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Agri-environment conservation set-asides have co-benefits for connectivity

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Abstract

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

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).

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-limitedspecies (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 (Tscharntke 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 (~0.5-4%

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.

511   ### Acknowledgements

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
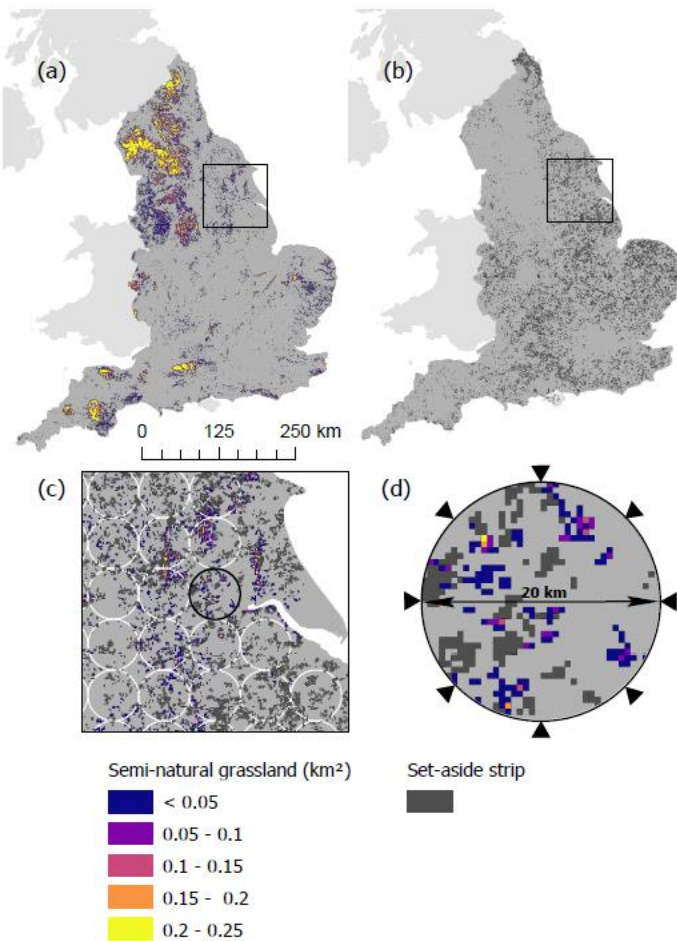
Figures

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
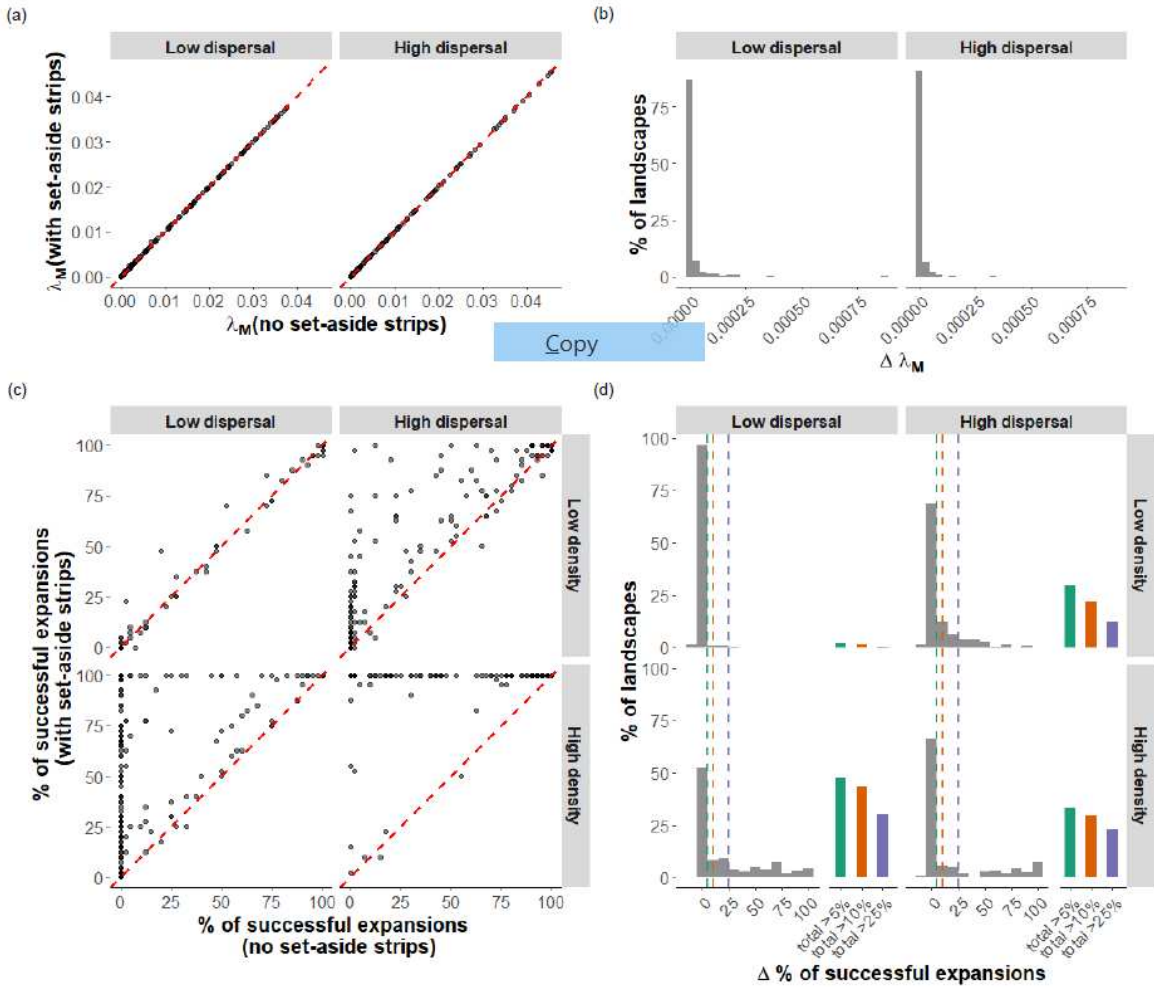
Figure 2. The impacts of the current distribution of set-aside strips on species persistence

