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

## Keywords:

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

## Introduction

Recent centuries have seen a global transformation in land use as a consequence of large scale land conversion of (semi-) natural habitats to croplands and pasture, which now cover ~37% of land surface worldwide (Goldewijk 2001, Ramankutty et al. 2008). Changes in land use towards agricultural production not only threaten biodiversity within converted land (Foley et al. 2005, 2011, Newbold et al. 2015), but can also threaten biodiversity found in remaining, isolated fragments of natural habitat (Crooks and Sanjayan 2006, Hanski 2015). Biodiversity responses to habitat fragmentation are less predictable than responses to habitat loss (Fahrig 2003, Hodgson et al. 2009), but habitat networks which exhibit high fragmentation are at particular risk from threats from climate change (Travis 2003, Oliver et al. 2015). Designing conservation strategies which increase habitat connectivity should help mitigate these environmental stressors (Opdam and Wascher 2004, Hodgson et al. 2011, Saura et al. 2014, Scriven et al. 2015), helping species respond and adapt to climate change. In addition to distributional effects, increasing connectivity is expected to be beneficial for many other important ecological processes, such as facilitating gene flow (Cushman et al. 2006; Keyghobadi 2007) and allowing inter-patch movements so that individuals may acquire appropriate resources within their lifetimes (Taylor et al. 1993).

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

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

Here, we examine the connectivity effects of set-aside strips for species within semi-natural grasslands in England. We examine connectivity within each of 267 20 km diameter circular landscapes by modelling metapopulation persistence within each landscape (metapopulation capacity; Hanski and Ovaskainen, 2000), and range expansion across each landscape (progression of a simulated expansion from one edge of the landscape to the other, using the Incidence Function Model; Hanski, 1994). Our models are parameterized for flying insects, such as butterflies, which are sensitive to habitat fragmentation (Hanski et al. 1995, Summerville and Crist 2001, Hill et al. 2001), threatened by agricultural intensification (Thomas 2016, Habel et al. 2019), and have the potential to benefit from small-scale AESs e.g. via availability of nectar and larval host-plant resources (Feber and Smith 1995). We examine benefits of AESs for each landscape by comparing landscape-scale persistence and expansion in landscapes with and without the inclusion of set-aside strips, according to 2015 locations of AES options in England (Natural England, 2016). Specifically, we examine the hypotheses that set-aside strips provisioned through AESs can have a positive impact on the persistence and range expansion of metapopulations of grassland species. We also test the hypothesis that the effectiveness of set-aside strip patches is greatest at intermediate quantities of of non-AES semi-natural grassland habitat within the landscape. Finally, we examine whether alternative spatial arrangements (e.g. varying the spatial aggregation/increasing the area; see Table 1) of these small scale set-aside patches could be more beneficial, testing the hypothesis that the current distribution of set-asides is not optimal, because positioning was not designed with connectivity in mind.

## Materials and Methods

### *Study area*

We assessed connectivity impacts of set-aside strips for grassland species within England, UK. To split England into regional landscapes, we defined 267 non-overlapping 20 km diameter (31,400 ha) circular landscapes arranged on a regular grid (Figure 1). The size of our landscapes was chosen to be large enough to observe ecologically meaningful rates of range expansion (recent northwards range expansion of UK butterflies has been calculated at an average rate of 14.3 – 17.6 km per decade, Hickling et al. 2006), whilst small enough to provide sufficient replication of study landscapes across England. We only included landscapes for which the entire area is located within England's land border.

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

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

We mapped the positions of AES habitat recreation sites subsidized under the Environmental Stewardship Scheme (ESS). The ESS was the agri-environment scheme in England open to applications from 2005-2015, with landowner agreements (5-10 years in length) running until 2025. We conducted all analyses on data for agreements live as of 1st July 2015, before any agreements under the replacement post-2015 scheme came into operation, therefore avoiding any hand-over effects on AES abundance or distribution. We used a spatial dataset (Environmental Stewardship Scheme Options (points); Natural England, 2016) which identifies specific management options operating within each ESS-managed field in England. We selected uncropped set-aside strips (41 separate set-aside strip codes, Table S1) as a key type of commonly implemented AES option which creates grassland habitat within agricultural land in England and which feature in AES across the world. Within the ESS dataset, each field parcel containing an AES option (such as a set-aside strip) is recorded as a single point located at the centroid of the field. Each point is associated with additional information, including the total area of the AES option within that field. We extracted points representing locations and areas of all types of ESS set-aside strip and mapped the area of set-aside strip within each 500 m grid cell across England. From these data it is not possible to identify the precise location of set-aside strips within each field, but it is possible to quantify the total set-aside strip area per land parcel. Therefore, we ran models at 500 m grid cell size, a resolution which allowed models to run at as fine a scale as possible without introducing unjustified precision due to the uncertainty in the precise locations of set-aside strips within fields (most fields in England are <500 m).

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

We used the concept of metapopulation capacity ($\lambda_M$) (Hanski and Ovaskainen (2000); see Appendix S1 for additional details) to assess species persistence within each of our 267 study landscapes. $\lambda_M$ is a spatially explicit measure of the ability of a network of habitat patches to support an equilibrium metapopulation, based on the size and position of patches and the dispersal ability of a species. A non-extinct equilibrium occupancy solution exists for the landscape if and only if $\lambda_M > \delta$, where $\delta$ is the persistence threshold value as determined by the extinction and colonization properties of the species. $\lambda_M$ can be compared between landscapes to assess the relative ability of networks of habitat patches to support persistent metapopulations. We expect the addition of set-aside strips to have a consistently positive impact on $\lambda_M$, but the magnitude of this impact will be dependent on the amount and spatial context of habitat addition. Calculations of metapopulation capacity are dependent on species dispersal ability and so we calculated $\lambda_M$ for each landscape and set-aside strip scenario, for each of two species types varying in their dispersal ability, selecting values likely to span sedentary and mobile flying insects (low: mean dispersal of 0.5 km per generation; high: mean dispersal of 2 km; see Appendix S1 for details of parameter selection).

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

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

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

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

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

The outcome of each simulation run was characterized as either a 'success' (the target cell was successfully colonized), an extinction (the metapopulation went extinct), or a 'timeout' (the metapopulation survived but failed to colonize the target cell in 200 generations). We re-ran simulations under reduced set-aside carrying capacity (50% of semi-natural grassland carrying capacity per unit area) to test the sensitivity of our results to our assumption that the quality of set-aside habitat was equivalent to other areas of semi-natural grassland within the landscape (Figure S7). These results show that reducing the carrying capacity of set-asides reduces expansion success to some extent, but this is dependent upon species traits and landscape scenario. Low quality set-asides (50% of SNG per-area carrying capacity) provide very little benefit to the range expansion of low density species (successful simulations increase by <1.2%). However, they can be effective at improving expansion for high density species, increasing expansion success by 14.8% and 18.2% in low and high dispersal species respectively, compared to increases of 23.0% and 19.2% for 100% carrying capacity set-asides.

