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1 **Agri-environment conservation set-asides have co-benefits for**
2 **connectivity**

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19 **Abstract**

20 Widespread declines in farmland biodiversity have led to state-funded schemes which take
21 land out of production to create (semi-)natural habitats for biodiversity (e.g. EU agri-
22 environment schemes; US Conservation Reserve Program). Common features of such
23 schemes are grassland strips at the edges of agricultural fields, and we examine potential
24 co-benefits of these biodiversity set-asides for contributing to grassland connectivity.
25 Although set-aside strips had negligible impact on landscape-scale species persistence
26 (using metapopulation models parameterized for flying insects run on 267 landscapes of
27 ~30,000 ha across England), they nonetheless improved connectivity in 74% (198/267) of
28 landscapes (comparing landscapes with and without set-asides), as shown by range
29 expansion rates increasing by up to 100%. Benefits of set-aside strips varied according to
30 species type (high/low dispersal, high/low population density), but had little benefit for
31 species with low dispersal and small population sizes, which generally failed to expand.
32 High dispersal/high density species were already successful expanders regardless of set-
33 asides (>75% of simulations were successful without set-asides) although expansion rates
34 were still improved when set-asides were added. Whilst alternative strategies for
35 placement of set-aside strips (more/less aggregated), revealed no consensus 'better'
36 strategy across species types, set-aside benefits were generally greatest in landscapes with
37 intermediate availability of semi-natural grassland (0.5- 4% cover). We conclude that
38 small-scale set-asides have the potential to improve connectivity, which we expect to help
39 some species track climate change, and connect habitat patches within existing climate

40 space for others. However, set-asides are unlikely to benefit low dispersal species which
41 are probably at greatest risk from agricultural intensification.

42 **Keywords:**

43 Connectivity, agri-environment schemes, range expansion, metapopulation, persistence

44 **Introduction**

45 Recent centuries have seen a global transformation in land use as a consequence of large
46 scale land conversion of (semi-) natural habitats to croplands and pasture, which now
47 cover ~37% of land surface worldwide (Goldewijk 2001, Ramankutty et al. 2008). Changes
48 in land use towards agricultural production not only threaten biodiversity within
49 converted land (Foley et al. 2005, 2011, Newbold et al. 2015), but can also threaten
50 biodiversity found in remaining, isolated fragments of natural habitat (Crooks and
51 Sanjayan 2006, Hanski 2015). Biodiversity responses to habitat fragmentation are less
52 predictable than responses to habitat loss (Fahrig 2003, Hodgson et al. 2009), but habitat
53 networks which exhibit high fragmentation are at particular risk from threats from climate
54 change (Travis 2003, Oliver et al. 2015). Designing conservation strategies which increase
55 habitat connectivity should help mitigate these environmental stressors (Opdam and
56 Wascher 2004, Hodgson et al. 2011, Saura et al. 2014, Scriven et al. 2015), helping species
57 respond and adapt to climate change. In addition to distributional effects, increasing
58 connectivity is expected to be beneficial for many other important ecological processes,
59 such as facilitating gene flow (Cushman et al. 2006; Keyghobadi 2007) and allowing inter-

60 patch movements so that individuals may acquire appropriate resources within their
61 lifetimes (Taylor et al. 1993).

62 The question of how best to arrange habitat within agricultural landscapes to conserve
63 biodiversity is difficult. Whilst much theoretical and empirical evidence suggests that large
64 blocks of continuous habitat are best for supporting viable populations under current
65 environments (Diamond 1975, Margules and Pressey 2000, Hodgson et al. 2009, but see
66 Ovaskainen 2002), this arrangement may not be optimal for conserving species under
67 climate change (i. e. species undergoing distributional shifts) if large blocks of habitat are
68 isolated from one another and dispersal between locations is therefore extremely rare. The
69 size and location of habitat patches is central to the persistence of metapopulations of
70 species in habitat networks (Hanski 1999), but the spatial location of patches which is best
71 for population persistence may not be the best landscape design for enabling range shifting
72 (Hodgson et al. 2011). Range shifts along latitudinal and elevational gradients (Parmesan
73 and Yohe 2003, Hickling et al. 2006, Moritz et al. 2008) are linked to habitat connectivity
74 (Krosby et al. 2010), and the addition of stepping stone habitat patches can facilitate range
75 expansion by linking larger blocks of habitat (Uezu et al. 2008, Kramer-Schadt et al. 2011,
76 Leidner and Haddad 2011, Saura et al. 2014) despite contributing a relatively low total area
77 of habitat. Habitat connectivity may also help species adapt to climate change within their
78 current ranges, for example, if better connectivity increases gene flow and so facilitates the
79 spread of climate tolerant traits (Sexton et al. 2011; Kremer et al. 2012, although gene flow
80 can also have negative impacts on local adaptation – e.g. see Lenormand 2002).

81 Agri-environment schemes (AESs) are policy initiatives which aim to reduce negative
82 environmental impacts of agriculture by financially incentivizing farmers to carry out
83 specified management practices, and schemes of varying forms can be found across the
84 world, including in Europe (Arnalds 2011, Batáry et al. 2015), North America (Robinson
85 2006); Central America (Sierra and Russman 2006), East Asia (Zhang et al. 2008, Kim and
86 Banfill 2012, Nomura et al. 2013) and Australasia (Sobels et al. 2001, Wilson 2004). Many
87 AESs include provision for setting aside small patches of land within the agricultural matrix
88 such as set-aside buffer strips at the edges of agricultural fields, which provide habitat and
89 foraging resources for wild birds, pollinating insects and other agriculturally beneficial
90 arthropods (Landis et al. 2000, Marshall and Moonen 2002, Olson and Wäckers 2006), as
91 well as reducing runoffs of agrochemicals and soil erosion (Haycock et al. 1996, Snoo and
92 Wit 1998, USDA 2000). In addition, it has been suggested that these types of AES set-asides
93 could offer secondary connectivity co-benefits (e.g. Donald and Evans 2006), which could
94 support species' persistence within current distributions, and/or improve species'
95 capacities to track climate changes across landscapes.

96 Here, we examine the connectivity effects of set-aside strips for species within semi-natural
97 grasslands in England. We examine connectivity within each of 267 20 km diameter
98 circular landscapes by modelling metapopulation persistence within each landscape
99 (metapopulation capacity; Hanski and Ovaskainen, 2000), and range expansion across each
100 landscape (progression of a simulated expansion from one edge of the landscape to the
101 other, using the Incidence Function Model; Hanski, 1994). Our models are parameterized
102 for flying insects, such as butterflies, which are sensitive to habitat fragmentation (Hanski
103 et al. 1995, Summerville and Crist 2001, Hill et al. 2001), threatened by agricultural

104 intensification (Thomas 2016, Habel et al. 2019), and have the potential to benefit from
105 small-scale AESs e.g. via availability of nectar and larval host-plant resources (Feber and
106 Smith 1995). We examine benefits of AESs for each landscape by comparing landscape-
107 scale persistence and expansion in landscapes with and without the inclusion of set-aside
108 strips, according to 2015 locations of AES options in England (Natural England, 2016).
109 Specifically, we examine the hypotheses that set-aside strips provisioned through AESs can
110 have a positive impact on the persistence and range expansion of metapopulations of
111 grassland species. We also test the hypothesis that the effectiveness of set-aside strip
112 patches is greatest at intermediate quantities of of non-AES semi-natural grassland habitat
113 within the landscape. Finally, we examine whether alternative spatial arrangements
114 (e.g. varying the spatial aggregation/increasing the area; see Table 1) of these small scale
115 set-aside patches could be more beneficial, testing the hypothesis that the current
116 distribution of set-asides is not optimal, because positioning was not designed with
117 connectivity in mind.

118 **Materials and Methods**

119 ***Study area***

120 We assessed connectivity impacts of set-aside strips for grassland species within England,
121 UK. To split England into regional landscapes, we defined 267 non-overlapping 20 km
122 diameter (31,400 ha) circular landscapes arranged on a regular grid (Figure 1). The size of
123 our landscapes was chosen to be large enough to observe ecologically meaningful rates of
124 range expansion (recent northwards range expansion of UK butterflies has been calculated
125 at an average rate of 14.3 – 17.6 km per decade, Hickling et al. 2006), whilst small enough

126 to provide sufficient replication of study landscapes across England. We only included
127 landscapes for which the entire area is located within England's land border.

128 ***Mapping semi-natural grassland habitat and set-aside strip locations***

129 Grassland habitat data were derived from the 2015 Land Cover Map (Rowland et al, 2017).
130 The LCM2015 provides 25 m resolution land cover data across Britain and from this we
131 extracted cells corresponding to semi-natural grassland (SNG) classes ('Neutral Grassland',
132 'Calcareous Grassland', 'Acid Grassland' and 'Fen, Marsh and Swamp') across England. We
133 aggregated these to produce a 500 m resolution raster representing the area of SNG within
134 each grid cell. The precision of AES data (see below) required the habitat data to be at 500
135 m resolution.

136 We mapped the positions of AES habitat recreation sites subsidized under the
137 Environmental Stewardship Scheme (ESS). The ESS was the agri-environment scheme in
138 England open to applications from 2005-2015, with landowner agreements (5-10 years in
139 length) running until 2025. We conducted all analyses on data for agreements live as of 1st
140 July 2015, before any agreements under the replacement post-2015 scheme came into
141 operation, therefore avoiding any hand-over effects on AES abundance or distribution. We
142 used a spatial dataset (Environmental Stewardship Scheme Options (points); Natural
143 England, 2016) which identifies specific management options operating within each ESS-
144 managed field in England. We selected uncropped set-aside strips (41 separate set-aside
145 strip codes, Table S1) as a key type of commonly implemented AES option which creates
146 grassland habitat within agricultural land in England and which feature in AES across the
147 world. Within the ESS dataset, each field parcel containing an AES option (such as a set-

148 aside strip) is recorded as a single point located at the centroid of the field. Each point is
149 associated with additional information, including the total area of the AES option within
150 that field. We extracted points representing locations and areas of all types of ESS set-aside
151 strip and mapped the area of set-aside strip within each 500 m grid cell across England.
152 From these data it is not possible to identify the precise location of set-aside strips within
153 each field, but it is possible to quantify the total set-aside strip area per land parcel.
154 Therefore, we ran models at 500 m grid cell size, a resolution which allowed models to run
155 at as fine a scale as possible without introducing unjustified precision due to the
156 uncertainty in the precise locations of set-aside strips within fields (most fields in England
157 are <500 m).