(a-b) and range expansion (c-d) for each species type (low/high dispersal = mean dispersal

of 0.5km / 2 km; low/high density = 10 / 1,000 individuals ha$_{-1}$). (a) Metapopulation

capacity (λ_M) of landscapes in the presence and absence of set-aside strips. Red dashed line

indicates 1:1 line of no change. (b) Distribution of changes in metapopulation capacity

across landscapes ($\Delta\lambda_M=\lambda_M$[with set-aside strips])- λ_M[without set-aside strips]). (c) Range

expansion (measured as percentage of successful cross-landscape expansions within the

IFM; 40 simulations per landscape) in the presence and absence of set-aside strips for each

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,
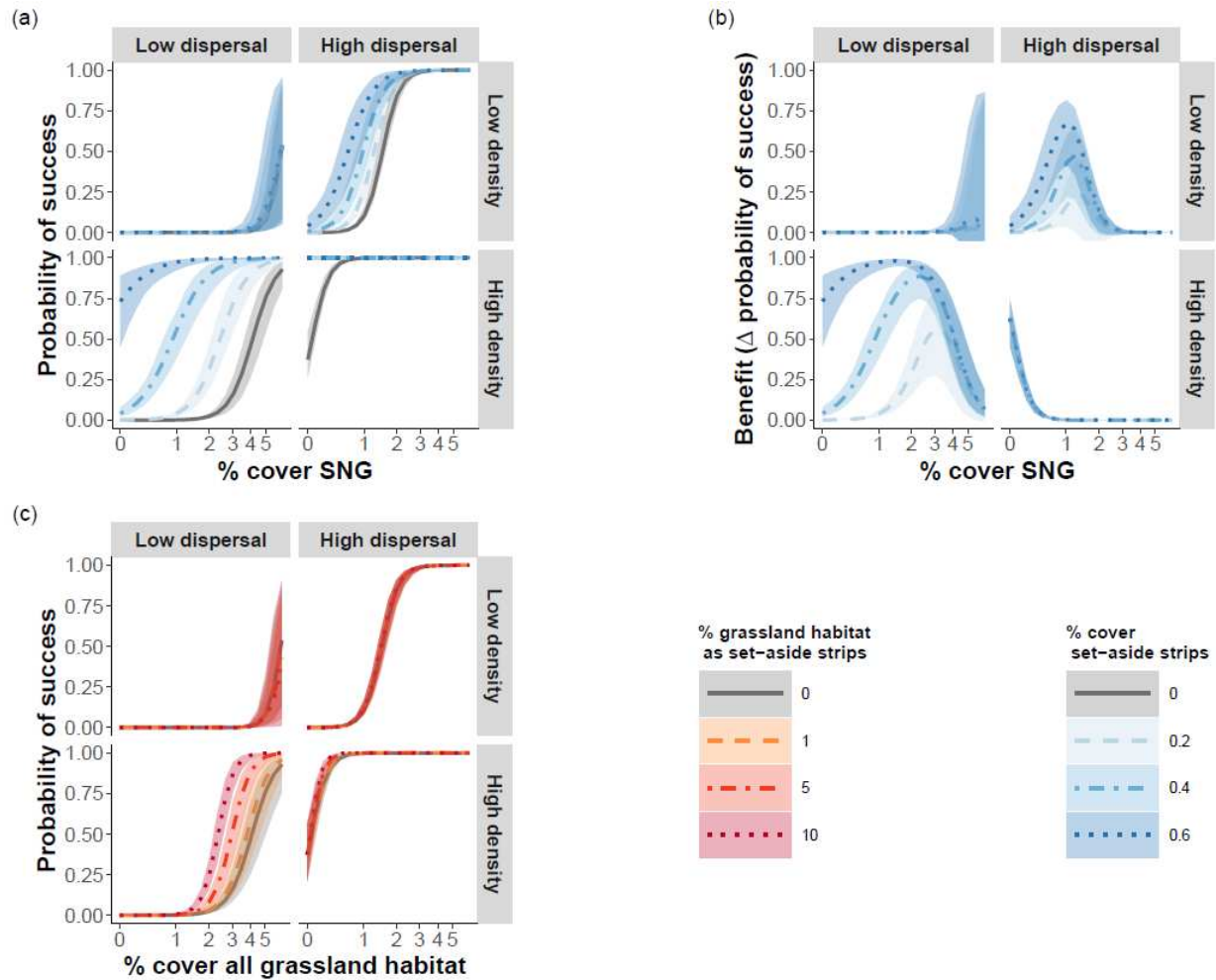
547   orange and purple bars.