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

We examined the relationship between semi-natural grassland cover within each 20 km diameter landscape and the effectiveness of set-aside strips using a generalized linear mixed-effects model (GLMM, binomial error distribution and logit link function, using the *lme4* package in *R* software version 3.5.1). Due to the very minimal effects of set-aside strips on metapopulation persistence (see *Results*), we only analyzed the impact of local (within-landscape) grassland habitat availability on range expansion. We modelled the response of the logit of the ratio of successes to failures of 40 simulations (five repeats in each of eight directions) for each landscape/species type combination to the total area of SNG and set-aside strip within a landscape. We only analysed landscapes with <0.6% set-aside strip cover and <6.4% SNG cover due to extreme values driving negative covariance between total set-aside strip area and total habitat area (188 of 267 landscapes studied). Our GLMM had a random effects structure (random intercept only) featuring landscape identity (to account for pseudoreplication because each landscape contributed two sets of success/failure responses– simulations run with and without set-aside strips) and an observation-level random effect to account for overdispersion. We then selected a candidate fixed effects structure including effects of: % SNG cover (transformed by log(x+1)), % set-aside strip cover, species type, and the two-way interactions between these terms. We then performed backward stepwise model selection using likelihood-ratio tests to determine the fixed effects structure. We found no spatial autocorrelation in model residuals, examined by Moran's I where nearest neighbours are defined as the nearest 1, 9 or 25 landscapes. We used the best-fitting GLMM to assess the benefit of set-aside strips along a gradient of SNG cover by calculating the differences between expansion success probabilities with set-aside strips (i.e. at 0.2, 0.4, 0.6% cover), and without.

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

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

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

In order to examine if alternative placement of AESs could deliver greater benefits for connectivity, we assessed the persistence and expansion of metapopulations under five different AES configuration scenarios: a baseline SNG-only scenario containing no set-aside strips, and four scenarios with different placement of set-aside strip habitat patches (Table 1). Three scenarios ('current', 'random', 'aggregate') had the same area and frequency of set-asides but varied their placement, whilst the forth scenario ('double') tested the effect of increasing the area of each set-aside strip in its current location (equivalent to doubling the width of every set-aside strip). There are many different scenarios we could test, but these four allow us to examine both aggregation and area effects of habitat provisioning through AESs. Details of set-aside strip scenario construction are outlined in Appendix S1.

All analyses were performed in R software version 3.5.1 (R Core Team 2018).

## Results

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

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

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

### Impact of small scale set-asides on metapopulation persistence

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

### Impact of small scale set-asides on range expansion

Set-aside strips provided sizeable benefits for range expansion for three out of four species types modelled (Figure 2C, 2D). Species with low dispersal and low density did not benefit considerably from set-aside strips, with only 2% of landscapes exhibiting increased rates of successful range expansion of >5%. By contrast, the other three species types benefitted considerably from set-asides, with 30 to 48% of landscapes (n=267) showing improved range expansion when compared with no set-asides, with some landscapes showing increased rates of range expansion of up to 100% (Figure 2D, *upper right, lower left* and *lower right*). We set our threshold for reporting set-aside benefits at 5% improvement to range expansion success, but our conclusions remain qualitatively similar at higher thresholds of 10% and 25% improvement.

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

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

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

Using our GLMM, we examined the extent to which the effect of set-aside strips on range expansion was disproportionate to their area, by plotting success probabilities according to total grassland area under alternative SNG/set-aside strip compositions (Figure 3c). This illustrated that for one species type (low dispersal/high density), the effect of set-aside strips is disproportionate to area (at the same total area of all grassland habitat, success was higher when this was made up of a greater proportion of set-aside strips). For the other three species types, set-aside strips had no greater impact on expansion success than an equivalent quantity of SNG.

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

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

By contrast, range expansion benefits were improved by alternative placement scenarios of set-asides, compared with current locations, for species with high dispersal and/or species which occur at high densities (Figure 4, *upper right* and *lower left*). However, there was no consensus strategy for achieving improvements across species types because responses to spatial arrangement were species-specific (Figure 4); extinction-limitedspecies (low density/high dispersal) benefited most from aggregated patterns of set-aside strips, whilst colonization-limited species (high density/low dispersal) benefited most from random placement of set-asides. Doubling the area of set-aside strips proved the best strategy for only one species (low density, high dispersal type). Thus, the optimal strategy for placement of AESs to improve range expansion was highly dependent on species characteristics, and increasing set-aside area was outperformed by strategies to improve the spatial positioning of existing set-aside habitat (Figure 4, *lower left* and *lower right*).

## Discussion

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

Our metapopulation capacity analysis illustrates that set-aside strips have only negligible impacts on landscape-scale persistence, whereas our range expansion simulations show reduced rates of extinction for low density species when landscapes contain set-aside strips. This apparent discrepancy is probably due to different spatial and temporal processes in our expansion versus persistence models. Our expansion model simulates the dynamics of a metapopulation given an initial pattern of occupancy, which in this case is localised to only one grid cell at one edge of a landscape. This low, localised occupancy can inflate initial extinction rates (90% of extinctions occur when populations have moved < 3 km across the landscape and when no more than three individual grid cells have been colonized; Figure S6). Under these extreme initial conditions, small scale-set asides do appear to reduce localised extinctions for some species. Metapopulation capacity, on the other hand, is used to calculate extinction thresholds and does this with no consideration of initial occupancy, instead it considers the *equilibrium* occupancy expected in the long term regardless of starting conditions. Our findings show that set-aside strips may stave off local extinctions in small, isolated populations for long enough for range expansion to take hold, but that set-asides do not facilitate long-term equilibrium persistence in whole landscapes where metapopulations would otherwise be unable to persist.The mechanisms by which set-aside strips benefit range expansion differ according to species' traits. For species which are limited by high extinction rates (i.e. our low density/high dispersal species), the presence of set-aside strips can prevent the localized extinction of small populations, likely through a rescue effect. This allows range expansion to progress past the stringent initial conditions of our simulations and, more widely, allows individual patches to resist extinction long enough to contribute towards the progression of expansion. This is supported by our finding that, with no change in total area, the 'aggregated' spatial scenario improves upon the 'current' distribution of set-aside strips for range expansion rates for this species because fewer, larger patches are better at resisting extinction. Further, it is for these species that reducing the quality of set-aside patches has the greatest impact, because it increases localized extinction rates. For species which are limited by their ability to colonize new patches (i.e. our high density/low dispersal species), set-aside strips appear to act as stepping stones of breeding habitat during range expansion. Stepping stones are useful because they reduce the distances over which individuals must disperse to colonize new patches, and we see that for this species, the 'random' scenario, which minimizes inter-patch distances, is indeed the most effective. This benefit comes despite the fact that the probability of extinction for low density species in individual set-aside strips is relatively high (0.43 for each time step/generation for a median set-aside of 0.23 ha). It is for this species only that set-aside strips have an impact over and above what is expected based on their area alone (Figure 3c), likely due to the less aggregated spatial arrangement of set-asides relative to SNG.