158 ***Quantifying benefits of set-aside strips for landscape-scale species' persistence***

159 We used the concept of metapopulation capacity (λ_M) (Hanski and Ovaskainen (2000); see
160 Appendix S1 for additional details) to assess species persistence within each of our 267
161 study landscapes. λ_M is a spatially explicit measure of the ability of a network of habitat
162 patches to support an equilibrium metapopulation, based on the size and position of
163 patches and the dispersal ability of a species. A non-extinct equilibrium occupancy solution
164 exists for the landscape if and only if $\lambda_M > \delta$, where δ is the persistence threshold value as
165 determined by the extinction and colonization properties of the species. λ_M can be
166 compared between landscapes to assess the relative ability of networks of habitat patches
167 to support persistent metapopulations. We expect the addition of set-aside strips to have a
168 consistently positive impact on λ_M , but the magnitude of this impact will be dependent on
169 the amount and spatial context of habitat addition. Calculations of metapopulation capacity

170 are dependent on species dispersal ability and so we calculated λ_M for each landscape and
171 set-aside strip scenario, for each of two species types varying in their dispersal ability,
172 selecting values likely to span sedentary and mobile flying insects (low: mean dispersal of
173 0.5 km per generation; high: mean dispersal of 2 km; see Appendix S1 for details of
174 parameter selection).

175 ***Quantifying benefits of set-aside strips for range expansion***

176 We simulated the expansion of species across each of the 267 landscapes using the
177 Incidence Function Model (IFM; Hanski (1994); see Appendix S1 for additional details of
178 IFMs). Range expansions have been observed to occur in many directions depending on the
179 ecological context e.g. along climate gradients or in-filling within a species' range, and so
180 we simulated range expansion across each landscape along eight equally-spaced compass-
181 directions (method adapted from Hodgson et al. 2011 & Scriven et al., 2019; Figure 1).

182 For each simulation (individual model run of expansion in a single direction), we created
183 'source' and 'target' habitat patches at either edge of the landscape, each of which consisted
184 of a single grid cell with 100% habitat cover. At the beginning of each simulation, the
185 'source' was the only occupied patch in the landscape. The simulation was run until the
186 'target' was colonized, or alternatively the metapopulation had gone extinct within the
187 landscape, up to a maximum of 200 generations (time steps; i.e. 100 years for bivoltine
188 species, or 200 years for univoltine species). Range expansion of British butterflies is
189 reported at an average speed of 14.3 – 17.6 km per decade (Hickling et al. 2006), and so we
190 deemed 200 generations to be a sufficient timeframe within which to observe range
191 expansion across a 20 km landscape, if it was to occur.

192 The total grassland and AES habitat area within each grid cell was multiplied by the
193 population density to give a carrying capacity for each habitat patch. Once colonized, a
194 patch was assumed to be occupied at its carrying capacity by the next time step. As such,
195 the extinction probability of each occupied patch was defined as $1/n$ where n is the
196 carrying capacity of that patch. Within the IFM, the addition of set-aside strip patches has a
197 consistently positive impact on the range expansion; situations in which the 'no set-aside
198 strips' scenario performs better than scenarios which include set-asides are indicative of
199 the stochasticity of the model.

200 The progression of IFM simulations is dependent upon species dispersal ability as well as
201 population density, and so we ran our simulations for four different 'species types'; high
202 and low dispersal (see above; 'low' = mean dispersal distance of 0.5 km per generation;
203 'high' = mean dispersal distance of 2 km per generation) and high and low density ('low'
204 density = 10 individuals ha^{-1} ; 'high' density = 1,000 individuals ha^{-1} (see Appendix S1 for
205 details of parameter selection). Simulations were repeated five times for each of the eight
206 source-target pairs (40 simulations per landscape).

207 The outcome of each simulation run was characterized as either a 'success' (the target cell
208 was successfully colonized), an extinction (the metapopulation went extinct), or a 'timeout'
209 (the metapopulation survived but failed to colonize the target cell in 200 generations). We
210 re-ran simulations under reduced set-aside carrying capacity (50% of semi-natural
211 grassland carrying capacity per unit area) to test the sensitivity of our results to our
212 assumption that the quality of set-aside habitat was equivalent to other areas of semi-
213 natural grassland within the landscape (Figure S7). These results show that reducing the

214 carrying capacity of set-asides reduces expansion success to some extent, but this is
215 dependent upon species traits and landscape scenario. Low quality set-asides (50% of SNG
216 per-area carrying capacity) provide very little benefit to the range expansion of low density
217 species (successful simulations increase by <1.2%). However, they can be effective at
218 improving expansion for high density species, increasing expansion success by 14.8% and
219 18.2% in low and high dispersal species respectively, compared to increases of 23.0% and
220 19.2% for 100% carrying capacity set-asides.

221 ***Assessing the importance of local habitat availability for small scale set-aside*** 222 ***effectiveness***

223 We examined the relationship between semi-natural grassland cover within each 20 km
224 diameter landscape and the effectiveness of set-aside strips using a generalized linear
225 mixed-effects model (GLMM, binomial error distribution and logit link function, using the
226 *lme4* package in R software version 3.5.1). Due to the very minimal effects of set-aside
227 strips on metapopulation persistence (see *Results*), we only analyzed the impact of local
228 (within-landscape) grassland habitat availability on range expansion. We modelled the
229 response of the logit of the ratio of successes to failures of 40 simulations (five repeats in
230 each of eight directions) for each landscape/species type combination to the total area of
231 SNG and set-aside strip within a landscape. We only analysed landscapes with <0.6% set-
232 aside strip cover and <6.4% SNG cover due to extreme values driving negative covariance
233 between total set-aside strip area and total habitat area (188 of 267 landscapes studied).
234 Our GLMM had a random effects structure (random intercept only) featuring landscape
235 identity (to account for pseudoreplication because each landscape contributed two sets of

236 success/failure responses– simulations run with and without set-aside strips) and an
237 observation-level random effect to account for overdispersion. We then selected a
238 candidate fixed effects structure including effects of: % SNG cover (transformed by
239 $\log(x+1)$), % set-aside strip cover, species type, and the two-way interactions between
240 these terms. We then performed backward stepwise model selection using likelihood-ratio
241 tests to determine the fixed effects structure. We found no spatial autocorrelation in model
242 residuals, examined by Moran's I where nearest neighbours are defined as the nearest 1, 9
243 or 25 landscapes. We used the best-fitting GLMM to assess the benefit of set-aside strips
244 along a gradient of SNG cover by calculating the differences between expansion success
245 probabilities with set-aside strips (i.e. at 0.2, 0.4, 0.6% cover), and without.

246 ***Assessing the extent to which set-aside strip effects are proportionate to area***

247 We further examined whether the contribution of set-aside strips to range expansion
248 success was disproportionate to their area or whether it was simply in line with
249 expectations given the scale of habitat addition. We plotted our GLMM to represent success
250 probability as a function of % cover of all grassland habitat (set-aside strips plus SNG), and
251 plotted alternative curves representing success probabilities for different proportions of
252 set-aside (0%, 1%, 5% and 10% of total grassland being made up of set-aside strips).
253 Where effects are proportionate to area, we would expect success probabilities to be the
254 same, regardless of the composition of grassland in terms of SNG and set-aside strips.

255 ***Assessing alternative placement scenarios for small scale set-aside effectiveness***

256 In order to examine if alternative placement of AESs could deliver greater benefits for
257 connectivity, we assessed the persistence and expansion of metapopulations under five
258 different AES configuration scenarios: a baseline SNG-only scenario containing no set-aside
259 strips, and four scenarios with different placement of set-aside strip habitat patches (Table
260 1). Three scenarios ('current', 'random', 'aggregate') had the same area and frequency of
261 set-asides but varied their placement, whilst the fourth scenario ('double') tested the effect
262 of increasing the area of each set-aside strip in its current location (equivalent to doubling
263 the width of every set-aside strip). There are many different scenarios we could test, but
264 these four allow us to examine both aggregation and area effects of habitat provisioning
265 through AESs. Details of set-aside strip scenario construction are outlined in Appendix S1.
266 All analyses were performed in R software version 3.5.1 (R Core Team 2018).

267 **Results**

268 ***Area of land managed as AES set-aside strips***

269 Across England, 34,127 ha of land were managed as set-aside strips under the
270 Environmental Stewardship Scheme, equivalent on a national scale to 5.2% total grassland
271 area when mapped in combination with semi-natural grassland areas (total area = 624,598
272 ha). Under the 2015 distribution of set-aside strips, total areas of land within study
273 landscapes classified as set-aside strip varied from 0 to 368 ha, with a median of 63.8 ha (0
274 to 1.17 % cover, median = 0.203%; Figure S1a), with other semi-natural grassland making
275 up 0 to 23,652 ha with a median of 175 ha (0 to 75.3 % cover, median = 0.557%; Figure

276 S1b). The proportion of total grassland amount made up of set-aside strips had a median of
277 28.4% (Figure S1c).

278 ***Impact of small scale set-asides on metapopulation persistence***

279 We found no sizeable benefits of set-aside strips for metapopulation persistence for either
280 low or high dispersal species (Figure 2A, 2B; median increase in metapopulation capacity =
281 0.003%). Regardless of exact position of the persistence threshold value (which depends
282 on the reproductive rate of a species), the inclusion of set-aside strips would not increase
283 metapopulation capacity sufficiently to facilitate landscape-scale persistence in otherwise
284 non-persistent landscapes in any more than 1% (3/267) of landscapes for any given
285 threshold, assuming a threshold > 0.00001 (a threshold which would represent extremely
286 high rates of colonization relative to extinction).

287 ***Impact of small scale set-asides on range expansion***

288 Set-aside strips provided sizeable benefits for range expansion for three out of four species
289 types modelled (Figure 2C, 2D). Species with low dispersal and low density did not benefit
290 considerably from set-aside strips, with only 2% of landscapes exhibiting increased rates of
291 successful range expansion of $>5\%$. By contrast, the other three species types benefitted
292 considerably from set-asides, with 30 to 48% of landscapes (n=267) showing improved
293 range expansion when compared with no set-asides, with some landscapes showing
294 increased rates of range expansion of up to 100% (Figure 2D, *upper right, lower left* and
295 *lower right*). We set our threshold for reporting set-aside benefits at 5% improvement to

296 range expansion success, but our conclusions remain qualitatively similar at higher
297 thresholds of 10% and 25% improvement.

298 ***Importance of grassland availability for set-aside effectiveness***

299 We found that set-aside strips had a positive impact on range expansion for three of the
300 four species types we modelled, although the magnitude of benefit was dependent upon the
301 availability of non-set-aside grassland within the study landscape (Figure 3; Table S2). The
302 greatest benefits of set-asides were generally in landscapes with intermediate quantities of
303 grassland, as revealed by humped relationships between grassland cover and expansion
304 benefit (Figure 3B, *upper left* and *lower right*). However, strong colonizers (i.e. high density
305 and high dispersal species) showed greatest expansion benefits from set-aside strips where
306 grassland cover was low (all landscapes where benefits were observed had <1% grassland
307 cover) (Figure 3B, *lower right*). Even though species with low density and low dispersal
308 generally failed to benefit from set-asides, benefits were observed in a few landscapes
309 where grassland cover was highest (>3% grassland cover; Figure 3B, *upper left*).