548

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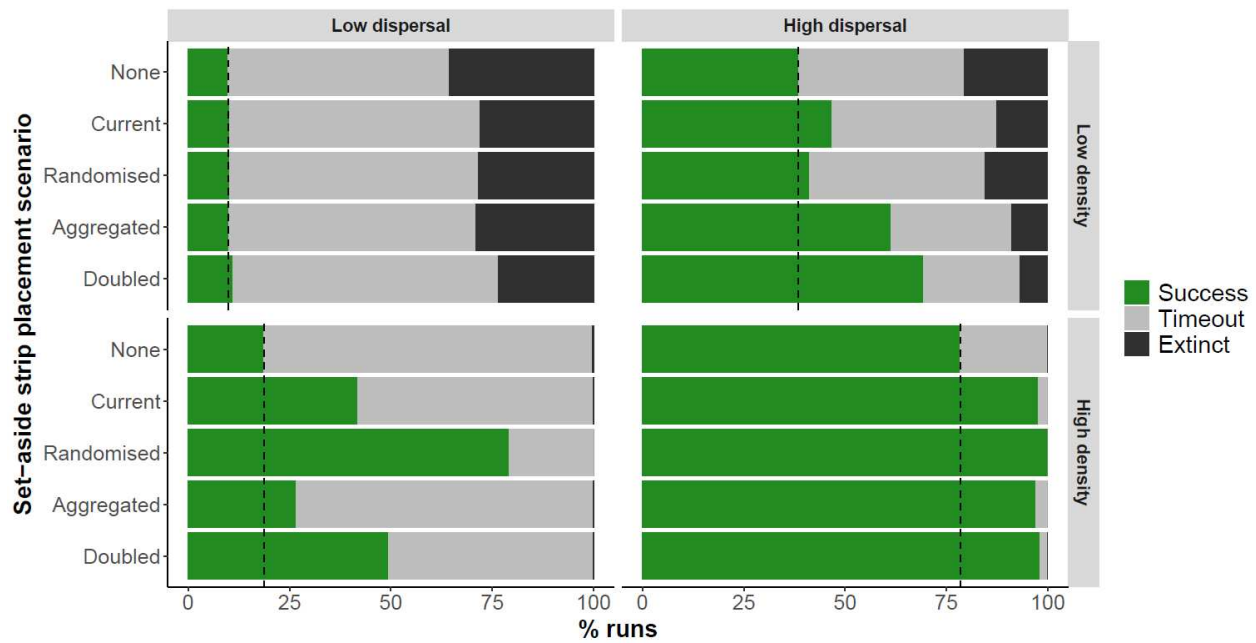
560   resamples.