Range shifts in response to climate change are well documented (e.g. Walther et al. 2002, Chen et al. 2011) and habitat availability has been shown to be a key factor influencing rates of range shifting (Hill et al. 1999, Platts et al. 2019). Integrating stepping-stone habitat within landscapes has been identified as an effective way of facilitating range shifts (Hodgson et al. 2012, Saura et al. 2014, Hannah et al. 2014) and our study shows that agri-environment options such as set-aside field margin strips can serve this stepping-stone function for dispersal-limited species. However, it is clear that expansion is also dependent on other species traits which influence localized extinction rates (Burton et al., 2010; Lawson et al, 2012) and indeed we observe that for density-limited species, reducing patch-wise extinction rates is most beneficial for expansion success. Whilst our models did not examine whether or not the expansion benefits of set-aside strips will be sufficient to enable species to track climate fully (we do not model shifts in climate envelopes), our simulations illustrate that AES options which introduce large numbers of small habitat patches into agricultural landscapes can make a sizable contribution to connectivity. We expect that current policies which incentivize the establishment of small-scale set asides within agricultural land may help reduce climate-driven declines of farmland species by facilitating range shifts and movement of individuals across landscapes, despite not affecting landscape-scale persistence within a species' current range.

However, our results show that small-scale set asides are not universally beneficial across different types of species. For species which are strong dispersers and occur at high densities, range expansion is generally successful regardless of set-asides. For species which are both poor dispersers and occur at low densities, set-aside strips are too small and inter-patch distances too great to provide substantial benefit. We expect that many rare species of conservation concern are poor dispersers with low density (e.g. 75% of declining UK butterflies Fox et al. (2015) have been classed as sedentary by Pollard and Yates (1994)). Therefore, small scale set-asides are unlikely to help conserve the most threatened species, which will require species-specific habitat recreation and conservation management. Hence, small scale set-asides may primarily benefit species with sufficient dispersal ability (> 500 m mean dispersal per generation in our models) to colonize these additional patches or sufficient resistance to extinction to survive within very small patches (e.g. due to high population densities; >10 individuals ha$^{-1}$ in our models).

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

Our analysis uses patch-based metapopulation models which consider individual dispersal events to occur without bias in direction, and without explicit dispersal mortality (except in so much as dispersal frequency declines with distance), and these models have been criticised for not explicitly considering these processes (e.g. Ruxton et al., 1997; Conradt et al., 2000). As a consequence, our results will probably apply best to those species for which habitat boundaries do not represent a significant barrier to movement and for which rates of mortality during dispersal are low. The impact of matrix quality on movements between habitat patches is complex; whilst for many species habitat-matrix boundaries may act as barriers to movement (Mair et al. 2015; Scriven et al. 2016) and increase dispersal mortality (Nowicki et al., 2014), for others, non-habitat matrix can increase movement speeds (Crone et al. 2019). However, given that the relative importance of these processes is unclear for most species, we ran our models under the conservative assumption that the matrix did not affect dispersal or mortality processes.

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

This study represents a theoretical analysis of the contributions of AES set-aside strips to species persistence and connectivity. Our analysis is based only on those set-aside strips provisioned through AESs; doubtless there are many field margins and grassy verges that may also contribute to connectivity, but these have yet to be comprehensively mapped across England. An empirical validation of our findings could be achieved by examining changes in species distributions over time, using citizen science occurrence records (e.g. UKCEH Biological Records Centre data), specifically examining changes in landscape occupancy and rates of range expansion in relation to local set-aside availability. Our range expansion results do align with empirical assessments of distributional shifts within the UK which highlight the importance of additional habitat at the leading edge of expansions for a diverse range of taxa including grassland flying insects (Platts et al., 2019), and that for certain species, small amounts of extra habitat can have big effects on range expansion (Hill et al., 2001).National AES programs are expensive and environmental subsidies should be carefully designed to make best use of public funds. In testing how well the existing distribution of set-aside strips fares against alternative strategies of spatial distribution, we found that altering the aggregation or area of set-aside strips could substantially improve range expansion, but there was no clear consensus on which strategy was universally better. Previous studies surveying biodiversity in AES habitat restoration sites have shown that sites located close to source habitat (i.e. with reduced isolation) show greater species abundance and diversity (Knop et al., 2010; Alison et al., 2016) but it is generally unclear whether AES sites act as ecological sinks, or support source populations. Our simulations illustrate that reduced inter-patch distances are beneficial for dispersal limited species (i.e. our random scenario), but in situations where trade-offs are necessary between inter-patch distances and aggregation, prioritising proximity could be costly for low density species. Species-specific responses to set-asides are likely to affect conclusions about the extent to which land set-aside for nature is better integrated within or aggregated away from agricultural production (e.g. Fischer et al. 2008, Phalan et al. 2011), and we suggest that issues of landscape connectivity should be better considered in these discussions.