310 ***Proportionality of set-aside strip effects***

311 Using our GLMM, we examined the extent to which the effect of set-aside strips on range
312 expansion was disproportionate to their area, by plotting success probabilities according to
313 total grassland area under alternative SNG/set-aside strip compositions (Figure 3c). This
314 illustrated that for one species type (low dispersal/high density), the effect of set-aside
315 strips is disproportionate to area (at the same total area of all grassland habitat, success
316 was higher when this was made up of a greater proportion of set-aside strips). For the

317 other three species types, set-aside strips had no greater impact on expansion success than
318 an equivalent quantity of SNG.

319 ***Testing alternative placement scenarios for set-asides***

320 The metapopulation persistence benefits of set-aside strips remained negligible regardless
321 of the placement of set-aside strips (i.e. aggregated, random or doubled; Figure S2). We also
322 examined how much additional set-aside strip area is required to substantially increase
323 metapopulation capacity given the current spatial placement of set-asides, by multiplying
324 areas of current set-aside strips by factors of 2, 5 and 10. We found that sizable increases in
325 λ_M are only found at 10 times the current set-aside areas, and these increases are limited to
326 landscapes with low values of λ_M in the absence of set-asides (i.e. those with low SNG
327 cover) (Figure S3). However, it may be that increases in metapopulation capacity could be
328 achieved through much lower total areas of set-aside strips if the spatial allocation of set-
329 asides could be optimized among landscapes, rather than relying on the existing pattern of
330 set-asides across England.

331 By contrast, range expansion benefits were improved by alternative placement scenarios of
332 set-asides, compared with current locations, for species with high dispersal and/or species
333 which occur at high densities (Figure 4, *upper right* and *lower left*). However, there was no
334 consensus strategy for achieving improvements across species types because responses to
335 spatial arrangement were species-specific (Figure 4); extinction-limited species (low
336 density/high dispersal) benefited most from aggregated patterns of set-aside strips, whilst
337 colonization-limited species (high density/low dispersal) benefited most from random
338 placement of set-asides. Doubling the area of set-aside strips proved the best strategy for

339 only one species (low density, high dispersal type). Thus, the optimal strategy for
340 placement of AESs to improve range expansion was highly dependent on species
341 characteristics, and increasing set-aside area was outperformed by strategies to improve
342 the spatial positioning of existing set-aside habitat (Figure 4, *lower left* and *lower right*).

343 **Discussion**

344 Increasing intensification of agricultural landscapes is reducing biodiversity (Foley et al.
345 2005, Reidsma et al. 2006, Newbold et al. 2015), and continuing habitat fragmentation is
346 reducing the resilience of populations in these landscapes (Thomas et al. 2004, Moritz and
347 Agudo 2013). Here, we find evidence to support our hypothesis that small scale
348 conservation set-asides, such as set-aside strips provisioned through state-funded AESs,
349 can improve landscape connectivity. Range expansion is observed at leading edges of
350 species ranges in many species responding to climate change (Hickling et al. 2006; Mason
351 et al. 2015) and our results suggest that set-aside strips could help facilitate shifts of this
352 nature. Connectivity is also important for many other processes such as in-filling within
353 species ranges, maintaining gene flow (Cushman et al. 2006; Keyghobadi 2007) and
354 allowing individuals to persist under challenging conditions within their existing range e.g.
355 moving to find suitable microclimates (Woods et al., 2015). By contrast to range expansion
356 benefits and contrary to our predictions, set-aside strips did not benefit metapopulation
357 persistence within our landscapes. Metapopulation capacity closely approximates the sum
358 of contributions from individual habitat patches (Hanski and Ovaskainen 2000); our results
359 show that the inclusion of set-aside strips within landscapes has very little effect on

360 metapopulation capacity, and so we conclude that set-asides are insufficiently large to
361 contribute to increasing the equilibrium occupancy of landscapes.

362 Our metapopulation capacity analysis illustrates that set-aside strips have only negligible
363 impacts on landscape-scale persistence, whereas our range expansion simulations show
364 reduced rates of extinction for low density species when landscapes contain set-aside
365 strips. This apparent discrepancy is probably due to different spatial and temporal
366 processes in our expansion versus persistence models. Our expansion model simulates the
367 dynamics of a metapopulation given an initial pattern of occupancy, which in this case is
368 localised to only one grid cell at one edge of a landscape. This low, localised occupancy can
369 inflate initial extinction rates (90% of extinctions occur when populations have moved < 3
370 km across the landscape and when no more than three individual grid cells have been
371 colonized; Figure S6). Under these extreme initial conditions, small scale-set asides do
372 appear to reduce localised extinctions for some species. Metapopulation capacity, on the
373 other hand, is used to calculate extinction thresholds and does this with no consideration of
374 initial occupancy, instead it considers the *equilibrium* occupancy expected in the long term
375 regardless of starting conditions. Our findings show that set-aside strips may stave off local
376 extinctions in small, isolated populations for long enough for range expansion to take hold,
377 but that set-asides do not facilitate long-term equilibrium persistence in whole landscapes
378 where metapopulations would otherwise be unable to persist. The mechanisms by which
379 set-aside strips benefit range expansion differ according to species' traits. For species
380 which are limited by high extinction rates (i.e. our low density/high dispersal species), the
381 presence of set-aside strips can prevent the localized extinction of small populations, likely
382 through a rescue effect. This allows range expansion to progress past the stringent initial

383 conditions of our simulations and, more widely, allows individual patches to resist
384 extinction long enough to contribute towards the progression of expansion. This is
385 supported by our finding that, with no change in total area, the 'aggregated' spatial scenario
386 improves upon the 'current' distribution of set-aside strips for range expansion rates for
387 this species because fewer, larger patches are better at resisting extinction. Further, it is for
388 these species that reducing the quality of set-aside patches has the greatest impact, because
389 it increases localized extinction rates. For species which are limited by their ability to
390 colonize new patches (i.e. our high density/low dispersal species), set-aside strips appear
391 to act as stepping stones of breeding habitat during range expansion. Stepping stones are
392 useful because they reduce the distances over which individuals must disperse to colonize
393 new patches, and we see that for this species, the 'random' scenario, which minimizes
394 inter-patch distances, is indeed the most effective. This benefit comes despite the fact that
395 the probability of extinction for low density species in individual set-aside strips is
396 relatively high (0.43 for each time step/generation for a median set-aside of 0.23 ha). It is
397 for this species only that set-aside strips have an impact over and above what is expected
398 based on their area alone (Figure 3c), likely due to the less aggregated spatial arrangement
399 of set-asides relative to SNG.

400 Range shifts in response to climate change are well documented (e.g. Walther et al. 2002,
401 Chen et al. 2011) and habitat availability has been shown to be a key factor influencing
402 rates of range shifting (Hill et al. 1999, Platts et al. 2019). Integrating stepping-stone
403 habitat within landscapes has been identified as an effective way of facilitating range shifts
404 (Hodgson et al. 2012, Saura et al. 2014, Hannah et al. 2014) and our study shows that agri-
405 environment options such as set-aside field margin strips can serve this stepping-stone

406 function for dispersal-limited species. However, it is clear that expansion is also dependent
407 on other species traits which influence localized extinction rates (Burton et al., 2010;
408 Lawson et al, 2012) and indeed we observe that for density-limited species, reducing
409 patch-wise extinction rates is most beneficial for expansion success. Whilst our models did
410 not examine whether or not the expansion benefits of set-aside strips will be sufficient to
411 enable species to track climate fully (we do not model shifts in climate envelopes), our
412 simulations illustrate that AES options which introduce large numbers of small habitat
413 patches into agricultural landscapes can make a sizable contribution to connectivity. We
414 expect that current policies which incentivize the establishment of small-scale set asides
415 within agricultural land may help reduce climate-driven declines of farmland species by
416 facilitating range shifts and movement of individuals across landscapes, despite not
417 affecting landscape-scale persistence within a species' current range.

418 However, our results show that small-scale set asides are not universally beneficial across
419 different types of species. For species which are strong dispersers and occur at high
420 densities, range expansion is generally successful regardless of set-asides. For species
421 which are both poor dispersers and occur at low densities, set-aside strips are too small
422 and inter-patch distances too great to provide substantial benefit. We expect that many
423 rare species of conservation concern are poor dispersers with low density (e.g. 75% of
424 declining UK butterflies Fox et al. (2015) have been classed as sedentary by Pollard and
425 Yates (1994)). Therefore, small scale set-asides are unlikely to help conserve the most
426 threatened species, which will require species-specific habitat recreation and conservation
427 management. Hence, small scale set-asides may primarily benefit species with sufficient
428 dispersal ability (> 500 m mean dispersal per generation in our models) to colonize these

429 additional patches or sufficient resistance to extinction to survive within very small
430 patches (e.g. due to high population densities; >10 individuals ha^{-1} in our models).

431 Connectivity benefits also vary according to the quantity of habitat within landscapes.
432 Previous studies (Tschardt et al. 2012), have proposed that conservation management
433 activities such as habitat recreation (e.g. set-aside strips) should be most effective in
434 landscapes with intermediate structural complexity, i.e. landscapes with an intermediate
435 quantity of habitat availability. Our findings broadly support this hypothesis for range
436 expansion and show that focusing set-asides in landscapes with intermediate quantities of
437 semi-natural habitat is a good strategy for efficient allocation of conservation resources
438 (Concepción et al. 2008, 2012, Jonsson et al. 2015). Whilst targeting habitat addition to
439 intermediate landscapes may not be the best strategy for all species, very strong expanders
440 (high density/high dispersal species) are already successful without additional habitat, and
441 very poor expanders (low density/low dispersal species) struggle regardless of habitat
442 addition. Therefore, prioritizing set-aside strips within intermediate landscapes ($\sim 0.5\text{-}4\%$
443 habitat) is a good strategy for maximizing range expansion benefits for those species for
444 which it is beneficial.

445 Our analysis uses patch-based metapopulation models which consider individual dispersal
446 events to occur without bias in direction, and without explicit dispersal mortality (except in
447 so much as dispersal frequency declines with distance), and these models have been
448 criticised for not explicitly considering these processes (e.g. Ruxton et al., 1997; Conradt et
449 al., 2000). As a consequence, our results will probably apply best to those species for which
450 habitat boundaries do not represent a significant barrier to movement and for which rates

451 of mortality during dispersal are low. The impact of matrix quality on movements between
452 habitat patches is complex; whilst for many species habitat-matrix boundaries may act as
453 barriers to movement (Mair et al. 2015; Scriven et al. 2016) and increase dispersal
454 mortality (Nowicki et al., 2014), for others, non-habitat matrix can increase movement
455 speeds (Crone et al. 2019). However, given that the relative importance of these processes
456 is unclear for most species, we ran our models under the conservative assumption that the
457 matrix did not affect dispersal or mortality processes.

