid squares containing historical landfill sites tend to have higher species  
279 richness across multiple taxa than other nearby squares, and may also support a rarer  
280 assemblage of birds. Among target grid squares, those containing larger ex-landfill sites  
281 again tend to have higher species richness across multiple taxa. However, it should be noted  
282 that despite statistical significance, effect sizes were extremely small. For example, our  
283 models predicted an estimated richness of 70.6 ( $\pm$  s.e. 1.1) bird species in target squares,  
284 compared to 66.4 ( $\pm$  s.e. 1.0) and 63.2 ( $\pm$  s.e. 0.9) species in matched land-use and different  
285 land-use squares respectively (Supplementary Fig. 3): an addition of only a few species to  
286 an already large assemblage. Similarly, predictions of estimated species richness of birds in  
287 target squares increased from 67.5 ( $\pm$  s.e. 1.0) species at 5 % coverage of landfill, to 78.3 ( $\pm$   
288 s.e. 1.6) at 50 % coverage. Proportional effect sizes were similarly small for other taxa  
289 (Supplementary Figs. 4-9). Therefore, whilst presence of ex-landfill sites appears to be  
290 associated with an increase in landscape-scale biodiversity richness, it should not be  
291 concluded that the ex-landfill sites are the richest possible land-use for conservation  
292 purposes; indeed, it is possible that these brownfield sites have relatively low species  
293 richness themselves, but increase beta diversity within landscapes by increasing habitat  
294 heterogeneity and providing niches that are distinct from those already present in the  
295 surrounding area. If this were the case, one would predict that the positive effect of  
296 increasing area within target sites should level off or decline as area exceeds 50 % (because  
297 habitat heterogeneity would decline once brownfield became too dominant in a square). We

298 were unable to assess this because few squares had >50 % coverage of ex-landfill in our  
299 dataset (Supplementary Fig. 1). One would also predict that the positive effect of ex-landfill  
300 sites might be more pronounced, and thus more detectable, in human-altered landscapes  
301 with low habitat heterogeneity (e.g. largely agricultural landscapes) compared to those with  
302 high habitat heterogeneity. Further field research is necessary to determine what proportion  
303 of full landscape-scale assemblages can be supported on brownfield sites themselves,  
304 which types of species are added to the assemblage by their occupation of brownfields, and  
305 which specific features of brownfield sites and their surrounding landscapes are responsible  
306 for driving the observed increase in landscape-scale assemblage richness. However, the  
307 contrasting effects of brownfield site age on plants and other taxa suggests the early-  
308 successional habitats associated with brownfield sites may be an important factor. Birds,  
309 moths and odonates are all relatively mobile taxa capable of rapidly colonising suitable early-  
310 successional habitat on recently-abandoned brownfield sites, but these sites may  
311 subsequently become less valuable as succession proceeds (e.g. Broughton et al., 2021).  
312 By contrast, plants are less mobile, and assemblages might colonise ex-landfill sites  
313 gradually over a period of years to decades post-closure.

314 Effects upon the index of rarity were only found for birds, not for other taxa. It is possible that  
315 this difference can be ascribed to statistical power, given that the BBS was by some margin  
316 the largest of the three in use (Supplementary Table 1). However, it is also conceivable that  
317 it represents a genuine ecological pattern relating to the way in which certain rare bird  
318 species respond to and/or make use of brownfield sites within the landscape (e.g. Broughton  
319 et al., 2021): by contrast to other taxa under study, birds are highly mobile, and also might  
320 respond more strongly to the reduced disturbance from humans and predators associated  
321 with brownfield sites (Kamp et al., 2015). As above, this point might be clarified by further  
322 research into species with particularly strong associations with brownfield sites.