## *Conclusions*

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

## Acknowledgements

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## Author contributions

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

# Tables

*Table 1: Summary of the five habitat configuration scenarios, including one baseline (no set-aside strip) scenario and four alternative set-aside strip configuration scenarios. (SNG: semi-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 |

# Figures

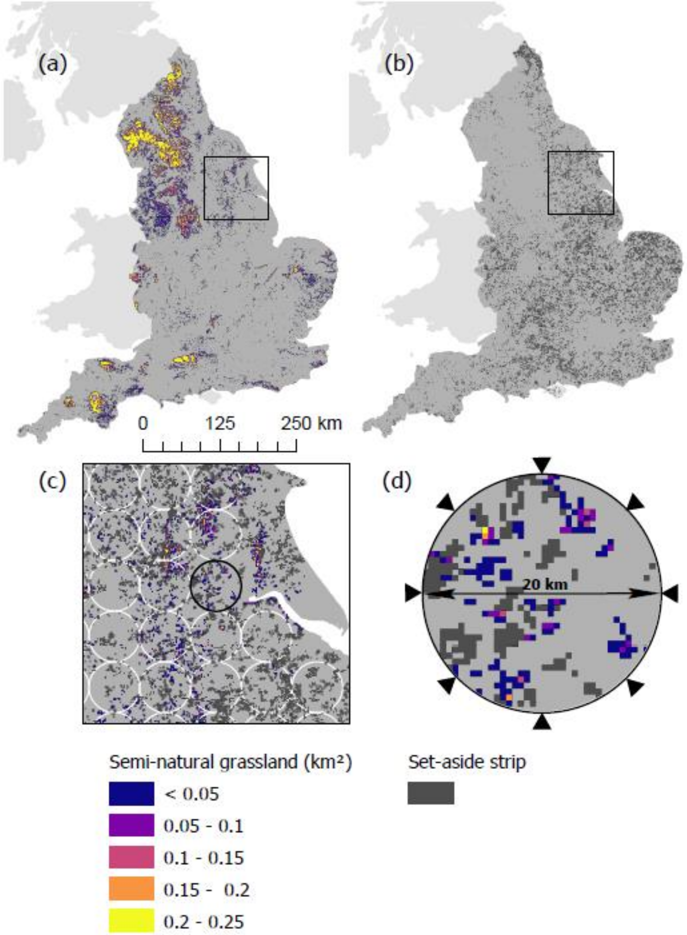

Figure 1: Maps of study design and landscape contexts (500m resolution). (a) The distribution of semi-natural grassland (SNG) cover within England, UK. (b) The distribution of set-aside strip-containing gridcells. (c) An example region indicating the layout of 20 km diameter circular landscapes (n=267).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

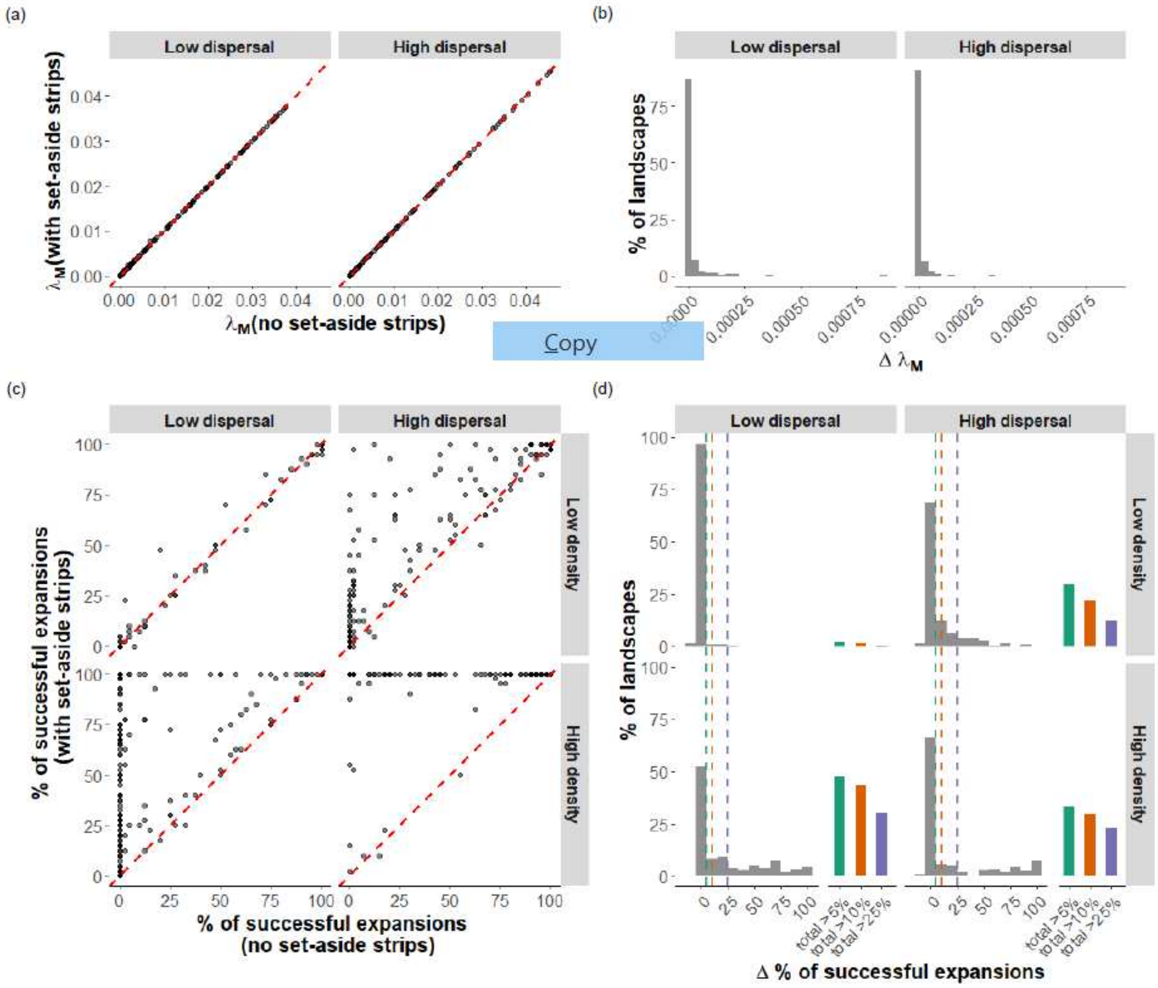

Figure 2. The impacts of the current distribution of set-aside strips on species persistence (a-b) and range expansion (c-d) for each species type (low/high dispersal = mean dispersal of 0.5km / 2 km; low/high density = 10 / 1,000 individuals $ha^{-1}$). (a) Metapopulation capacity ($\lambda_M$) of landscapes 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])- $\lambda_M$[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