458 Our models assume that spatial configuration, as well as the amount of habitat, is important
459 for determining metapopulation processes and species persistence. There is considerable
460 debate regarding the relative importance of habitat amount and configuration (the 'habitat
461 amount hypothesis'; reviewed by Villard & Metzger, 2014), with some suggesting that
462 habitat amount alone can explain patterns in e.g. species persistence (Fahrig, 2013).
463 However, there is also empirical evidence to support the importance of spatial
464 configuration for both species persistence and range expansion in many circumstances (e.g.
465 Lawson et al., 2012; Saura et al., 2013; Hanski et al., 2017). Arguably, much of the
466 disagreement may be driven by changes in the relative effect of configuration versus
467 amount along gradients of habitat quantity (Villard & Metzger, 2013). Patch-based
468 metapopulation models of the kind used in this study have been used to predict the
469 occupancy and movement of real-life species, particularly butterflies, within landscapes
470 where habitat cover is relatively low and highly fragmented (e.g. Hanski & Ovaskainen,
471 2000; Wilson et al., 2010; Hanski et al., 2017), and so we expect these models to also
472 produce realistic predictions in our study system.

473 This study represents a theoretical analysis of the contributions of AES set-aside strips to
474 species persistence and connectivity. Our analysis is based only on those set-aside strips
475 provisioned through AESs; doubtless there are many field margins and grassy verges that
476 may also contribute to connectivity, but these have yet to be comprehensively mapped
477 across England. An empirical validation of our findings could be achieved by examining
478 changes in species distributions over time, using citizen science occurrence records (e.g.
479 UKCEH Biological Records Centre data), specifically examining changes in landscape
480 occupancy and rates of range expansion in relation to local set-aside availability. Our range
481 expansion results do align with empirical assessments of distributional shifts within the UK
482 which highlight the importance of additional habitat at the leading edge of expansions for a
483 diverse range of taxa including grassland flying insects (Platts et al., 2019), and that for
484 certain species, small amounts of extra habitat can have big effects on range expansion (Hill
485 et al., 2001). National AES programs are expensive and environmental subsidies should be
486 carefully designed to make best use of public funds. In testing how well the existing
487 distribution of set-aside strips fares against alternative strategies of spatial distribution, we
488 found that altering the aggregation or area of set-aside strips could substantially improve
489 range expansion, but there was no clear consensus on which strategy was universally
490 better. Previous studies surveying biodiversity in AES habitat restoration sites have shown
491 that sites located close to source habitat (i.e. with reduced isolation) show greater species
492 abundance and diversity (Knop et al., 2010; Alison et al., 2016) but it is generally unclear
493 whether AES sites act as ecological sinks, or support source populations. Our simulations
494 illustrate that reduced inter-patch distances are beneficial for dispersal limited species (i.e.
495 our random scenario), but in situations where trade-offs are necessary between inter-patch

496 distances and aggregation, prioritising proximity could be costly for low density species.
497 Species-specific responses to set-asides are likely to affect conclusions about the extent to
498 which land set-aside for nature is better integrated within or aggregated away from
499 agricultural production (e.g. Fischer et al. 2008, Phalan et al. 2011), and we suggest that
500 issues of landscape connectivity should be better considered in these discussions.

501 ***Conclusions***

502 Our results show that agri-environmental conservation interventions can have important
503 biodiversity co-benefits for connectivity and improve the extent to which species are able
504 to traverse landscapes and thus respond to changes in environmental conditions despite
505 having minimal impact on metapopulation persistence. The magnitude of range expansion
506 benefits are not universal across species or landscapes, but can be considerable (e.g. up to
507 100% improvement in range expansion in highly dispersive species). Thus, land
508 management activities can have important landscape connectivity co-benefits which
509 should be carefully weighed up in the evaluation of environmental policies and the design
510 of future schemes.

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517 **Author contributions**

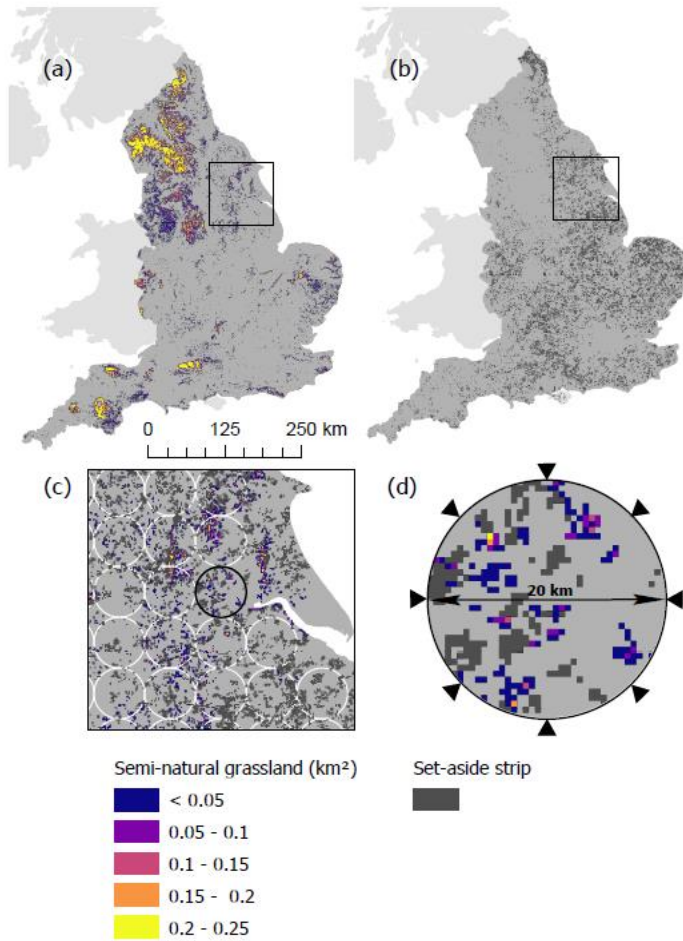
518 KRDT, JKH, CJM, JAH and NJ designed the research. JAH provided code for metapopulation
519 models. KRDT ran the models, analyzed the data. KRDT wrote the initial draft of the paper
520 with contributions from all authors.

521 **Tables**

522 *Table 1: Summary of the five habitat configuration scenarios, including one baseline (no set-*
 523 *aside strip) scenario and four alternative set-aside strip configuration scenarios. (SNG: semi-*
 524 *natural grassland; ESS: Environmental Stewardship Scheme).*

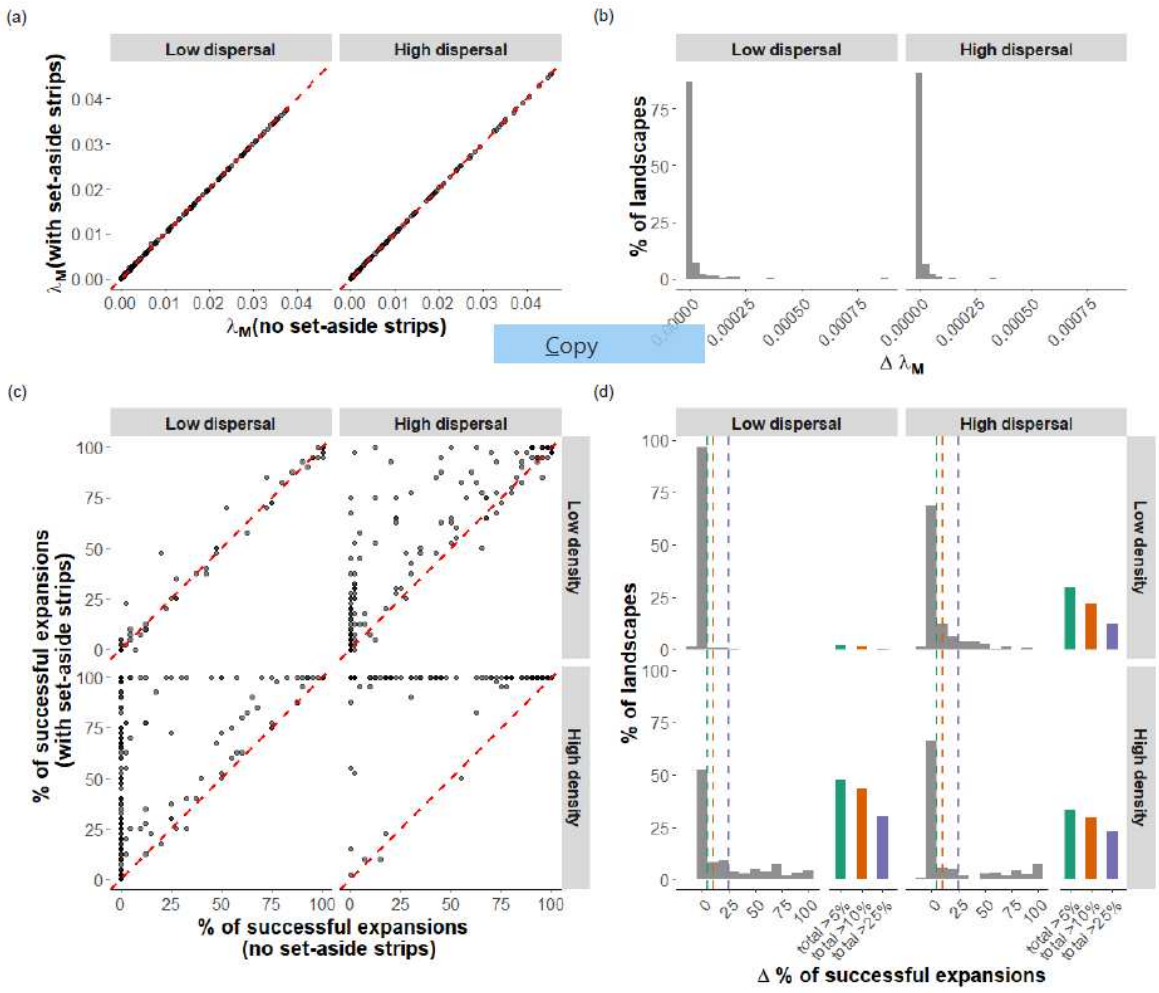
Scenario	Description	Total set-aside strip area (Ha)	Mean nearest neighbor distance (set-aside strip patches only, km)
No set-aside strips	SNG only	0	n.a.
Current set-aside strips	SNG + ESS set-aside strips	34,127	1.221
Randomized set-aside strips	SNG + ESS set-aside strips redistributed randomly	34,127	0.941
Aggregated set-aside strips	SNG + ESS set-aside strips aggregated into a single patch positioned in the location of one of the existing set-aside strips (selected randomly)	34,127	2.526
Doubled set-aside strips	SNG + ESS set-aside strips doubled in area (i.e. doubled width of every set-aside strip)	68,254	1.221

