



Combining occupancy and dispersal models to predict the conservation benefits of land-use change

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Abstract

Context Economic incentives for habitat creation in productive agricultural land are an important tool for halting biodiversity loss. Given inevitable funding constraints, assessing the cost-effectiveness of potential habitat creation strategies should be a priority.

Objectives We make model predictions of changes in the populations of ten woodland-affiliated bird species over time across a set of contrasting woodland creation scenarios in a 25 × 25-km square of primarily arable land in England.

Methods Using an economic agent-based model of landowners who make economically rational decisions on land use in response to financial incentives for woodland creation, we created a suite of potential landscapes with varying spatial configurations (and amounts) of newly planted woodland. We then parameterised an individual-based model for each of ten woodland bird species, and used these models to simulate dispersal and settlement across the altered landscapes.

Results Across all bird species, population increases were greater when woodland creation plots were clumped together than when randomly sited. When woodland plots were adjacent to existing woodland, increases were comparable to those in the clumped

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arrangements, except at lower planting densities, where wood-adjacent planting was more beneficial for birds. In all cases, benefits were very gradual, typically taking at least thirty years to be fully realised.

Conclusions Our study demonstrates that the cost-effectiveness of woodland creation, in terms of subsequent benefits to biodiversity, is strongly determined by its spatial configuration. Short-term biodiversity targets for woodland birds are unlikely to be well served by woodland creation, given the time required for newly planted trees to reach maturity. We recommend the use of interim targets, but emphasise that current rates of woodland creation may only result in modest changes in woodland bird populations.

Keywords Agriculture · Biodiversity · Woodland birds · Restoration ecology · Agent-based model · Individual-based model

Introduction

Habitat creation is likely to be a large component of future land-use planning if global targets on halting biodiversity loss and mitigating climate change are to be met. Given that approximately 40% of the Earth's land surface is currently occupied by agriculture of some form, such restoration will frequently occur on productive land (Staddon et al. 2021), and gains in ecosystem services and biodiversity must be balanced against potential losses in food production and food security (Lu et al. 2013; Delzeit et al. 2017).

Where agricultural land is privately owned, economic incentives must be provided to induce pro-conservation changes in land management, due to the opportunity costs of habitat creation falling on private landowners (Green et al. 2018). Given constrained public spending, there is an onus on maximising the return on expenditure on such economic incentives, in terms of environmental benefit (where 'benefit' is measured in terms of biodiversity, carbon storage, or similar environmental metric), and hence a need for accurate forecasts of the impacts of any given incentive-based scheme.

Such forecasts are not trivial to produce. As well as accounting for the purely ecological mechanics of ecosystem functions, they must contend with spatial variation in agricultural productivity, and hence spatial variation in the opportunity cost that must be

met by subsidy payments before a landowner is likely to enrol land in a habitat creation scheme (Simpson et al. 2023). This heterogeneity of costs will have knock-on effects on the relative economic feasibility of different spatial patterns of land-use change, and must be explicitly accommodated when estimating the cost–benefit trade-offs of any prospective restoration scenario (Adams et al. 2010).

In the United Kingdom, ambitious plans for reforestation—628,000 hectares created by 2050—are closely linked not only to the legally binding target of a net-zero economy by 2050 (HM Government 2018; Rayment 2021), but to targets relating to biodiversity and species abundance (Stanford and Spain 2023; The Environmental Targets (Biodiversity) (England) Regulations 2023). However, not all expenditure delivers equal ecological benefits. The locations of newly planted woodlands in relation to each other and to existing woodland—as well as their individual patch sizes—are likely to have a profound impact on their value to biodiversity and biomass (van Dorp and Opdam 1987; Jacquemyn et al. 2003), as could the nature of the previous land use (Graham et al. 2017).

The optimal planting design for biodiversity maximisation is not necessarily obvious (Fahrig 2020). To take a very simplistic example, numerous small, randomly scattered woodland patches may be relatively poor for maintaining populations of a diverse assemblage of species, but facilitate greater landscape connectivity, whilst fewer, larger woods may offer localised better-quality habitats, but poorer connectivity (Cunningham et al. 2008; Martensen et al. 2012). However, recent research has suggested that biodiversity in restored or newly created habitats is largely influenced by colonisation from nearby populations, emphasising the importance of establishing new habitats close to existing habitat fragments (Watts and Hughes 2024). Similarly, a modelling study by Synes et al. (2020) found that creating new habitats near existing patches of the same habitat type typically provides the greatest benefits for both species range expansion and patch occupancy across various landscapes. However, these and similar studies rarely address the trade-offs between productivity and biodiversity, or the role of economic factors in determining the targeting of woodland creation.