561

Figure 4. The effect of alternative set-aside strip configuration scenarios on the outcome of

simulation runs, for each of the four species types. The outcome of each run was classified

as either an extinction (the metapopulation went globally extinct), a timeout (the

metapopulation survived the 200 generations of the simulation but failed to colonize the

'target' cell) or a success (the metapopulation successfully colonized the 'target' cell). Each

species type was simulated 10,680 times under each scenario (267 landscapes x 8

directions x 5 repeats). Dashed lines indicate the baseline proportion of successful

simulation runs when no set-aside strips are present.

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Supplementary materials

Supplementary Figures

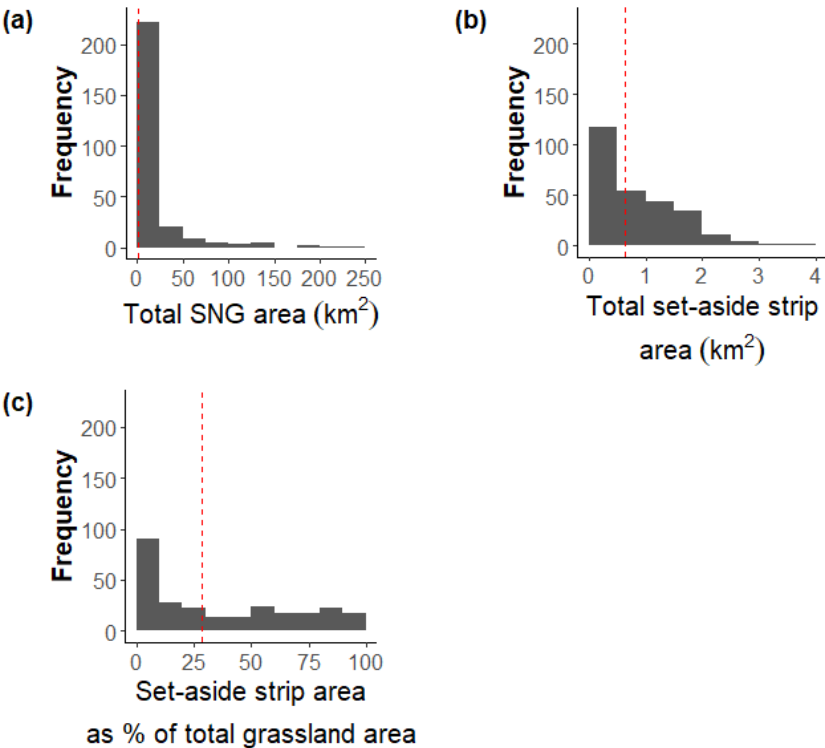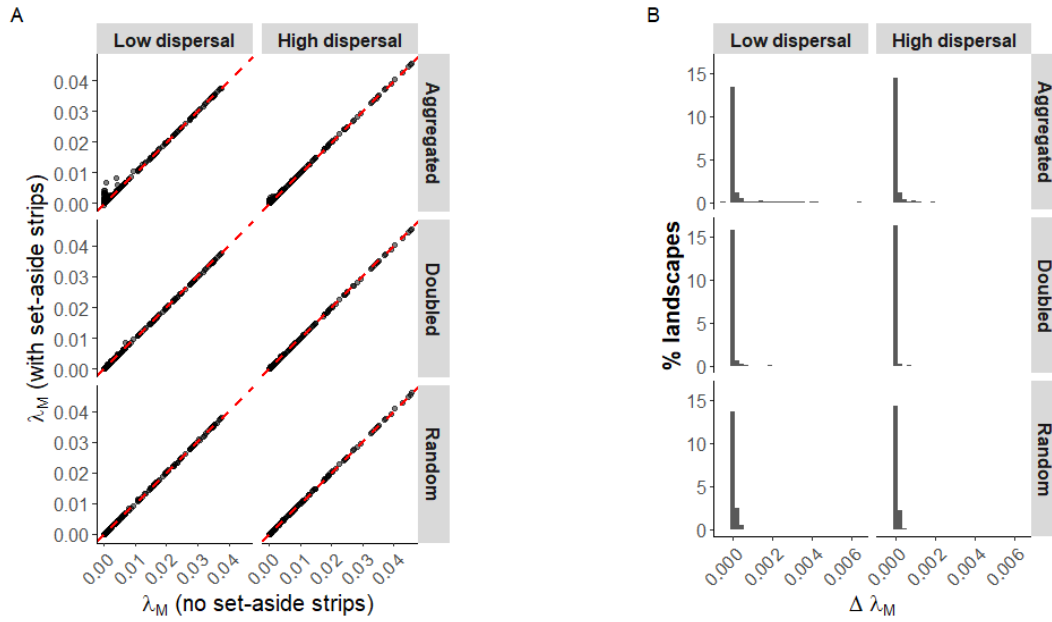**Figure S1. Summary of habitat quantity and composition within landscapes**