323 Effects were mainly absent in butterflies across all analyses (after FDR correction), apart  
324 from a negative effect of brownfield sites on habitat specialist species. The absence of

325 positive effects matching those in other taxa seems unlikely to be a consequence of low  
326 statistical power, given that such effects were variously detected in moths, dragonflies and  
327 damselflies, all of which were recorded incidentally by a subset of WCBS butterfly recorders  
328 (Supplementary Table 1) and therefore had lower power; nonetheless, the timing of the  
329 WCBS recording window (July-August) might potentially mask effects by precluding the  
330 possibility of recording early-flying species known occasionally to colonise brownfield sites  
331 (e.g. Grizzled Skipper *Pyrgus malvae* (Slater, 2007)). An alternative, but unconfirmed,  
332 explanation, is that interactions between the traits of butterflies and those of their larval host  
333 plants reduce the likelihood of butterflies (especially habitat specialists) colonising brownfield  
334 sites. Butterfly distributions are strongly tied to the presence of larval host plants, even at  
335 very local scales (Clausen et al., 2001). Under the C-S-R strategy model for plants (Grime,  
336 1974), larval hostplants of the most widespread and abundant wider countryside generalist  
337 butterflies tend to have competitive or ruderal strategies (Dennis et al., 2004), occupying  
338 productive habitats (Hodgson, 1993), and therefore might not benefit from low-fertility or  
339 polluted soils (Hard et al., 2019) on ex-landfill sites. Many of the habitat specialist butterfly  
340 species resident in the UK are associated with host plants that are themselves habitat  
341 specialists of calcareous grassland (Asher et al., 2001), with requirements unsuited to  
342 colonising ex-landfill sites. Even in cases where host plants can occur on ex-landfill sites, the  
343 typical traits of habitat specialist butterflies (low mobility, closed population structure, and  
344 inherently limited geographic distribution) may make colonisation by the butterflies unlikely.  
345 Other major forms of brownfield sites (e.g. disused quarries) may provide favourable  
346 conditions for habitat specialist butterflies and their host plants (Beneš et al., 2003; Schmitt,  
347 2003; Slater, 2007; Turner et al., 2009), as well as a range of other taxa (Tropék et al.,  
348 2010), and could therefore generate landscape-scale benefits similar to those from ex-landfill  
349 sites detected in this study for butterflies and other taxa.

#### 350 4.1. Conclusions

351 Our findings warn that current policies of unrestricted, or even preferential, development  
352 upon brownfield sites (such as former landfills) could have unintended negative outcomes for  
353 biodiversity richness, by destroying the unique ecological communities that can develop on  
354 such sites. Further research is necessary to establish whether particular features of  
355 brownfield sites and their management can provide an indication of their likely biodiversity  
356 value, and therefore enable more considered decision-making about the individual merits of  
357 different brownfield sites at the planning stage. In the meantime, our results imply that to  
358 minimise loss of biodiversity, development upon brownfield sites could be targeted towards  
359 smaller sites (i.e. those with the least positive influence to lose), or sites in areas with a high  
360 density of other brownfield sites (therefore, likely to retain some regional benefit).

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370

#### 371 **Author contributions**

372 This study was instigated and primarily designed by C.J.M., M.J.B., P.D. and W.M.M., in  
373 discussion with N.A.D.B. and D.B.R. The statistical analysis was conducted by C.J.M., who

374 also prepared the first draft of the paper. All authors contributed substantially to revising the  
375 paper.

376

### 377 **Competing interests**

378 The authors declare no competing interests.

379

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381

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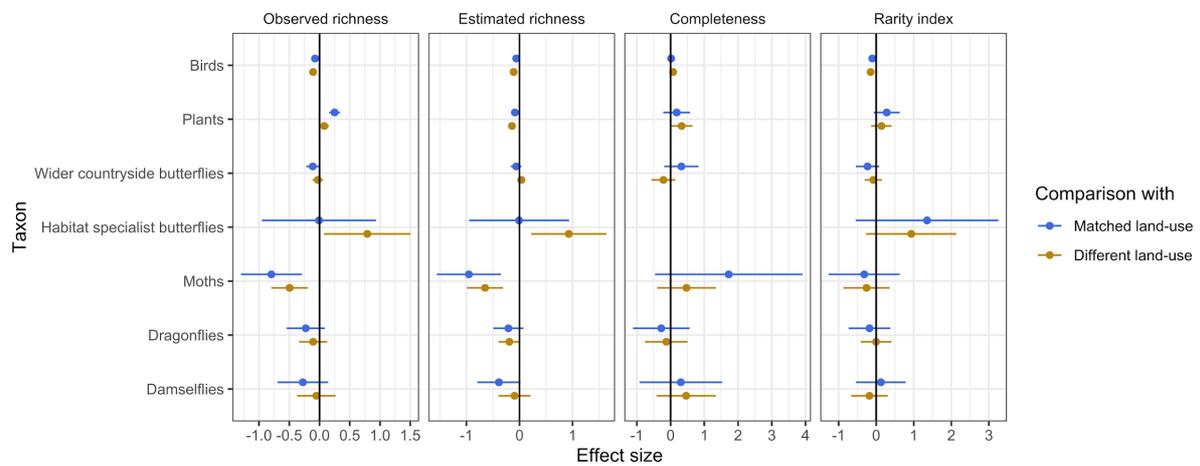
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488 **Figure 1.** Presence of brownfield (historical landfill) sites in the landscape promotes species  
489 richness in multiple taxa. For each combination of response variable and taxon, target  
490 squares (with > 5% landfill by area) were compared to matched and neighbouring squares  
491 (nearest neighbours with respectively the same, and different, modal land-use compared to  
492 the target square). Estimated species richness was significantly higher in target squares  
493 than matched and/or neighbouring squares for birds, plants, moths (with similar trends for  
494 dragonflies and damselflies), but not for wider countryside or habitat specialist butterflies.  
495 Effect sizes (ES) are from Poisson- or binomial-family models with log link functions, such  
496 that comparison square metrics = target square metrics  $\times e^{ES}$  (therefore, a negative ES  
497 indicates that metrics are lower in comparison squares than target squares, and vice versa).  
498 No comparisons were made between sampling completeness of squares for habitat  
499 specialist butterflies due to severe under-dispersion of data (Supplementary Fig 6).