525



527

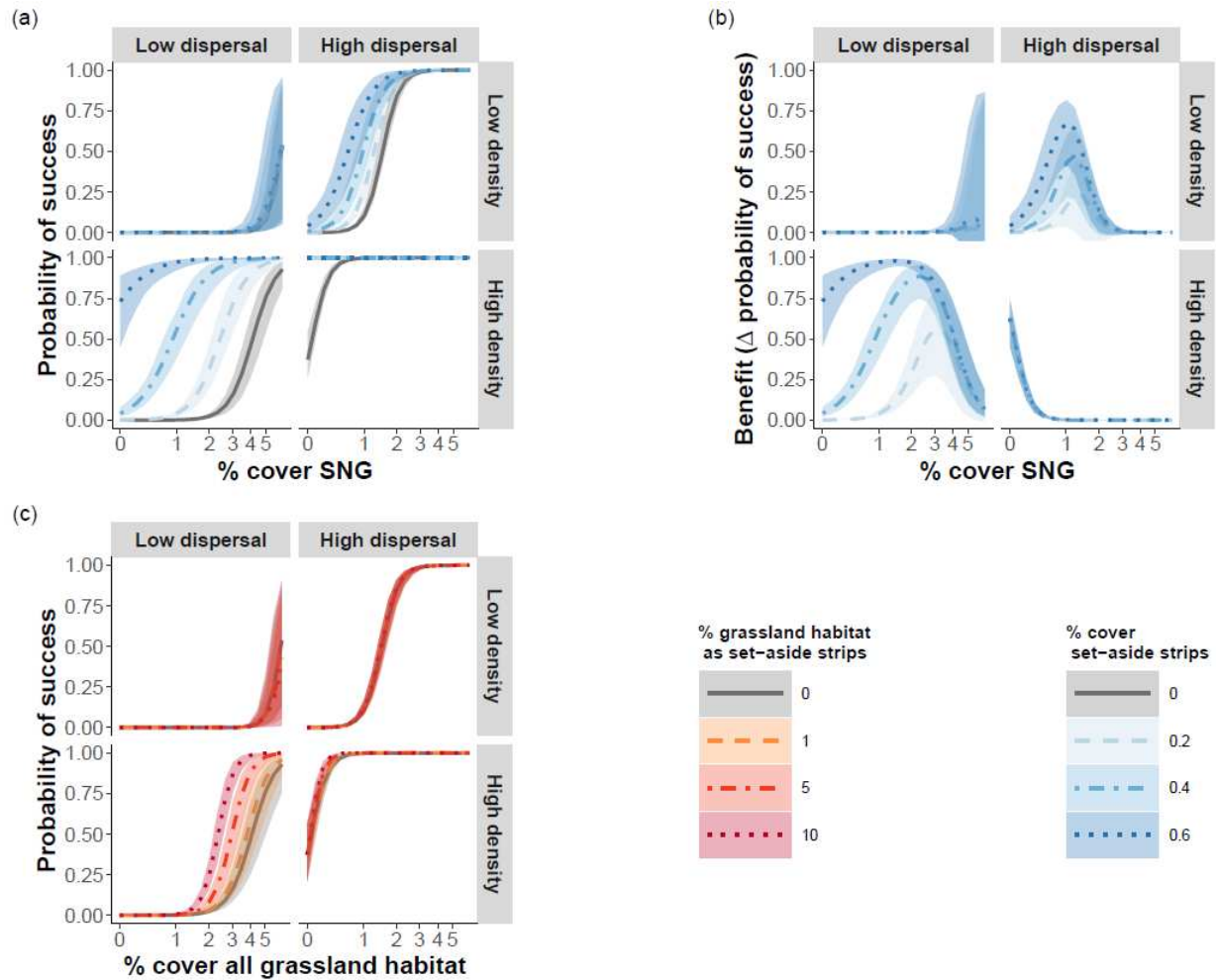
528 Figure 1: Maps of study design and landscape contexts (500m resolution). (a) The
 529 distribution of semi-natural grassland (SNG) cover within England, UK. (b) The distribution
 530 of set-aside strip-containing gridcells. (c) An example region indicating the layout of 20 km
 531 diameter circular landscapes (n=267). (d) An example landscape. Arrows indicate the eight
 532 compass directions in which expansion is tested within simulations (5 repeats per
 533 direction).



534

535 Figure 2. The impacts of the current distribution of set-aside strips on species persistence
 536 (a-b) and range expansion (c-d) for each species type (low/high dispersal = mean dispersal
 537 of 0.5km / 2 km; low/high density = 10 / 1,000 individuals ha⁻¹). (a) Metapopulation
 538 capacity (λ_M) of landscapes in the presence and absence of set-aside strips. Red dashed line
 539 indicates 1:1 line of no change. (b) Distribution of changes in metapopulation capacity
 540 across landscapes ($\Delta \lambda_M = \lambda_M[\text{with set-aside strips}] - \lambda_M[\text{without set-aside strips}]$). (c) Range
 541 expansion (measured as percentage of successful cross-landscape expansions within the
 542 IFM; 40 simulations per landscape) in the presence and absence of set-aside strips for each
 543 species type. Red dashed line indicates 1:1 line of no change. (d) Distribution of changes in

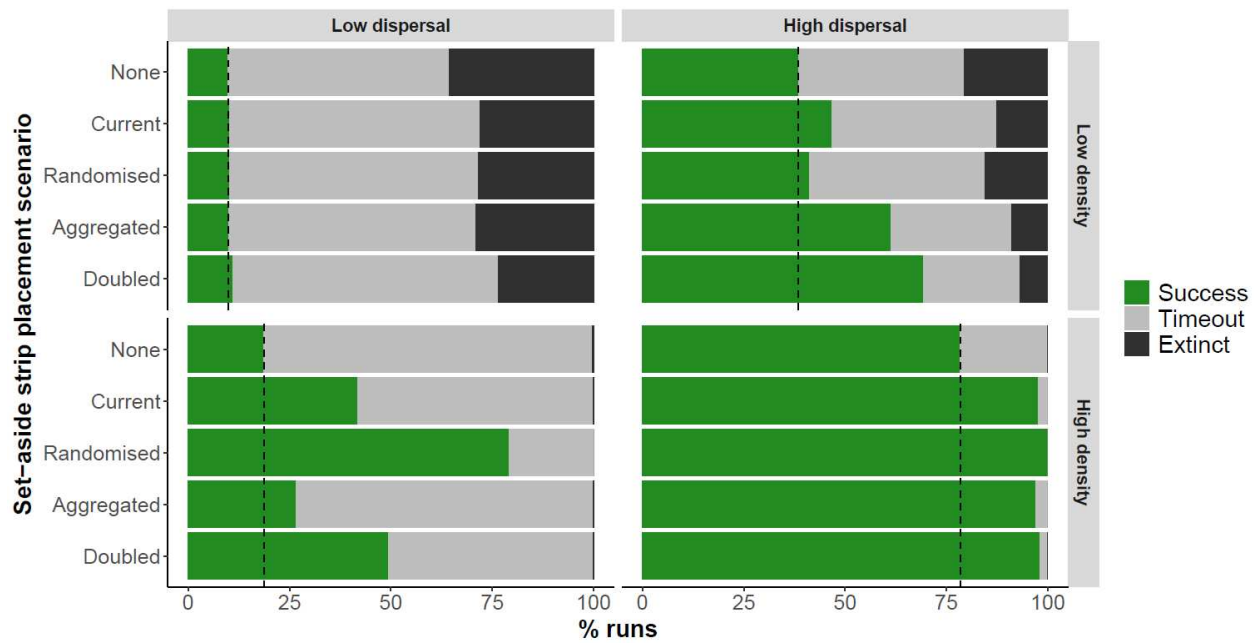
544 expansion success across landscapes. Green, orange and purple dashed lines indicate
545 thresholds of 5%, 10% and 25% respectively, and the total percentage of landscapes
546 exhibiting increases in expansion success above these thresholds are indicated by green,
547 orange and purple bars.



548

549 Figure 3. The impact of habitat cover on range expansion benefits of set-aside strips. (a)
 550 The relationship between cover of semi-natural grassland (SNG) and the probability of
 551 successful landscape crossing, as modelled using a generalized linear mixed-effects model,
 552 across four species types and for different quantities of set-aside strip addition. (b) The
 553 benefit of set-aside strip addition, where benefit is defined as the change in the probability
 554 of successful crossing after set-aside strip addition, calculated by subtracting the success
 555 probability of 0% set-aside strip addition from each of the other curves. (c) Probability of
 556 successful range expansion plotted as a function of % cover of all grassland habitat (SNG

557 and set-aside strips). Alternative lines illustrate grassland habitat made up of a varying
558 proportions of set-aside strips relative to SNG (0%, 1%, 5% and 10% set-aside strips).
559 Shaded areas indicate 95% confidence intervals calculated by bootstrapping with 1,000
560 resamples.



561

562 Figure 4. The effect of alternative set-aside strip configuration scenarios on the outcome of
 563 simulation runs, for each of the four species types. The outcome of each run was classified
 564 as either an extinction (the metapopulation went globally extinct), a timeout (the
 565 metapopulation survived the 200 generations of the simulation but failed to colonize the
 566 ‘target’ cell) or a success (the metapopulation successfully colonized the ‘target’ cell). Each
 567 species type was simulated 10,680 times under each scenario (267 landscapes x 8
 568 directions x 5 repeats). Dashed lines indicate the baseline proportion of successful
 569 simulation runs when no set-aside strips are present.

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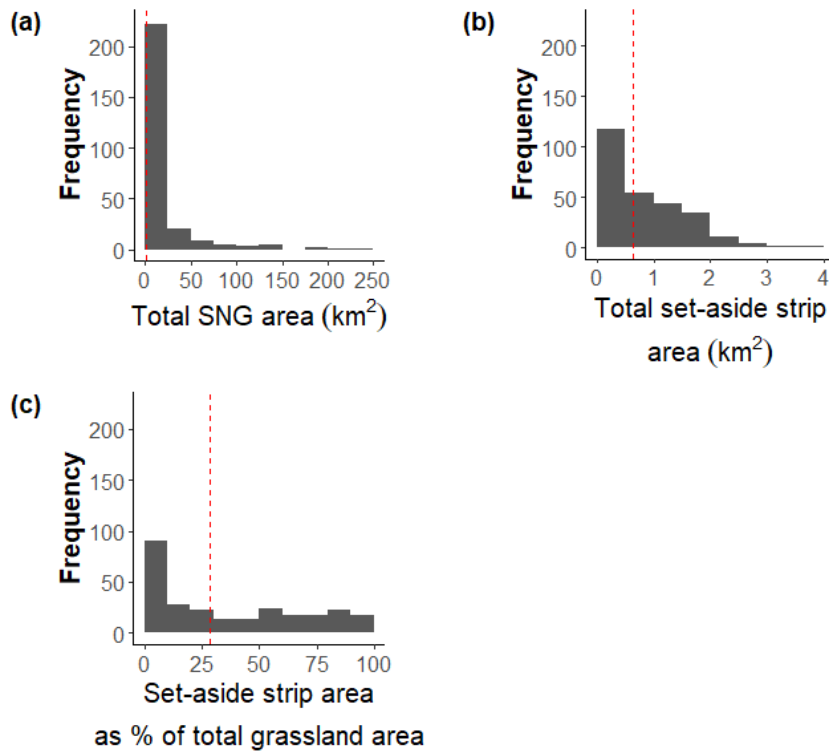
745 Wilson, G. A. 2004. The Australian Landcare movement: Towards 'post-productivist' rural
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750 Program in Ningxia Autonomous Region of China. - *China World Econ.* 16: 66–81.