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

Figure S2. Additional MPC scenarios

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]).*

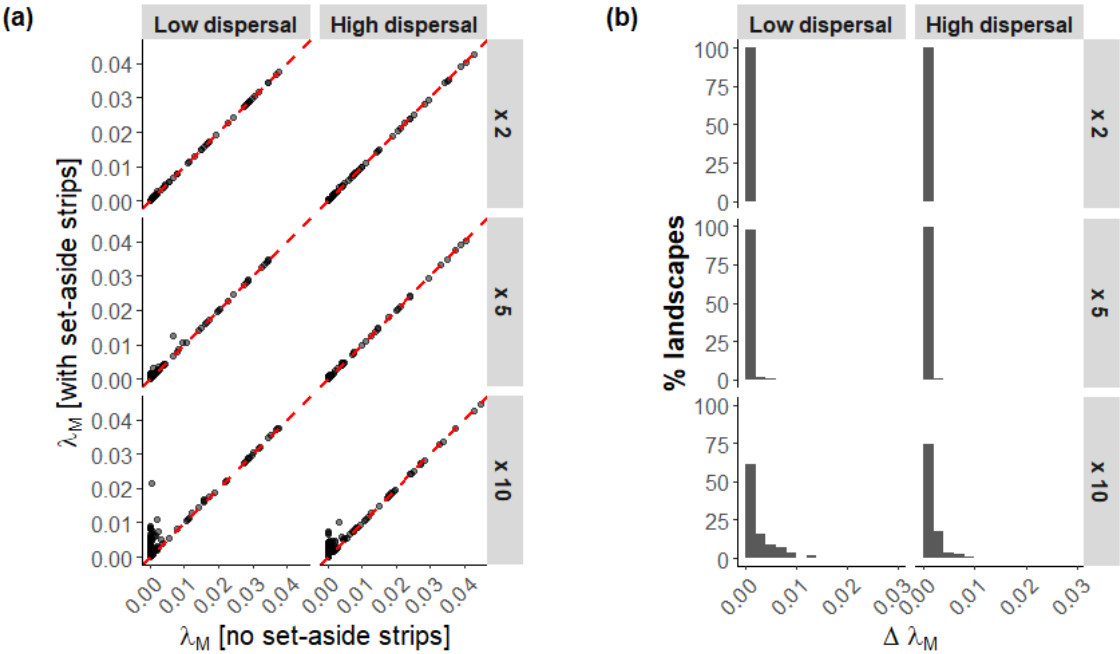767   **Figure S3. MPC under increasing set-aside area**

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) Metapopulation 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

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

landscape

Number of species
types benefiting from
margin addition

0   1   2   3
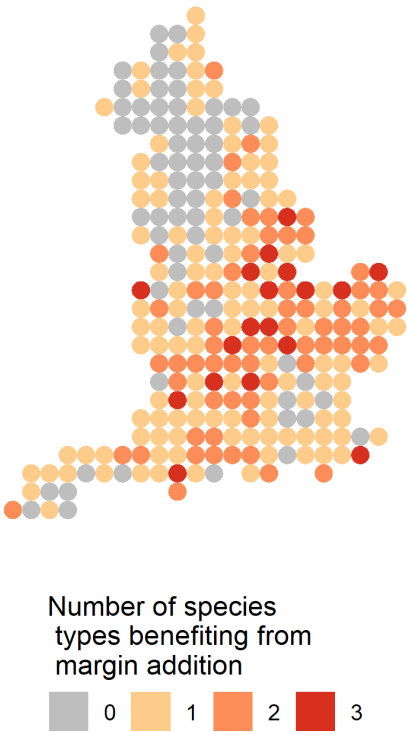
Figure S4: The number of species types (out of four) benefiting in range expansion from set-aside strips across all landscapes (n=267). Benefit is defined as >5% improvement in expansion success. At least one species benefited in 74% of landscapes (198/267).