New woodland planting is expected to be concentrated on the lowest-value (i.e. least agriculturally productive) farmland (HM Government 2018),

which is not necessarily found in areas most beneficial for wildlife (Armsworth 2014; Nthambi et al. 2024; Watts and Hughes, 2024). Nonetheless, regardless of the spatial correlation between opportunity costs and ecological benefits, there is the chance to positively influence the design of woodland creation schemes within such economic constraints. Identifying the spatial patterns of planting most conducive to meeting biodiversity targets will maximise the cost-efficiency of tax-payers' investment in economic incentive schemes designed to increase woodland cover.

The design of optimum planting schemes would ideally be based solely on empirical data, but there are various challenges to this approach beyond the perennial issue of limited funding for biodiversity monitoring. Firstly, the timescales involved in woodland development mean that appropriate long-term data rarely exist (Lira et al. 2019; Watts et al. 2020). Secondly, the occupancy of a given woodland patch, even at ecological equilibrium, may be determined in part by 'spillover' effects from both the contemporary surrounding landscape (MacArthur and Wilson 1967; Tscharrntke et al. 2012) and the legacies of historical land use (Dambrine et al. 2007; Auffret et al. 2015; Semper-Pascual et al. 2021; Bradfer-Lawrence et al. 2024)—hereafter referred to as spatial spillovers and temporal legacies, respectively.

These external influences make patch occupancy and abundance highly site-specific, so that predicting the effects of land-use change on biodiversity in any given patch requires the incorporation of landscape-scale data. The number of potential variables involved in assessing the colonisation potential of new woodlands by even a single taxon is considerable; size, age, isolation, and landscape context—among other factors—are known to influence habitat suitability of woodland patches, and relationships will differ among species (Lira et al. 2019; Haddou et al. 2022). Indeed, data limitations mean that there are few taxa for which such an attempt is feasible.

Together, these challenges necessitate an approach that combines diverse empirical information with process-based models to simulate landowner decision-making (over woodland planting), woodland development, and colonisation by wild species over time. In this study we use individual-based models (IBM) for a suite of woodland bird species to assess the biodiversity benefits of a range of realistic, economically

driven agent-based models (ABM) of woodland creation with different spatial rules.

Woodland birds have declined in the UK by 34% since 1970 (Eaton and Noble 2024), and are a key indicator taxon for biodiversity conservation. We only consider birds in the present paper, due to the large suite of datasets and models required, but many less-intensively studied taxa have also declined (Burns et al. 2023).

We run our IBMs across a real-world landscape modified by woodland planting schemes informed by an economic ABM (Simpson et al. 2023; Nthambi et al. 2024), which simulates the response of individual land managers to economic incentives for woodland planting given their opportunity costs of changing land use away from the current (agricultural) baseline. We also generate planting scenarios in which the landscape is considered as a whole (i.e. without multiple individual landowners), to simulate a situation in which planning decisions may be taken at a much larger strategic scale.

The suitability of habitat patches (i.e. discrete areas of land of a uniform land cover type) for birds in the study landscape is calculated by reference to two predictive models. The first (Finch et al. 2023) provides density estimates for each of our species, and the second (Bradfer-Lawrence et al. 2024) allows suitability values for individual woodland patches to be adjusted according to site-specific characteristics. The latter model accounts for spatial spillovers and temporal legacies by the incorporation of contemporary and historical landscape-scale data.

The IBMs simulate the extent and speed of colonisation of woodland patches by the ten most abundant bird species in the study area, comparing two basic scenarios of planting: (a) randomly scattered and (b) clumped together, with the assumption in each case that the cheapest parcels of land will be enrolled into the schemes first (Simpson et al. 2023). Importantly, in each case we estimate changes in the abundance of each species over a period of 100 years as the simulated woodlands age, grow and develop suitable habitat conditions, rather than assuming—as is typical in the modelling literature—that woodland matures immediately or at some unspecified future date (Finch et al. 2021, 2023; Synes et al. 2020). We also investigate the impacts of planting scenarios that exist at the extremes of a continuum from random scattering in the cheapest land (irrespective of current woodland

configuration) to planting exclusively on land adjacent to existing woodlands, as per the ‘Lawton Principles’ for creating effective ecological networks (Lawton et al. 2010).