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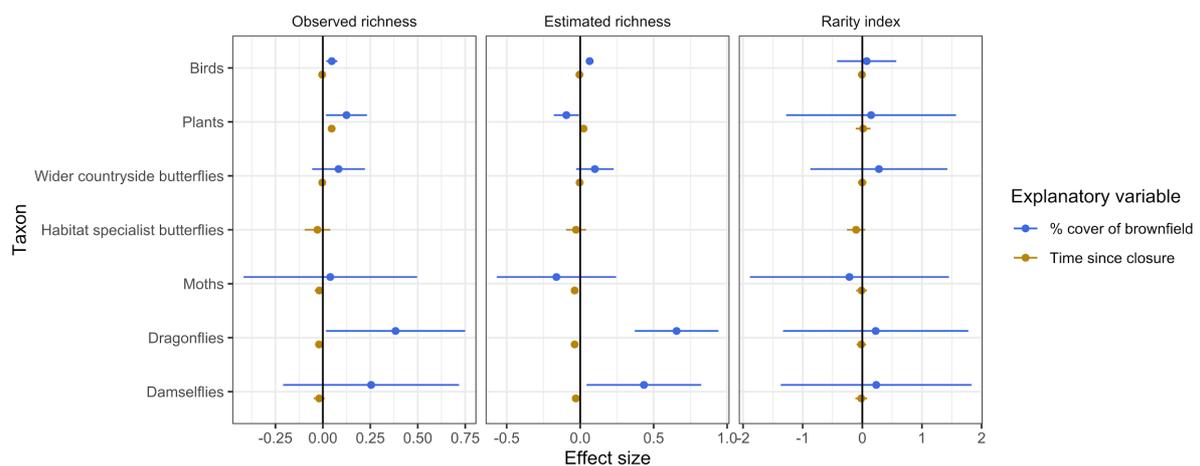
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504 **Figure 2.** Area and age of brownfield sites affect species richness in multiple taxa. For each  
505 combination of response variable and taxon, the relationship between response variable and  
506 the explanatory variable (either percentage cover of brownfield sites or time since landfill site  
507 closure in years) was assessed, among all target squares (with > 5% landfill by area).  
508 Estimated species richness increased significantly with increasing area of brownfield for  
509 birds and dragonflies (with trends in the same direction for damselflies). For birds, moths and  
510 dragonflies, species richness decreased significantly with increasing time since landfill site  
511 closure (with trends in the same direction for damselflies), whereas for plants, species  
512 richness increased significantly with increasing time since landfill site closure. Effect sizes  
513 (ES) indicate slopes fitted by Poisson- or binomial-family models with log link functions  
514 (therefore, a negative ES indicates that metrics decrease as area or age of brownfield sites  
515 increase, and vice versa). Analyses of the effect of area of brownfield on habitat specialist  
516 butterflies are not plotted in order to preserve clarity for other taxa (due to extremely wide  
517 error bars), but are summarised in Supplementary Table 4.

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