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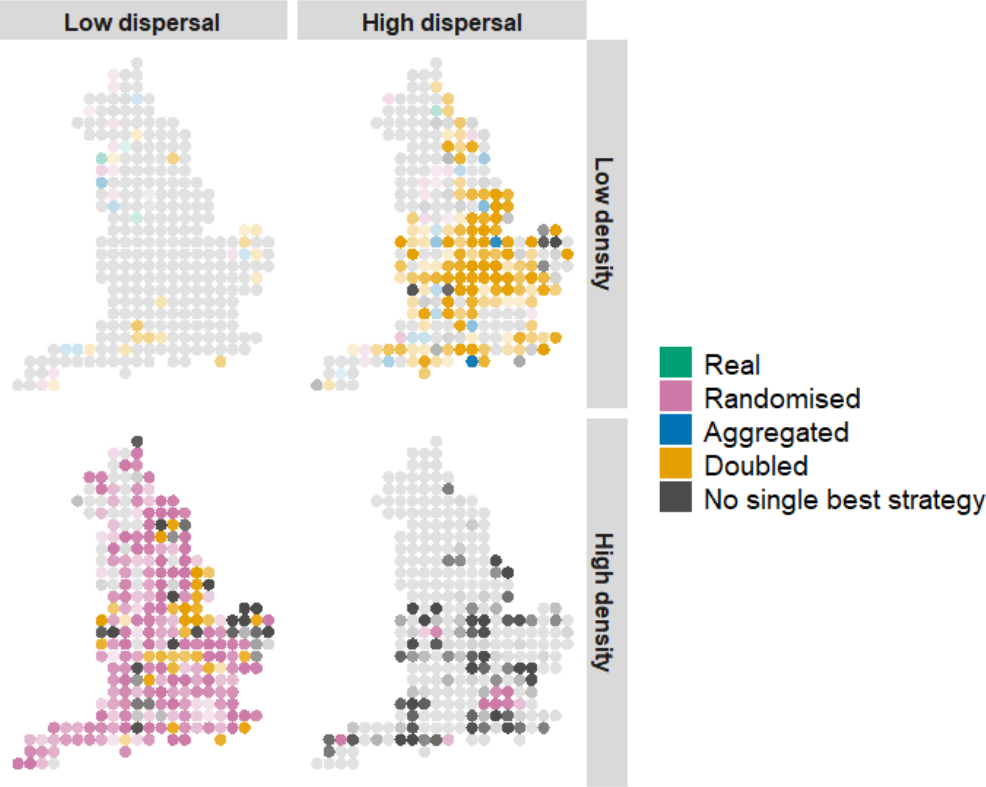

783

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**
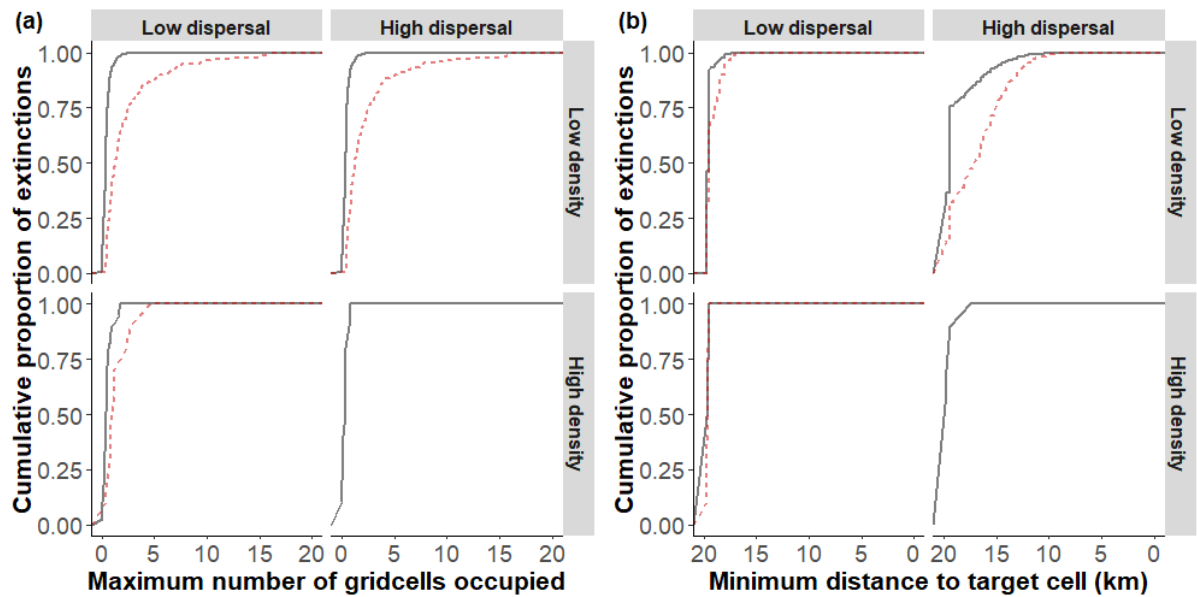