The study is designed to provide guidance for woodland creation strategy at the landscape scale, by estimating the cost-effectiveness—in terms of bird population increase per unit cost—of different spatial configurations of woodland creation. We discuss the implications of the study for land-use policy and future research.

Methods

Study area and species

The study area is a 25×25 km square in the Midlands of England, with lower-left corner 409000E, 239000N (British National Grid; Fig. 1). It contains a subset of woodlands that form part of the Woodland Creation & Ecological Networks (WrEN) Project, a long-term natural experiment covering 134 UK woodlands of varying age and size that provide a space-for-time substitution for studying the long-term effects of woodland creation on biodiversity in UK landscapes (Watts et al. 2016; Fuentes-Montemayor et al. 2022). The area is dominated by arable agriculture (59%)

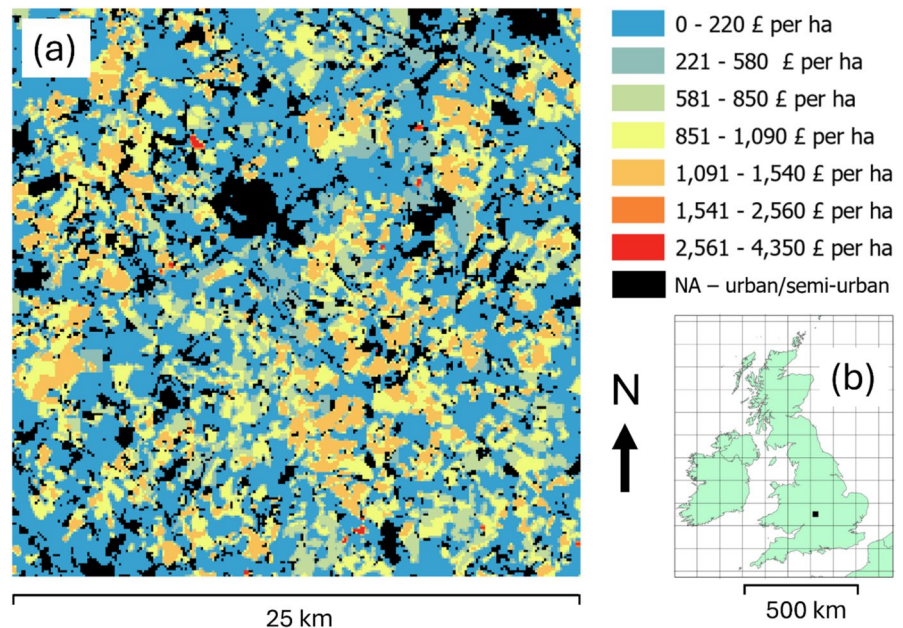
and improved grassland (31%); urban and semi-urban areas cover 6% of the land, and broadleaved woodland 4%.

We selected the ten bird species that are most abundant in woodlands in the English Midlands, according to the UK-wide estimates of Finch et al. (2023). Those estimates are based on UK Breeding Bird Survey data (Heywood et al. 2023), and modelled using optimisation-based mixture models. The models provide region-specific density estimates for each species in land-use categories taken from the UK Land Cover Map 2015, based on the proportional coverage of each land cover in 1-km bird survey squares (LCM2015; Rowland et al. 2017). We also used these data to calculate the degree of woodland specialisation that each species exhibits in the study area, dividing the total estimated abundance of each species in broadleaved woodland in the study area by its expected abundance if there were no habitat preference (i.e. the total abundance multiplied by the fraction of the land area covered by woodland).