751 **Supplementary materials**

752 **Supplementary Figures**

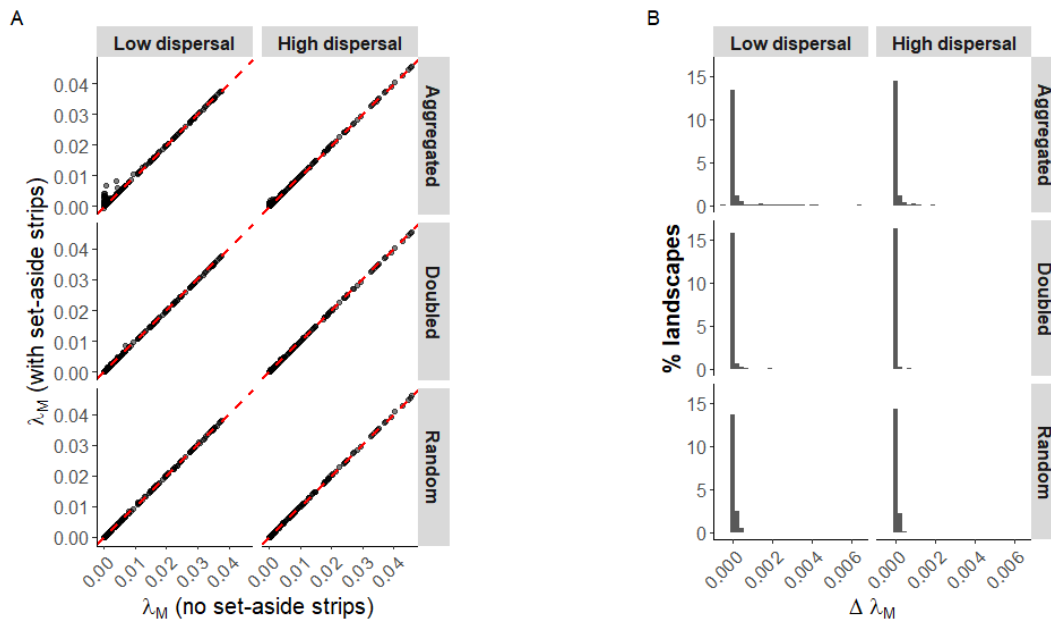
753 **Figure S1. Summary of habitat quantity and composition within landscapes**



754

755 Figure S1: The frequency of landscapes (n=267) according to (a)total quantity of semi-
756 natural grassland (SNG), (b) set-aside strip, and (c) the % of total habitat amount made up
757 of set-aside strips.

758 **Figure S2. Additional MPC scenarios**



759

760 *Figure S2: The impact of alternative set-aside strip spatial scenarios on metapopulation*

761 *persistence. (A) Comparison of the metapopulation capacity λ_M of landscapes (n=267) under*

762 *scenarios in the absence and presence of set-aside strips. Red dashed line indicates 1:1 line of*

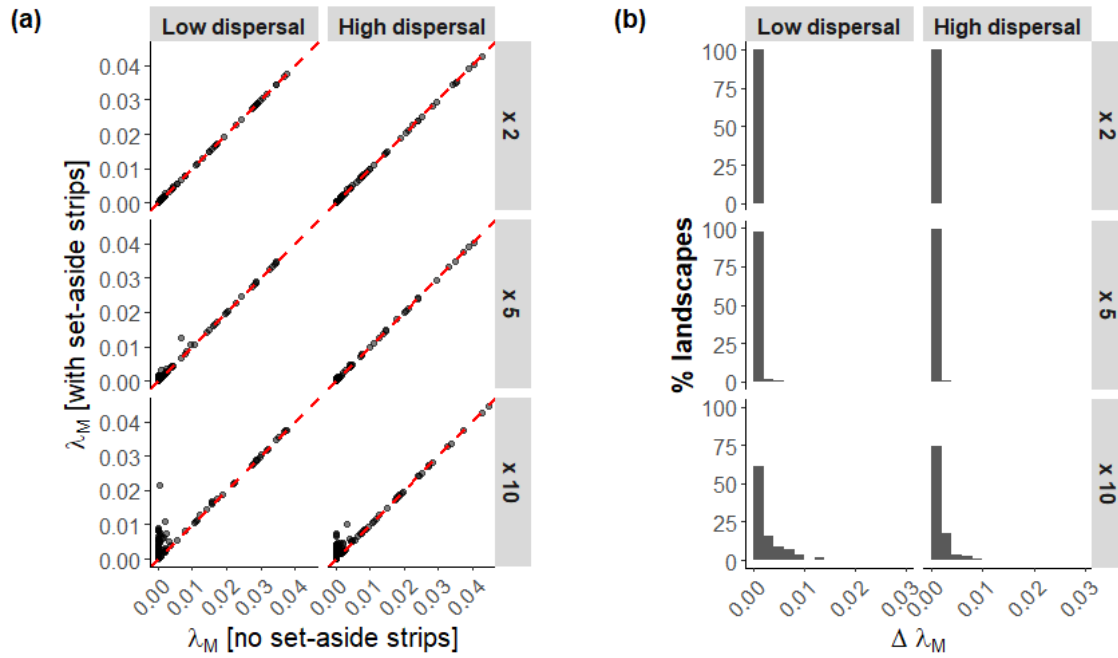
763 *no change in λ_M between scenarios. Blue dotted lines indicate hypothetical persistence*

764 *thresholds. (B) Distribution of the effect of set-aside strips on metapopulation capacity under*

765 *each scenario ($\Delta \lambda_M = \lambda_M$ [scenario with set-aside strips present] - λ_M [scenario with set-*

766 *aside strips absent]).*

767 **Figure S3. MPC under increasing set-aside area**



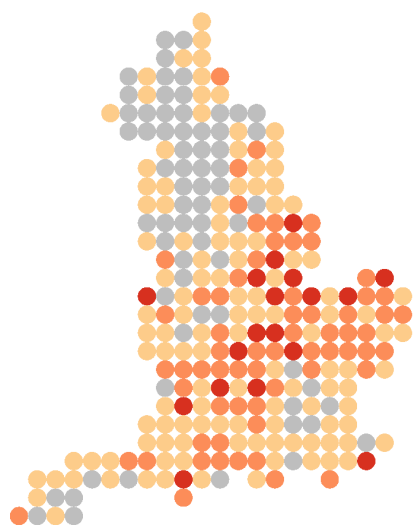
768

769 Figure S3. Metaopulation capacity (λ_M) values of landscapes under increasing quantities of
770 set-aside strips, equivalent to multiplying the areas of existing strips in their current
771 locations by 2, 5 and 10. (a) Metaopulation capacity of landscapes with and without set-
772 aside strips. Red dashed line indicates 1:1. (b) The frequency distribution of $\Delta \lambda_M$, calculated
773 as the difference between λ_M with and without set-aside strips

774

775 **Figure S4. Number of species types for which set-aside strips benefit range expansion in each**
776 **landscape**

777



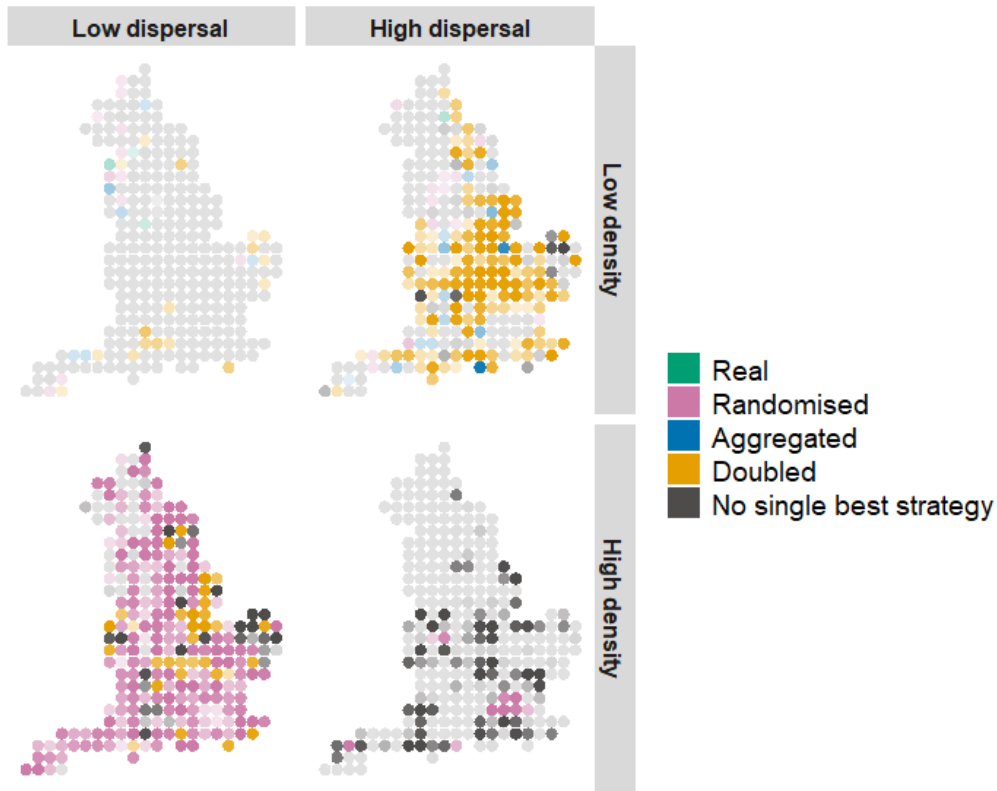
Number of species
types benefiting from
margin addition

Grey square	0	Yellow square	1	Orange square	2	Red square	3
-------------	---	---------------	---	---------------	---	------------	---

778

779 *Figure S4: The number of species types (out of four) benefiting in range expansion from set-*
780 *aside strips across all landscapes (n=267). Benefit is defined as >5% improvement in*
781 *expansion success. At least one species benefited in 74% of landscapes (198/267).*