788

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
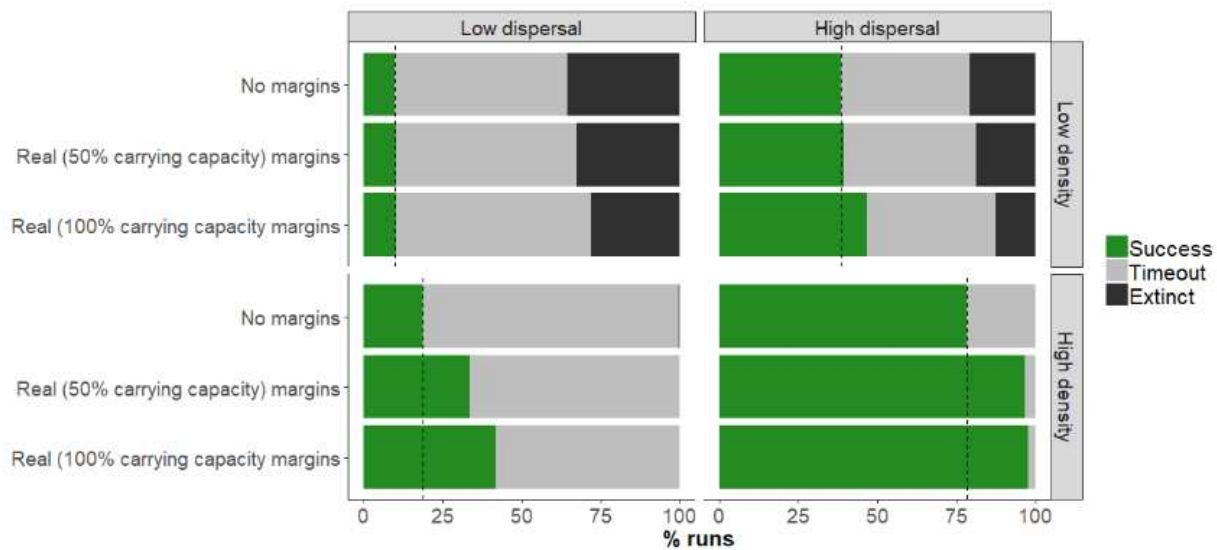
800   *Figure S7: Range expansion simulations assuming full and half carrying capacity in set-aside*

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.*

808 **Supplementary tables**

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 |

810

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

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

Appendix S2. MPC code

```r
 #####function for unscaled metapopulation capacity
# x & y: coordinates of patches (km)
# area: areas of habitat patches (km2)
# alpha: parameter which sets slope of negative
#          exponential dispersal kernel

mpc<-function(x,y,area,alpha=0.2){

  d<- as.matrix(dist(cbind(x,y)))
  M<- alpha^2/2/pi*exp(-alpha*d)*outer(area^2,area,'*')
  diag(M)<-0
  eg<-eigen(M, symmetric=F, only.values = FALSE)
  l_M=eg$values[1]
  return(l_M=eg$values[1])
}
```