Landowner economic agent-based model (Enrolled scenarios)

We employed outputs from the economic agent-based model of Nthambi et al. (2024), in which the same study area was conceptualised as a set of 1 km×1

Fig. 1 **a** Spatial distribution of opportunity costs in the study area, and **b** its location in the UK



km parcels, each owned by a separate landowner who manages their parcel to maximise profits. Land was assumed to be used for crop or livestock production, and the current value of each parcel was calculated using land-use and soil data from the Land Cover Plus Crops map (Rowland et al. 2017) and Soilscales,¹ together with gross margin data (revenue minus variable costs) from the Scotland's Rural College Farm Management Handbook. This allowed us to calculate the total gross margin values for each crop and livestock type, based on soil fertility. Each landowner was modelled as a discrete agent who chooses the best use of their land by comparing the returns (profits) from maintaining current farming practices with those from accepting a subsidy for woodland planting. Note that all agents share the same behavioural assumptions. We considered the larger two of the three per-farm woodland creation levels considered by Nthambi et al. (2024) so as to maximise the likelihood of detecting biodiversity impacts; these were 5 ha and 10 ha per 1km² parcel. Predicted enrolment in the woodland creation scheme was based on the maximum payment rate offered of £2056 per ha. This identified $n=16$ enrolled parcels under the 5ha area level (resulting in 80 ha of woodland creation) and $n=46$ for the 10ha area level (resulting in 460 ha of woodland creation). The per-ha payment cost is derived from a baseline of £528 per ha (the average gross margin of all agricultural parcels in the landscape) plus a £500 planting cost, for a total of £1028 per ha. Based on findings in Nthambi et al. (2024), we increased this to a flat-rate subsidy payment of £2056 per ha, to increase the likelihood of securing enrolment, and therefore a biodiversity response.

The economic ABM identifies 1-km parcels in which planting takes place, but does not specify which individual hectares are planted. We selected these hectares in four distinct ways: (1) 5 individual hectares planted in a random configuration in each enrolled 1-km parcel, (2) 5 ha planted in a single clump per parcel, (3) 10 individual hectares planted at random per parcel, (4) 10 ha planted in a single clump per parcel (Table 1). These planting patterns are always within the constraint that the cheapest hectares (in terms of the opportunity cost of foregone

Table 1 Scenario characteristics

Scenario	Category	Hectares/ km ²	Configura- tion	Total hectareage planted
1	Enrolled	5	Random	80
2	Enrolled	5	Clumped	80
3	Enrolled	10	Random	460
4	Enrolled	10	Clumped	460
5	Unenrolled	≤1	Random	458
6	Unenrolled	≤2	Random	460
7	Unenrolled	≤2	Clumped	460
8	Unenrolled	≤5	Random	460
9	Unenrolled	≤5	Clumped	460
10	Unenrolled	≤10	Random	460
11	Unenrolled	≤10	Clumped	460
12	Unenrolled	≤20	Random	460
13	Unenrolled	≤20	Clumped	460
14	Unenrolled	≤1	Wood- adjacent	438
15	Unenrolled	≤2	Wood- adjacent	456
16	Unenrolled	≤5	Wood- adjacent	460
17	Unenrolled	≤10	Wood- adjacent	460
18	Unenrolled	≤20	Wood- adjacent	460

In the third column, hectares/km² for unenrolled models are variable since planting occurs widely across the landscape and is only limited per km², not prescribed

In the fifth column, for scenarios 5–18, values are variable due to the fixed budget and differences in land values between planted hectares

agricultural profit per annum) are planted first, with the most expensive parcels in terms of opportunity costs planted last, known as ‘moving up the supply curve’.

These four patterns, which originate with the ABM, are hereafter referred to as ‘enrolled’ scenarios. In these scenarios, the maximum size of woodland clumps is necessarily limited; even where two adjoining landowners are enrolled, their planted areas will not adjoin except by chance.

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Landscape-scale decision process (unenrolled scenarios)

To provide a contrast with the landowner-level decision process of the ABM-derived enrolled scenarios, we also created fourteen further scenarios in which woodland could be planted in any non-woodland and non-urban land (i.e. a landscape-level decision process that bypasses the landowner ABM, hereafter referred to as the ‘unenrolled’ scenarios). In these scenarios, every hectare in the study area was ranked by agricultural land value, and a fixed budget was allocated for meeting the opportunity cost of removing land from production, plus the cost of planting. Beginning with the lowest-ranked, we moved up the list, selecting hectares to be planted until the budget was exhausted. This basic method was applied with three variations: (i) where there were multiple hectares of identical value available, they were selected at random (hereafter ‘random’), (ii) where available, hectares were preferentially selected if adjacent to hectares already selected (hereafter ‘clumped’), (iii) where available, hectares were preferentially selected if adjacent to existing woodlands (hereafter ‘wood-adjacent’). Note that there was no wood-adjacent condition for the enrolled scenarios, due to the rarity of existing woodland in the landscape; very few enrolled parcels would contain woodland.