782 **Figure S5. Maps indicating the ‘best scenario’ for range expansion in each landscape**

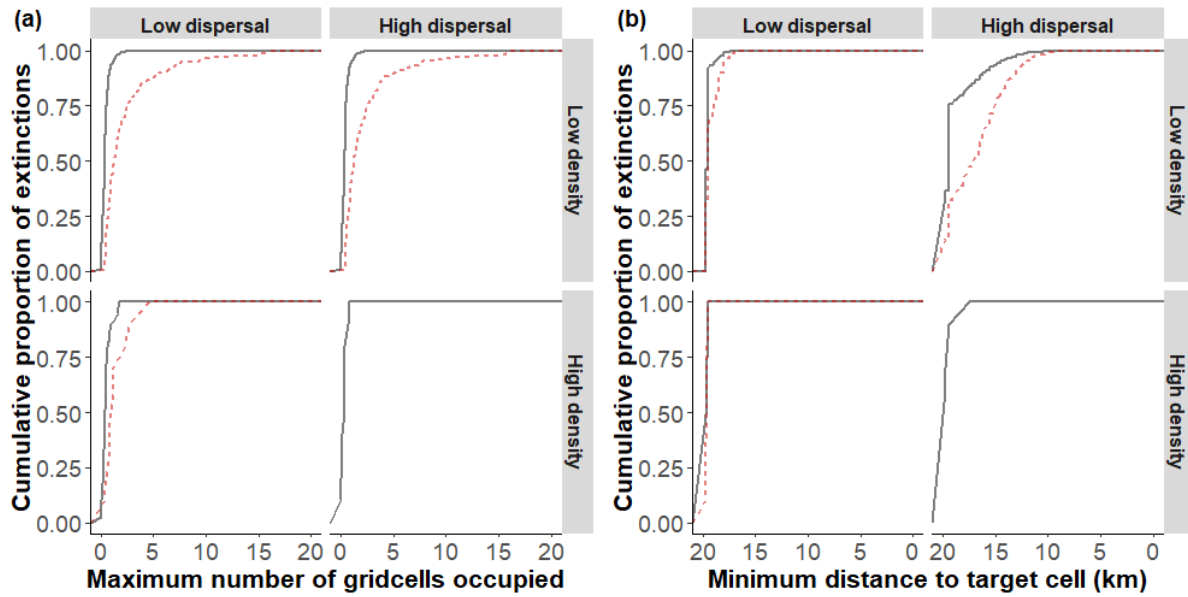


784 *Figure S5: The best scenario for facilitating range expansion for each of the species types.*

785 *Color illustrates the best scenario and transparency illustrates the magnitude of the benefit of*

786 *the best scenario when compared to the ‘no margins’ baseline.*

787 **Figure S6. Conditions of IFM simulations which result in extinction**



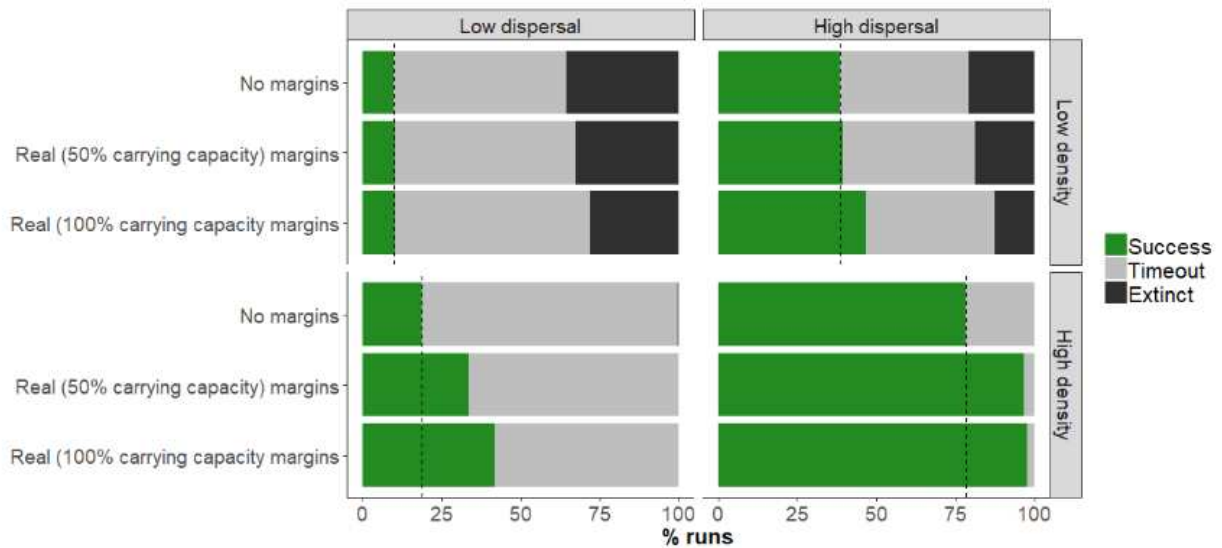
788

789 *Figure S6: Cumulative proportion of extinctions within Incidence-Function Model (IFM)*
790 *simulations related to (a) the maximum number of gridcells (500 m) which are ever occupied*
791 *within the simulation and (b) the minimum distance between occupied cells and the target*
792 *cell (edge of landscape) at the timestep (generation) before extinction occurs. Solid black line*
793 *indicates simulations under the 'no set-aside strips' scenario. Dashed red line indicates*
794 *simulations under the 'current set-aside strips' scenario.*

795

796

797 **Figure S7. Impact on range expansion of varying the carrying capacity of set-aside strip**
 798 **habitat**



799

800 *Figure S7: Range expansion simulations assuming full and half carrying capacity in set-aside*
 801 *strip patches for each of the four species types. The outcome of each run was classified as*
 802 *either an extinction (the metapopulation went globally extinct), a timeout (the*
 803 *metapopulation survived the 200 generations of the simulation but failed to colonize the*
 804 *'target' cell) or a success (the metapopulation successfully colonized the 'target' cell). Each*
 805 *species type was simulated 10,680 times under each scenario (267 landscapes x 8 directions x*
 806 *5 repeats). Dashed lines indicate baseline proportion of successful simulation runs when no*
 807 *set-aside strips are present.*

809 **Table S1. Set-aside strip option codes (Environmental Stewardship Scheme)**

Scheme	Code	Option Type	Option
ELS	EE1	Buffer strips	2m on cultivated land
ELS	EE2	Buffer strips	4m on cultivated land
ELS	EE3	Buffer strips	6m on cultivated land
ELS	EE4	Buffer strips	2m intensive grassland
ELS	EE5	Buffer strips	4m intensive grassland
ELS	EE6	Buffer strips	6m intensive grassland
ELS	EE12	Buffer strips	Supplement to add wildflowers to field corners and buffer strips on cultivated land
ELS	EF4	Arable land	Nectar flower mixture
ELS	EF11	Arable land	Uncropped cultivated set-aside strips for rare plants
ELS	EK1	Grassland outside the Severely Disadvantaged Areas (SDAs)	Take field corners out of management
HLS	HE10	Arable land	Floristically enhanced grass buffer strips (non-rotational)
OELS	OE1	Buffer strips	2m on rotational land
OELS	OE2	Buffer strips	4m on rotational land
OELS	OE3	Buffer strips	6m on rotational land
OELS	OE4	Buffer strips	2m organic grassland
OELS	OE5	Buffer strips	4m organic grassland
OELS	OE6	Buffer strips	6m organic grassland
OELS	EE12	Buffer strips	Supplement to add wildflowers to field corners and buffer strips on cultivated land
OELS	OF4	Arable land	Nectar flower mixture

OELS	OF11	Arable land	Uncropped cultivated set-aside strips for rare plants
OELS	OK1	Grassland outside the Severely Disadvantaged Areas (SDAs)	Take field corners out of management

811 **Table S2. GLMM model results**

812 *Table S2: Summary of fixed effects from generalized linear mixed effects model:*

813 *logit(success/failure) ~ log(% SNG cover + 1) * % set-aside strip cover * species type (p <*

814 *0.05*, p < 0.01**, p < 0.001***).*

Fixed effect	Coefficient	SE	z value	p
log(% SNG cover + 1)	12.670	1.785	7.099	<1.26e-12***
% set-aside strip cover	10.868	3.182	3.415	0.000638***
species2	16.353	2.791	5.858	4.68e-09***
species3	13.844	2.778	4.984	6.22e-07***
species4	24.668	2.840	8.685	<2e-16***
log(% SNG cover + 1): % set-aside strip cover	-5.370	1.307	-4.109	3.97e-05***
log(% SNG cover + 1) : species2	-3.093	1.737	-1.780	0.075014
log(% SNG cover + 1) : species3	-5.713	1.717	-3.328	0.000873***
log(% SNG cover + 1) : species4	-2.916	2.022	-1.442	0.149165
% set-aside strip cover : species2	-1.405	2.935	-0.479	0.632078
% set-aside strip cover : species3	9.715	2.937	3.308	0.000939***
% set-aside strip cover : species4	45.536	6.753	6.743	1.55e-11***

815 Species1 corresponds to the low density, low dispersal species type (density = 1,000 km⁻²; mean dispersal = 0.5 km).

816 Species2 corresponds to the low density, high dispersal species type (density = 1,000 km⁻²; mean dispersal = 2 km).

817 Species3 corresponds to the high density, low dispersal species type (density = 100,000 km⁻²; mean dispersal = 0.5 km).

818 Species4 corresponds to the high density, high dispersal species type (density = 100,000 km⁻²; mean dispersal = 2 km).

819 **Supplementary appendices**

820 **Appendix S1. Additional methodological details**

821 **Details of construction of alternative scenario layers**

822 ***No set-aside strips***

823 Raster layer at 500m resolution where the value of each cell represents the area of semi-
824 natural grassland (SNG) (according to the 2015 Land Cover Map; Rowland et al. 2017)
825 within that cell.

826 ***AES set-aside strips***

827 Raster layer at 500m resolution where the value of each cell represents the area of SNG
828 plus area of set-aside strip within that cell. Set-aside strip areas/locations were sourced
829 from the Environmental Stewardship Scheme (ESS) Options (points) dataset by Natural
830 England (accessed November 2016, [https://data.gov.uk/dataset/6c0f19e7-9a2d-4c50-
831 b548-3b7d4b9c18bb/environmental-stewardship-scheme-options-points](https://data.gov.uk/dataset/6c0f19e7-9a2d-4c50-b548-3b7d4b9c18bb/environmental-stewardship-scheme-options-points)). Only set-aside
832 strips in place as of July 2015 were included in analyses and this date was chosen because
833 2015 represented the peak of ESS agreements.

834 ***Randomized set-aside strips***

835 As for 'AES set-aside strips', except for the spatial location of set-aside strip patches. Set-
836 aside strips as present in the ESS dataset were redistributed by randomly assigning set-
837 aside strips to grid cells across England.