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

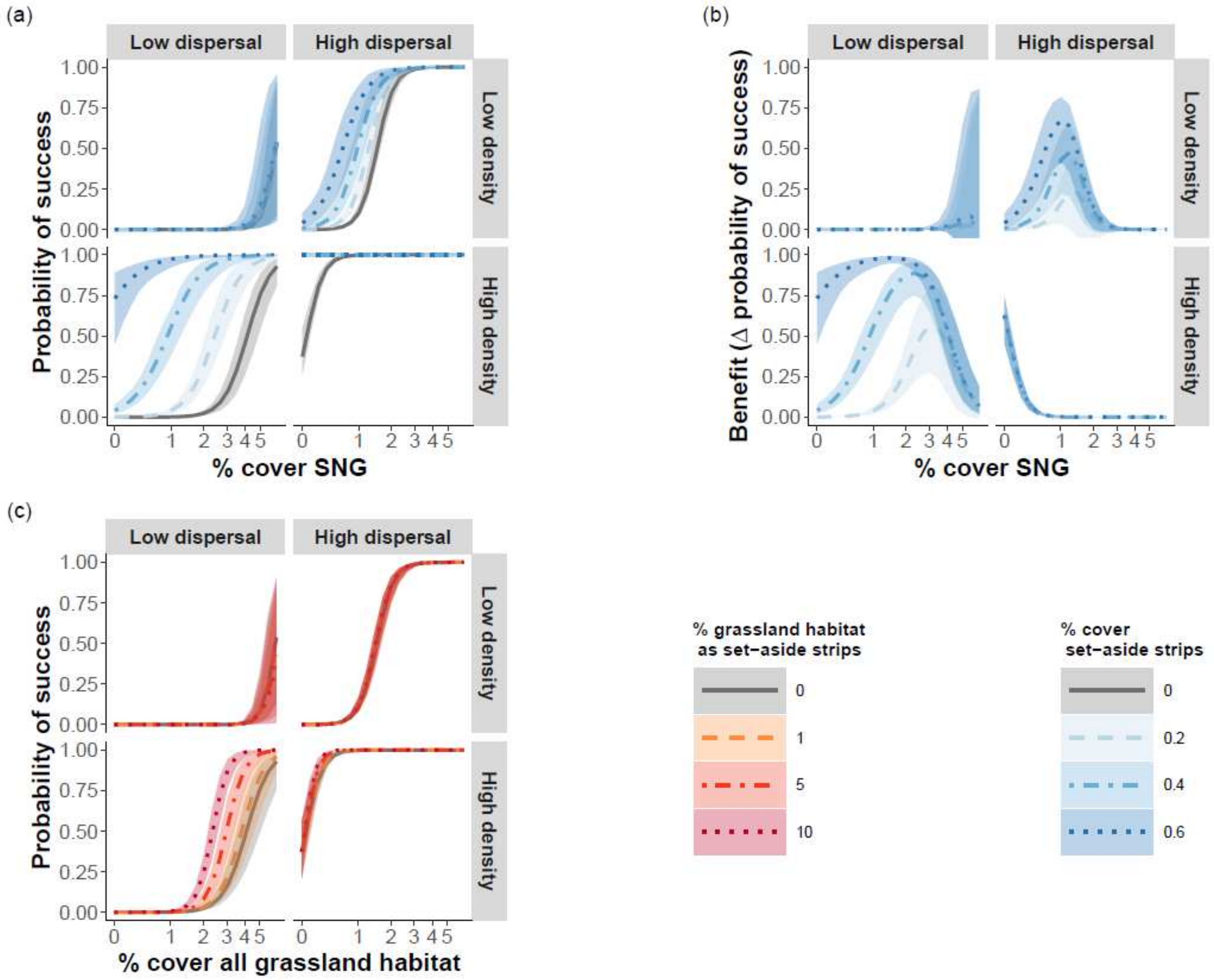

Figure 3. The impact of habitat cover on range expansion benefits of set-aside strips. (a) The relationship between cover of semi-natural grassland (SNG) and the probability of successful landscape crossing, as modelled using a generalized linear mixed-effects model, across four species types and for 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

and set-aside strips). Alternative lines illustrate grassland habitat made up of a varying proportions of set-aside strips relative to SNG (0%, 1%, 5% and 10% set-aside strips).

Shaded areas indicate 95% confidence intervals calculated by bootstrapping with 1,000 resamples.

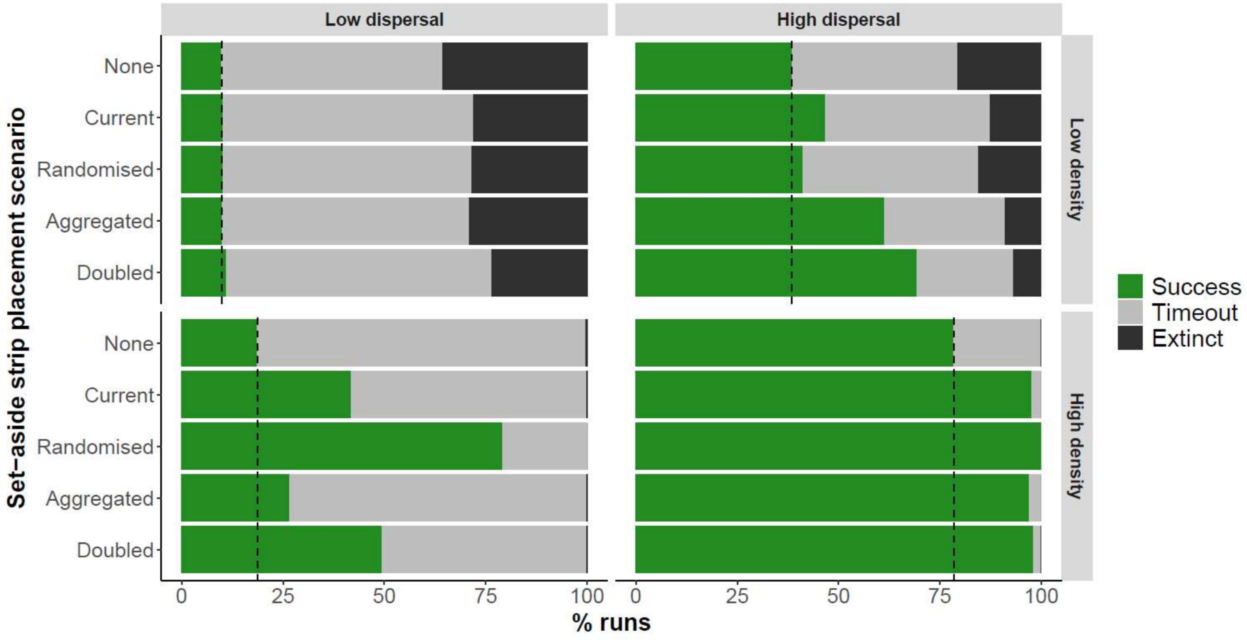

Figure 4. The effect of alternative set-aside strip configuration scenarios on the outcome of simulation runs, for each of the four species types. The outcome of each run was classified as either an extinction (the metapopulation went globally extinct), a timeout (the metapopulation survived the 200 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