For comparability with the enrolled scenarios, we selected an annual budget of £230,000, which was equivalent to the cost of planting the maximum hectareage from the enrolled scenarios (460 ha) in land of the minimum value available across the whole study area. The budget acts as a constraint on an optimal conservation planning solution, whereby we ignore the individual landowner decision-making process. The unenrolled scenarios are thus better conceived of as a compulsory buy-out or regulatory solution.

For each of the three planting arrangements, we applied five levels of restriction, limiting planting to 1, 2, 5, 10, or 20 ha in any given km² (Table 1), in order to control the maximum clump size, and thereby provide comparison with the enrolled scenarios. Note that since the clumped planting of a single hectare per km² is not logically possible, the clumped scenario for 1 ha/km² is omitted.

Individual-based model: habitat suitability

For each species we created a single habitat suitability map (see below) representing the before-planting condition, and then a 100-years map series for each scenario, beginning with planting, and updated annually to reflect changes in woodland age and structure.

All map data were downloaded as, or converted to, 1-ha (100×100 m) rasters. Map cells were also organised into patches of contiguous land cover, which were used to represent discrete population sub-units in the IBM (see below). For the more dominant land cover classes (e.g. arable and horticultural, and improved grassland), creating patches from contiguous cells of the same land cover would have resulted in several individual patches far in excess of 10 km². Since the IBM assumes that birds in a given patch are able to disperse freely to any adjacent patch, regardless of their estimated dispersal range, such large patches would have allowed artificially rapid dispersal across certain parts of the landscape. To counter this artefact, we limited patches to 1 km², splitting anything larger into multiple parts.

We constructed habitat suitability maps for each species in which each patch was assigned a value between 0 and 100, calculated as follows (Eq. 1):

$$V_{ic} = \frac{AdjD_{ic}}{D_{imax}} \cdot 100 \quad (1)$$

where V_{ic} is the raw habitat suitability of patches in land cover c for species i , D_{ic} is the density of species i in land cover c in the Midlands region estimated by Finch et al. (2023), and D_{imax} is the highest estimated density for species i across all land-cover types in the region. To address the exclusion of trees outside woodlands in the LCM2015 map data (Rowland et al. 2017) and in the density estimates from Finch et al. (2023), we adjusted D_{ic} values in each non-woodland patch by incorporating data from the LIDAR-based Vegetation Object Model (Environment Agency 2022)—which provides height-above-ground data of vegetation at 1 m resolution—as follows (Eq. 2):

$$AdjD_{ic} = (1 - pToW) \cdot D_{ic} + pToW \cdot D_{iBLW} \quad (2)$$

where $pToW$ is the proportion of the patch occupied by trees outside woodland, and D_{iBLW} is the density of species i in broad-leaved woodland.

The habitat suitability of individual woodland patches was adjusted using parameter estimates from Bradfer-Lawrence et al. (2024), in which the occupancy probability of each species was modelled as a function of both patch-scale and local-landscape-scale (3km radius) variables in a Bayesian hierarchical model. This framework accounts for imperfect detectability when estimating species-level occupancy (Kery and Royle, 2016). The model is based on bird survey data from 125 woodlands of the WrEN Project (Whytock et al. 2018; Bradfer-Lawrence et al. 2024). In the present study, each woodland patch was first assigned an occupancy probability for each species according to the following equations (Eqs. 3 and 4):

$$x_{ij} = a_i + \sum_{y=1}^9 b_{yi} \cdot \text{var}_{yj} \quad (3)$$

$$O_{ij} = \frac{e^{x_{ij}}}{1 + e^{x_{ij}}} \quad (4)$$

where O_{ij} is the occupancy probability of species i in patch j , a_i is the intercept for species i , and b_{yi} is species i 's co-efficient for variable y . The first four of the nine variables are patch-based: area (ha), shape (the ratio of patch perimeter divided by the perimeter of a circle with the same area), age (years), and structural heterogeneity (standard deviation of diameter at breast-height of trees in the patch). The other five variables describe properties of a 3-km buffer surrounding each patch: proportion covered by trees outside woodland, livestock density, proportion of agricultural land that is arable, proportion covered by woodland, and proportion of woodland that is more than 100 years old (Bradfer-Lawrence et al. 2024).