Appendix S3. IFM code

```
###############################################################################
# ifm()                                                                       #
#                                                                             #
# Adapted from Hodgson et al. (2011)                                          #
#                                                                             #
# IFM function. Seeds occupancy in single cell at base of invasion axis,      #
# which it gives 100% habitat cover, and simulation continues until cell      #
# at opposite edge of landscape (also given 100% cover) is occupied, or       #
# else number of generations > 'simtime', the population goes globally        #
# extinct, or global occupancy >95%.                                          #
#                                                                             #
###############################################################################
# Arguments:                                                                  #
#                                                                             #
# x - vector of x-coordinates of habitat patches (in km)                      #
# y - vector of y-coordinates of habitat patches (in km)                      #
# n - vector of carrying capacity of habitat patches (calculated as          #
#   patch area * density)                                                     #
# alpha - slope of negative exponential dispersal kernel                      #
# density - population density (in individuals per km2)                       #
# simtime - number of generations at which to cut off simulations             #
# rot - angle of invasion (0 = South to North)                                #
# cellsize - cell size of gridded data (used for creating habitat start       #
#   and end cells), measured in km                                            #
```

```r
    # landscapesize - radius of landscape in km                              #
    ###############################################################################


ifm <- function(x,y,n,alpha,density,
                 rot, simtime=200, cellsize=0.5, landscapesize=10){

  x <- x-min(x)-landscapesize # make all coordinates relative, where the
                              # centre of the landscape is (0,0)
  y <- y-min(y)-landscapesize
  le <- length(x)
  D <-( -sin(rot)*x + cos(rot)*y ) # distance along invasion axis
                                   # (start at low end)
  far <- max(D)
  W <-  x*cos(rot) + y*sin(rot) # width-ways distance from centre of axis
  dw <- data.frame(D, W)

  start_edge_cand <- dw[which(dw$D == min(D)),] # cells at starting edge
                                                # of landscape

  # Where there are multiple cells at starting edge, pick the one that is
  # nearest the centre of axis of invasion. Where the axis goes between 2
  # cells, pick the one adjacent & offset anti-clockwise from the axis.

  if (nrow(start_edge_cand > 1)){
```

```r
      start_edge_cand$Wplus <- start_edge_cand$W - 0.1
    start <- as.numeric(
              rownames(start_edge_cand)[
                which(
                  abs(
                    start_edge_cand$Wplus) == min(
                      abs(start_edge_cand$Wplus)))])
  } else {
    start <- as.numeric(rownames(start_edge_cand))
  }

  # start = cell number of starting cell (of all cells incl. zeros)

  # x- and y-coordinates of starting cell
  start_x <- x[start]
  start_y <- y[start]

  # Where there are multiple cells at ending edge, pick the one that
  # is nearest the centre of axis of invasion. Where the axis goes
  # between 2 cells, pick the one adjacent & offset anti-clockwise from
  # the axis.

  endedge <- D[rank(D) == max(rank( D ))]
  end_edge_cand <- dw[which(dw$D == max(D)),]
  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
```

```r
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
```

```r
conn<-rep(0,le)#the connectivity
for(j in 1:le){
  if( occ0[j] ){
    conn[-j] <- conn[-j]+(n[-j]/density)*alpha^2/2/pi*
      n[j]*exp(-alpha*
                sqrt( (x[-j] - x[j])^2 + (y[-j] - y[j])^2 )
      )#close kernel
  }#close if
}#close j loop

###########output for t=0#############
tis<- data.frame(t=0,no=sum(n*occ0)/sum(n),co=mean(occ0),
                 do=far-max(D[occ0])
)

######here is the actual simulation#######
for(i in 1:simtime){
  pcol<- 1-exp(-conn)
  pext<- pex*(1-pcol)#extinction prob with rescue effect
  occ1<- (occ0*(1-pext) + (!occ0)*(pcol)) > runif(le)#the new occupancy
  tis<- rbind(tis,c(t=i,no=sum(n*occ1)/sum(n),co=mean(occ1),
                    do= if(mean(occ1)>0){far-max( D[occ1])}else{
                      far-min( D )}
  ))#the results
  #############test for ending###########
```

```r
      if( sum(occ1)==0 ){break}

      if( (mean(occ1)>=0.95)){break}

      if( occ1[end_new]==TRUE ) {break} # end id not same here - NAs removed

    ###########update connectivity#######

    for(j in 1:le){

      if( occ0[j] & !occ1[j]){

        conn[-j] <- conn[-j] - (n[-j]/density)*

          alpha^2/2/pi*n[j]*exp(-alpha*

                                    sqrt( (x[-j] - x[j])^2 + (y[-j] - y[j])^2 )

          )#close kernel

      }#close if

      if( !occ0[j] & occ1[j]){

        conn[-j] <- conn[-j] + (n[-j]/density)*

          alpha^2/2/pi*n[j]*exp(-alpha*

                                    sqrt( (x[-j] - x[j])^2 + (y[-j] - y[j])^2 )

          )#close kernel

      }#close if

    }#close j loop

    ##############

    occ0<- occ1

  }#end time series

  return(list(tis=tis,time=i,rot=rot))#return this

}#end the function
```

Supplementary references

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