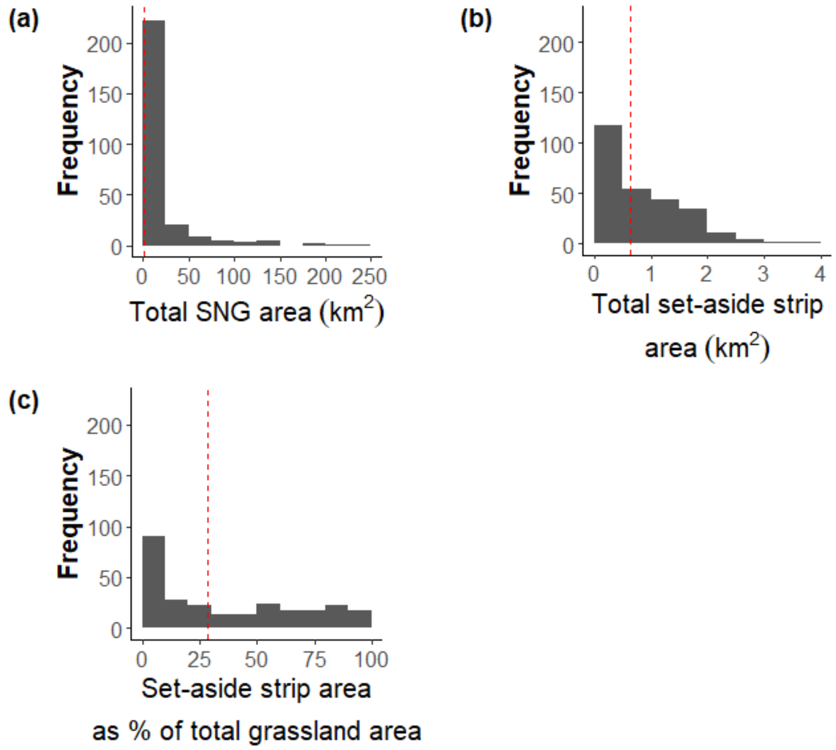


Figure S1: The frequency of landscapes (n=267) according to (a)total quantity of semi-natural grassland (SNG), (b) set-aside strip, and (c) the % of total habitat amount made up of set-aside strips.

## Figure S2. Additional MPC scenarios

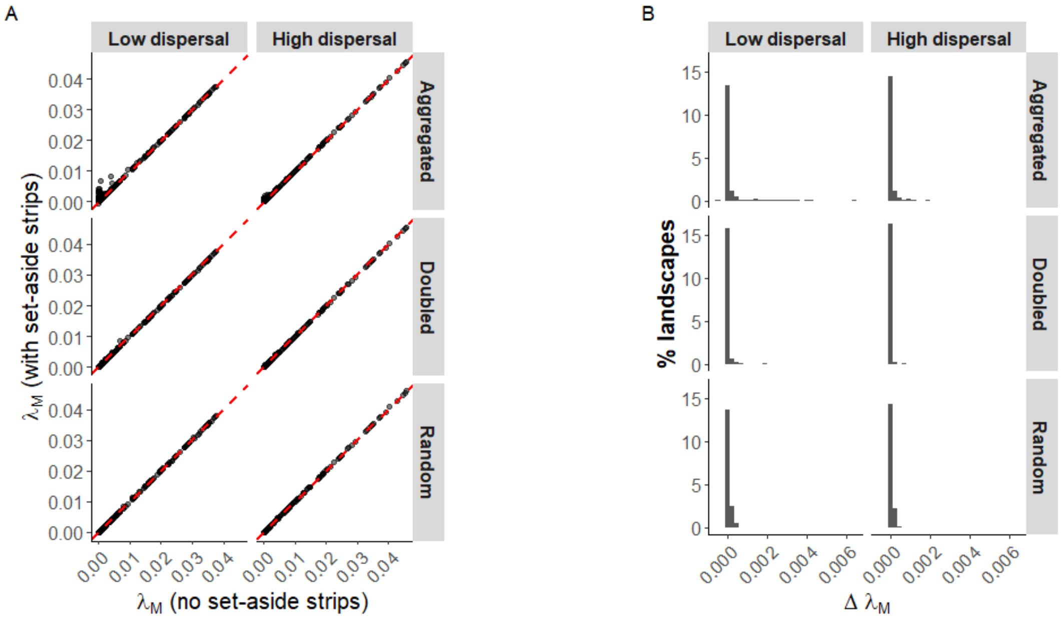


*Figure S2: The impact of alternative set-aside strip spatial scenarios on metapopulation persistence. (A) Comparison of the metapopulation capacity $\lambda_M$ of landscapes (n=267) under scenarios in the absence and presence of set-aside strips. Red dashed line indicates 1:1 line of no change in$\lambda_M$ between scenarios. Blue dotted lines indicate hypothetical persistence thresholds. (B) Distribution of the effect of set-aside strips on metapopulation capacity under each scenario ($\Delta\lambda_M = \lambda_M$ [scenario with set-aside strips present] - $\lambda_M$ [scenario with set-aside strips absent]).*