Two variables (age and structural heterogeneity) could not be measured for every woodland patch. Three patches in the study area are WrEN sites, and their ages and structural heterogeneity were known from field surveys. For other patches, ages were assigned randomly in line with the distribution of known woodland ages in 3-km buffers around WrEN sites in England (Bradfer-Lawrence et al. 2024). Since woodland age is the main driver of structural heterogeneity (Fuentes-Montemayor et al. 2022), we fitted a non-linear regression model to age and structure data from the WrEN sites using the *nprob* function in the R package *robustbase* (Maechler et al. 2024), then used

the model to predict structure values for non-WrEN sites based on their randomly assigned ages.

We combined V_{ij} (the raw habitat suitability value for species i in patch j) and O_{ij} estimates to produce a habitat suitability value H_{ij} for each woodland patch as follows (Eq. 5):

$$H_{ij} = O_{ij} \cdot V_{ij} \quad (5)$$

Because O_i can be no higher than 1, its mean across all woodland patches will be lower than 1, and, in turn, the mean of H_i will be lower than V_i , the modelled density (i.e. H_{ij} will always be artificially low). We therefore apply an adjustment to the carrying capacity of the patch, as described in the following section. For non-woodland patches, we assumed $H_{ij} = V_{ij}$.

Our woodland dataset does not contain woodlands younger than ten years old, so rather than extrapolating beyond the range of the data, we categorised all newly planted woodland as semi-natural grassland for the first ten years, and as eleven-year-old broad-leaved woodland for the following year, aging annually thereafter.

Individual-based model: dispersal and settlement

We used the *RangeShiftR* package in R (Malchow et al. 2021) to model multi-generation dispersal and settlement across the landscape of the ten bird species into newly planted woodland. Based on *Rangeshifter* 2.0 (Bocedi et al. 2021), *RangeShiftR* implements an individual-based, spatially explicit, stochastic model that simulates population dynamics, dispersal, and settlement. The model operates in raster-based maps of habitat suitability, values of which are used to scale the maximum potential carrying capacity, which is applied either to individual cells discretely, or to groups of cells considered as a single patch. Habitat suitability maps may be continuously altered during the course of a single simulation, thereby allowing users to account for landscape change—such as woodland maturation—over time. Demography and dispersal variables (Table 2) are organised in Leslie matrix formulations, with density-dependent regulation applied to adult fecundity. Data were taken from the British Trust for Ornithology (2023) and Storchová and Hořák (2018), and dispersal data from Paradis et al. (1998).

Table 2 Demographic and dispersal variables for the study species used in the IBMs

Species	Eggs laid per year	Adult annual survival	Juvenile annual survival	Maximum lifespan (years)	Dispersal distance (km)	Long-range dispersal (km)
Long-tailed tit	10	0.44	0.25	11	8.3	83
Woodpigeon	3	0.607	0.52	18	10.7	107
Blue tit	11	0.53	0.38	11	5.3	53
Robin	10	0.42	0.41	19	6	60
Chaffinch	4.5	0.59	0.53	16	3.6	36
Great tit	15	0.54	0.38	15	5.3	53
Blackcap	5	0.436	0.356	14	41.2	412
Wren	13	0.319	0.263	7	8.9	89
Blackbird	10	0.65	0.564	22	3.3	33
Song thrush	10	0.563	0.463	18	7	70

The strength of density dependence is mediated via the variable $1/b$ (which is equivalent to carrying capacity for stage-structured models, and which acts on fecundity; Bocedi et al. 2020). For each species in our models, we derived the value of $1/b$ from preliminary model runs in landscapes where all cells were aggregated in a single patch, and habitat suitability was set at 100. In such model runs, the population should stabilise around the value of D_{imax} , but we also further adjusted D_{imax} to account for the lowered mean suitability value of woodland patches that occurs when occupancy model predictions are incorporated (Eq. 5), as follows (Eq. 6):

$$D_{imaxAdj} = D_{imax} \cdot \frac{1}{\text{mean}(O_{iW})} \quad (6)$$

This adjustment ensures that the mean habitat suitability of woodland patches will equal V_i for broad-leaved woodland. However, it will also cause suitability values in non-woodland to be inflated. The latter were therefore adjusted downwards by multiplying by $D_{imax}/D_{imaxAdj}$.