838 ***Aggregated set-aside strips***

839 As for ‘AES set-aside strips’, except that for each individual farm/holding (as identified by
840 ‘AGREF’ agreement codes in the ESS dataset) all set-aside strip patches were aggregated
841 such that the total set-aside strip area on each farm was assigned to a single patch at the
842 centroid of the farm.

843 ***Doubled set-aside strips***

844 As for ‘AES set-aside strips’, except the area of set-aside strip within each grid cell is
845 doubled. Equivalent to, for example, doubling the width (or carrying capacity) of each set-
846 aside strip.

847 **Construction of metapopulation models**

848 ***Metapopulation capacity***

849 Specifically, the metapopulation capacity is defined as the leading eigenvalue of the
850 landscape matrix, M, consisting of elements

851
$$m_{ij} = \begin{cases} f(d_{ij})A_i & i \neq j \\ 0 & i = j \end{cases}$$

852 where A_i is the area of patch i and $f(d_{ij})$ is a function describing the effect of inter-patch
853 distance (d_{ij}) on dispersal. Dispersal is defined here as a negative exponential function,

854
$$f(d_{ij}) = \frac{\alpha^2}{2\pi} A_i A_j \exp(-\alpha d_{ij})$$

855 where α is the parameter setting the slope of the curve and therefore the dispersal ability
856 of the species and the mean dispersal distance is $2/\alpha$.

857 ***Incidence Function Model***

858 The effect of inter-patch distance (d_{ij}) on dispersal, $f(d_{ij})$, was defined by a negative
859 exponential function as follows:

$$860 \quad f(d_{ij}) = \frac{\alpha^2}{2\pi} A_i A_j e^{-\alpha d_{ij}}$$

861 where A_i and A_j are the areas of patch i and j respectively and α is the parameter setting
862 the slope of the curve and therefore the dispersal ability of the species (the mean dispersal
863 distance is $2/\alpha$).

864 **Selection of species parameters**

865 ***Dispersal***

866 Mean dispersal distances calculated from negative exponential dispersal kernels fitted to
867 mark-release-recapture (MMR) data from European butterflies can be as high as 1.3 km
868 within individual studies (less than one generation) (1). As MMR data underestimate
869 dispersal (2, 3) and because colonization distances at the leading edge of the expanding
870 range of UK butterflies have been shown to be as high as 12 km over ~ 10 years (from
871 1995-1999 to 2005-2009; 4), we set our 'high' mean dispersal to 2 km. We set our lower
872 mean dispersal value at 0.5 km; this value approximately corresponds to mean dispersal
873 values calculated for more sedentary European butterflies (1) and below this value
874 metapopulations generally failed to expand their ranges at all in our IFM simulations.

875 ***Population density***

876 Published literature estimates population densities of European butterfly species as low as
877 <5 individuals ha⁻¹ (5) and as high as >4,000 individuals ha⁻¹ (6); in our models we define
878 'low' density at 10 individuals ha⁻¹ and 'high' density at 1,000 individuals ha⁻¹ to capture
879 this variation.

880

881 **Appendix S2. MPC code**

```
882 #####function for unscaled metapopulation capacity
883 # x & y: coordinates of patches (km)
884 # area: areas of habitat patches (km2)
885 # alpha: parameter which sets slope of negative
886 #      exponential dispersal kernel
887
888 mpc<-function(x,y,area,alpha=0.2){
889
890     d<- as.matrix(dist(cbind(x,y)))
891     M<- alpha^2/2/pi*exp(-alpha*d)*outer(area^2,area, '*')
892     diag(M)<-0
893     eg<-eigen(M, symmetric=F, only.values = FALSE)
894     l_M=eg$values[1]
895     return(l_M=eg$values[1])
896 }
```

897

898 **Appendix S3. IFM code**

```
899 #####
900 # ifm() #
901 # # #
902 # Adapted from Hodgson et al. (2011) #
903 # # #
904 # IFM function. Seeds occupancy in single cell at base of invasion axis, #
905 # which it gives 100% habitat cover, and simulation continues until cell #
906 # at opposite edge of landscape (also given 100% cover) is occupied, or #
907 # else number of generations > 'simtime', the population goes globally #
908 # extinct, or global occupancy >95%. #
909 # # #
910 #####
911 # Arguments: #
912 # # #
913 # x - vector of x-coordinates of habitat patches (in km) #
914 # y - vector of y-coordinates of habitat patches (in km) #
915 # n - vector of carrying capacity of habitat patches (calculated as #
916 # patch area * density) #
917 # alpha - slope of negative exponential dispersal kernel #
918 # density - population density (in individuals per km2) #
919 # simtime - number of generations at which to cut off simulations #
920 # rot - angle of invasion ( $\theta$  = South to North) #
921 # cellsize - cell size of gridded data (used for creating habitat start #
922 # and end cells), measured in km #
```

```

923 # Landscapesize - radius of landscape in km #
924 #####
925
926
927 ifm <- function(x,y,n,alpha,density,
928               rot, simtime=200, cellsize=0.5, landscapesize=10){
929
930   x <- x-min(x)-landscapesize # make all coordinates relative, where the
931                               # centre of the landscape is (0,0)
932   y <- y-min(y)-landscapesize
933   le <- length(x)
934   D <-( -sin(rot)*x + cos(rot)*y ) # distance along invasion axis
935                                       # (start at low end)
936   far <- max(D)
937   W <- x*cos(rot) + y*sin(rot) # width-ways distance from centre of axis
938   dw <- data.frame(D, W)
939
940   start_edge_cand <- dw[which(dw$D == min(D)),] # cells at starting edge
941                                               # of landscape
942
943   # Where there are multiple cells at starting edge, pick the one that is
944   # nearest the centre of axis of invasion. Where the axis goes between 2
945   # cells, pick the one adjacent & offset anti-clockwise from the axis.
946
947   if (nrow(start_edge_cand > 1)){

```

```

948 start_edge_cand$Wplus <- start_edge_cand$W - 0.1
949 start <- as.numeric(
950     rownames(start_edge_cand)[
951         which(
952             abs(
953                 start_edge_cand$Wplus) == min(
954                     abs(start_edge_cand$Wplus)))]
955 } else {
956     start <- as.numeric(rownames(start_edge_cand))
957 }
958
959 # start = cell number of starting cell (of all cells incl. zeros)
960
961 # x- and y-coordinates of starting cell
962 start_x <- x[start]
963 start_y <- y[start]
964
965 # Where there are multiple cells at ending edge, pick the one that
966 # is nearest the centre of axis of invasion. Where the axis goes
967 # between 2 cells, pick the one adjacent & offset anti-clockwise from
968 # the axis.
969
970 endedge <- D[rank(D) == max(rank( D ))]
971 end_edge_cand <- dw[which(dw$D == max(D)),]
972 if (nrow(end_edge_cand > 1)){

```

```

973 end_edge_cand$Wplus <- end_edge_cand$W + 0.1
974 end <- as.numeric(
975     rownames(
976         end_edge_cand)[
977             which(
978                 abs(
979                     end_edge_cand$Wplus) == min(
980                         abs(end_edge_cand$Wplus))]
981 ) else {
982     end <- as.numeric(rownames(end_edge_cand))
983 }
984
985 # end = cell number of ending cell (of all cells incl. zeros)
986
987 # x- and y-coordinates of ending cell
988
989 end_x <- x[end]
990 end_y <- y[end]
991
992 # Set up starting occupancy (all cells)
993 occ0 <- rep(FALSE, times=le)
994 occ0[start] <- TRUE
995
996 # Give starting and ending cells 100% habitat cover
997 n[start] <- cellsize^2 * density

```

```
998 n[end] <- cellsize^2 * density
999
1000 # Get rownumbers of non-habitat containing cells
1001 zeros <- which(n==0)
1002
1003 # Get rid of x, y, n elements with no habitat & redefine objects
1004 x <- x[-zeros]
1005 y <- y[-zeros]
1006 n <- n[-zeros]
1007 occ0 <- occ0[-zeros]
1008 D <- ( -sin(rot)*x + cos(rot)*y )
1009 le <- length(x)
1010
1011 # Dataframe of non-zero cell coordinates
1012 xy <- data.frame(x,y)
1013
1014 # Non-zero index of ending cell
1015 end_new <- which(xy$x==end_x & xy$y==end_y)
1016
1017
1018
1019 # Baseline probability of extinction
1020 pex<- pmin(1,1/n)
1021
```

```

1022 conn<-rep(0,le)#the connectivity
1023 for(j in 1:le){
1024   if( occ0[j] ){
1025     conn[-j] <- conn[-j]+(n[-j]/density)*alpha^2/2/pi*
1026     n[j]*exp(-alpha*
1027               sqrt( (x[-j] - x[j])^2 + (y[-j] - y[j])^2 )
1028               )#close kernel
1029   }#close if
1030 }#close j loop
1031
1032 #####output for t=0#####
1033 tis<- data.frame(t=0,no=sum(n*occ0)/sum(n),co=mean(occ0),
1034                 do=far-max(D[occ0])
1035 )
1036
1037 #####here is the actual simulation#####
1038 for(i in 1:simtime){
1039   pcol<- 1-exp(-conn)
1040   pext<- pex*(1-pcol)#extinction prob with rescue effect
1041   occ1<- (occ0*(1-pext) + (!occ0)*(pcol)) > runif(1e)#the new occupancy
1042   tis<- rbind(tis,c(t=i,no=sum(n*occ1)/sum(n),co=mean(occ1),
1043                   do= if(mean(occ1)>0){far-max( D[occ1])}else{
1044                       far-min( D )})
1045   )#the results
1046   #####test for ending#####

```



```

1047   if( sum(occ1)==0 ){break}
1048   if( (mean(occ1)>=0.95)){break}
1049   if( occ1[end_new]==TRUE ) {break} # end id not same here - NAs removed
1050   #####update connectivity#####
1051   for(j in 1:le){
1052     if( occ0[j] & !occ1[j]){
1053       conn[-j] <- conn[-j] - (n[-j]/density)*
1054         alpha^2/2/pi*n[j]*exp(-alpha*
1055           sqrt( (x[-j] - x[j])^2 + (y[-j] - y[j])^2 )
1056         )#close kernel
1057     }#close if
1058     if( !occ0[j] & occ1[j]){
1059       conn[-j] <- conn[-j] + (n[-j]/density)*
1060         alpha^2/2/pi*n[j]*exp(-alpha*
1061           sqrt( (x[-j] - x[j])^2 + (y[-j] - y[j])^2 )
1062         )#close kernel
1063     }#close if
1064   }#close j loop
1065   #####
1066   occ0<- occ1
1067 }#end time series
1068 return(list(tis=tis,time=i,rot=rot))#return this
1069 }#end the function

```

1070

1071 **Supplementary references**

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1088

1089