## Figure S3. MPC under increasing set-aside area

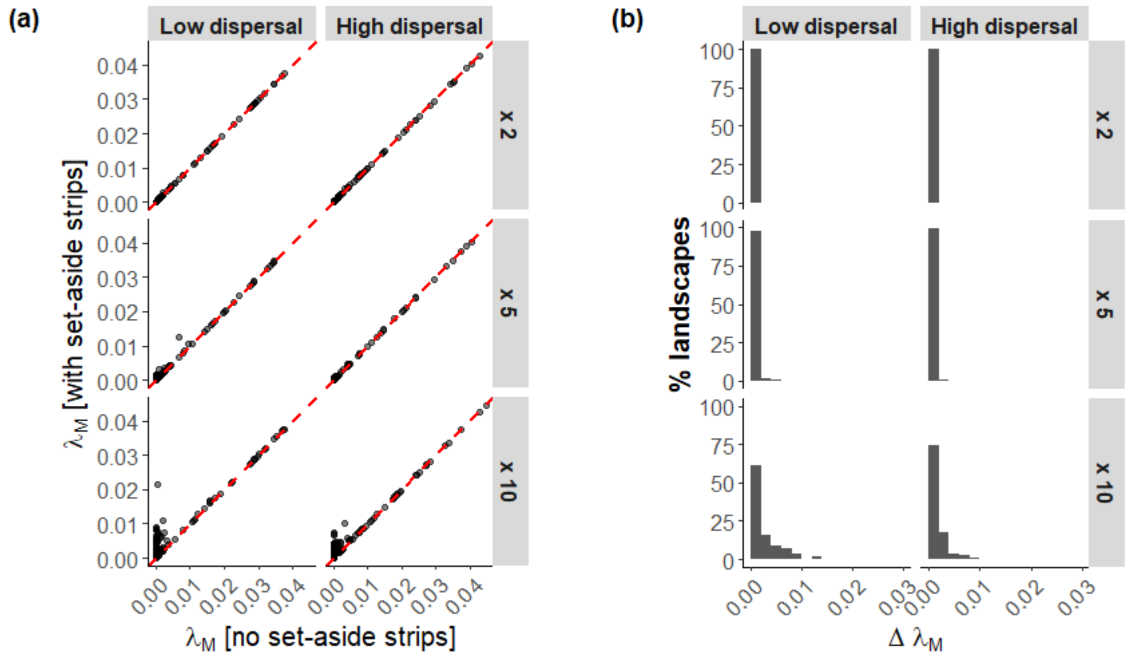


Figure S3. Metaopulation capacity ($\lambda_M$) values of landscapes under increasing quantities of set-aside strips, equivalent to multiplying the areas of existing strips in their current locations by 2, 5 and 10. (a) Metapopulation capacity of landscapes with and without set-aside strips. Red dashed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

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

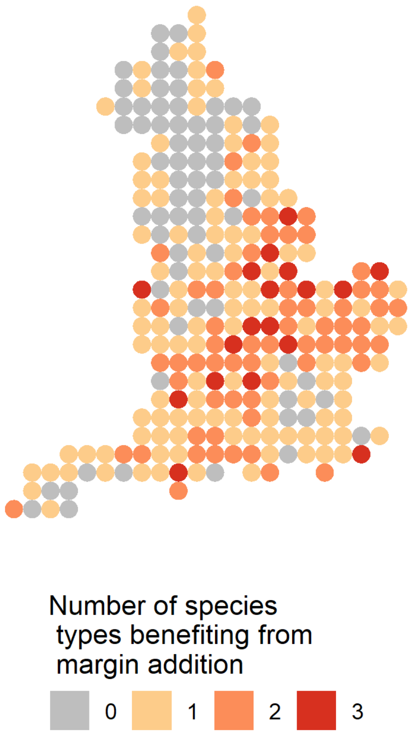
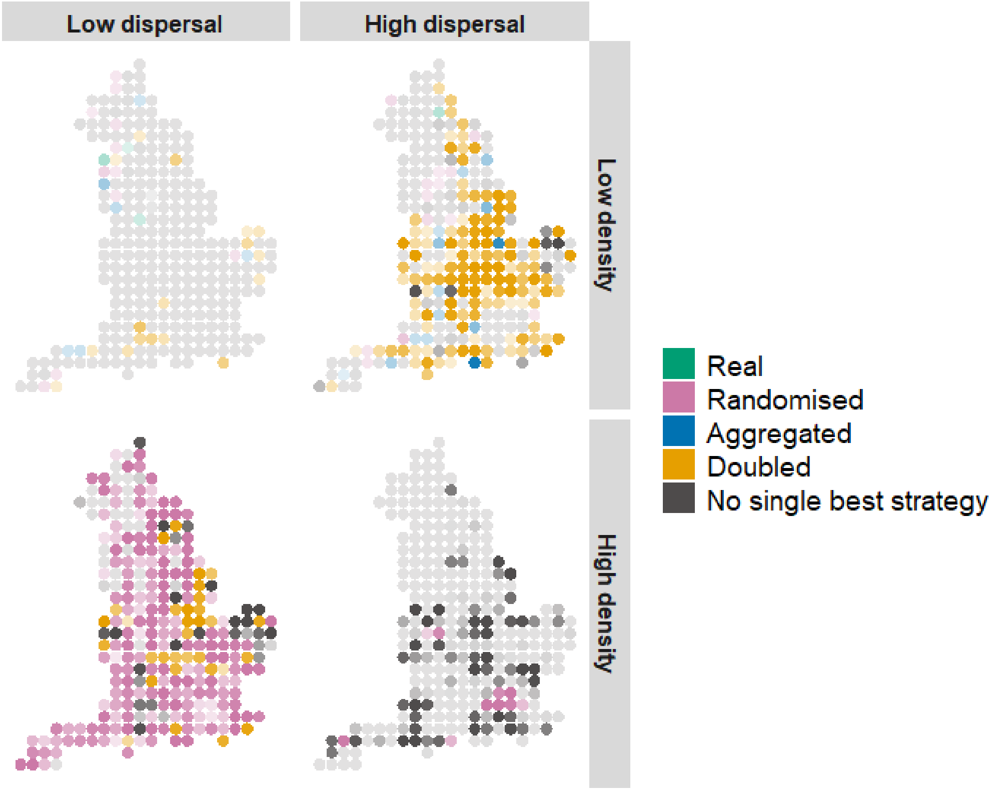


*Figure S4: The number of species types (out of four) benefiting in range expansion from set-aside strips across all landscapes (n=267). Benefit is defined as >5% improvement in expansion success. At least one species benefited in 74% of landscapes (198/267).*

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.*

### Figure S6. Conditions of IFM simulations which result in extinction

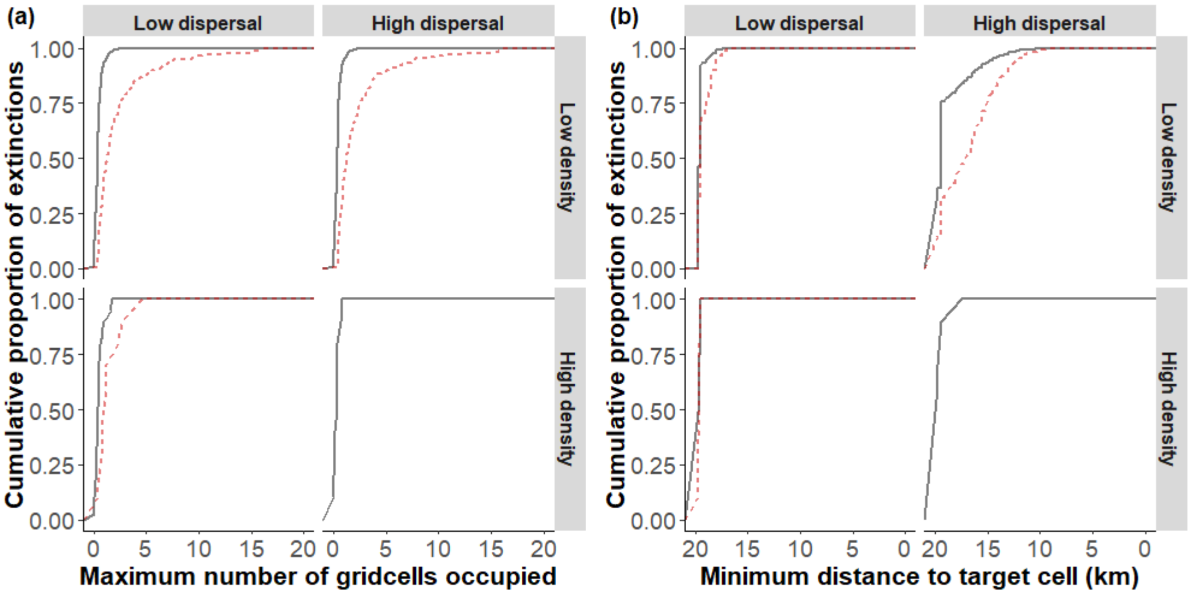


*Figure S6: Cumulative proportion of extinctions within Incidence-Function Model (IFM) simulations related to (a) the maximum number of gridcells (500 m) which are ever occupied within the simulation and (b) the minimum distance between occupied cells and the target cell (edge of landscape) at the timestep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

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

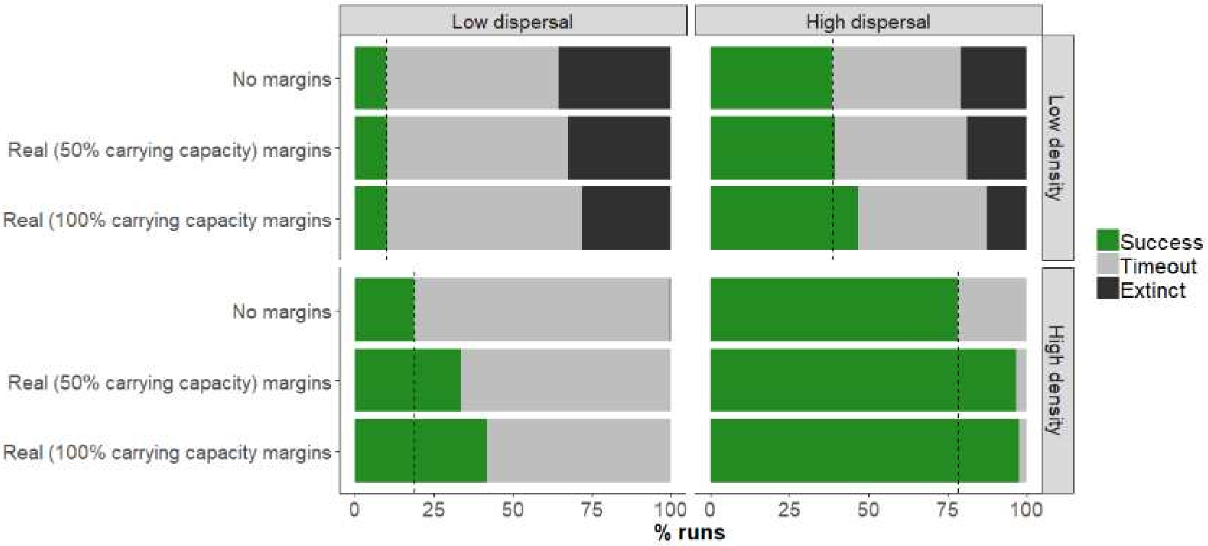


*Figure S7: Range expansion simulations assuming full and half carrying capacity in set-aside strip patches for each of the four species types. The outcome of each run was classified as either an extinction (the metapopulation went globally extinct), a timeout (the metapopulation survived the 200 generations 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 baseline proportion of successful simulation runs when no set-aside strips are present.*

# Supplementary tables

**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 |

## Table S2. GLMM model results

*Table S2: Summary of fixed effects from generalized linear mixed effects model: logit(success/failure) ~ log(% SNG cover + 1) * % set-aside strip cover * species type (p < 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*** |

Species1 corresponds to the low density, low dispersal species type (density = 1,000 $km^{-2}$; mean dispersal = 0.5 km).

Species2 corresponds to the low density, high dispersal species type (density = 1,000 $km^{-2}$; mean dispersal = 2 km).

Species3 corresponds to the high density, low dispersal species type (density = 100,000 $km^{-2}$; mean dispersal = 0.5 km).

Species4 corresponds to the high density, high dispersal species type (density = 100,000 $km^{-2}$; mean dispersal = 2 km).

# Supplementary appendices

## Appendix S1. Additional methodological details

### Details of construction of alternative scenario layers

#### *No set-aside strips*

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

#### *AES set-aside strips*

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

#### *Randomized set-aside strips*

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

### *Aggregated set-aside strips*

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

### *Doubled set-aside strips*

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

## Construction of metapopulation models

### *Metapopulation capacity*

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

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

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

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

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

### *Incidence Function Model*

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

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

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

## Selection of species parameters

### *Dispersal*

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

### ***Population density***

Published literature estimates population densities of European butterfly species as low as <5 individuals ha$^{-1}$ (5) and as high as >4,000 individuals ha$^{-1}$ (6); in our models we define ‘low’ density at 10 individuals ha$^{-1}$ and ‘high’ density at 1,000 individuals ha$^{-1}$ to capture this variation.

## 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                                       #
```

```
# 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)){
```

```
  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)){
```

```
  end_edge_cand$Wplus <- end_edge_cand$W + 0.1
  end <- as.numeric(
            rownames(
              end_edge_cand)[
                which(
                  abs(
                    end_edge_cand$Wplus) == min(
                      abs(end_edge_cand$Wplus)))])
} else {
  end <- as.numeric(rownames(end_edge_cand))
}

# end = cell number of ending cell (of all cells incl. zeros)

# x- and y-coordinates of ending cell

end_x <- x[end]
end_y <- y[end]

# Set up starting occupancy (all cells)
occ0 <- rep(FALSE, times=le)
occ0[start] <- TRUE

# Give starting and ending cells 100% habitat cover
n[start] <- cellsize^2 * density
```

```r
n[end] <- cellsize^2 * density

# Get rownumbers of non-habitat containing cells
zeros <- which(n==0)

# Get rid of x, y, n elements with no habitat & redefine objects
x <- x[-zeros]
y <- y[-zeros]
n <- n[-zeros]
occ0 <- occ0[-zeros]
D <-( -sin(rot)*x + cos(rot)*y )
le <- length(x)

# Dataframe of non-zero cell coordinates
xy <- data.frame(x,y)

# Non-zero index of ending cell
end_new <- which(xy$x==end_x & xy$y==end_y)



# Baseline probability of extinction
pex<- pmin(1,1/n)

```

```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###########
```

```
    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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