To find the correct value of $1/b$ for each species, we iteratively adjusted it between runs until each population attained an equilibrium of adults at $D_{imaxAdj}$ (Malchow et al. 2021).

Dispersal in *RangeShiftR* is modelled as three distinct processes: (1) emigration—the probability that an individual will leave its natal patch in a given year (we assumed a value of 0.1 for all species); (2) transfer—the pattern of movement undertaken after emigration (here we used a pair of negative exponential

distributions specifying the probability of moving given distances, one for ordinary dispersal (probability=0.99), and one for rare, long-range events (probability=0.01)); and (3) settlement—the likelihood of an individual remaining in a cell or patch to which it has dispersed; in this case it will remain if the ‘spare’ carrying capacity of the patch is ≥ 1 individual (Fig. 2).

Simulations and analyses

We ran simulations for each species in each of the eighteen scenarios (Table 1). Before the start of each simulation, species were assumed to occupy all pre-existing woodland patches to the extent that the habitat suitability (and hence carrying capacity) allowed. Simulations began with a 100-year burn-in period (so that species were at equilibrium in the landscape prior to planting), followed by the 100-year map series for each scenario (i.e. woodland planting occurred in year 101). Each species-scenario combination was repeated 20 times. We present results in terms of the percentage increase of each species’ population across the landscape per £100,000 of spending on woodland planting subsidies (note that this is purely for comparative purposes, and in some scenarios considerably less was spent).

Sensitivity testing

The sensitivity of IBM predictions to deviations in variable values was assessed in two ways. Firstly, we ran simulations for each species where each of the

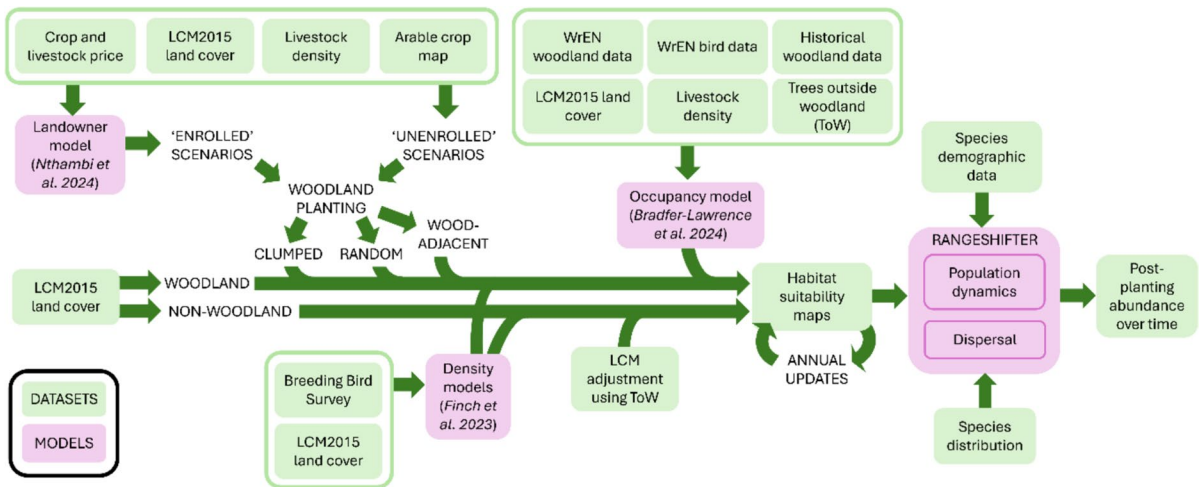


Fig. 2 Schematic of model and dataset structure. *ToW* the ‘trees outside woodland’ dataset. LCM2015 UK Land Cover Map 2015, *WrEN* Woodland Creation & Ecological Networks Project

nine variables (the eight in Table 2, as well as the $1/b$ multiplier) was altered $\pm 10\%$ in turn (with 20 repetitions per combination), then $\pm 25\%$ and $\pm 50\%$. These simulations used the ‘unenrolled’ scenarios 5 (random with $\leq 1 \text{ ha/km}^2$) and 18 (wood-adjacent with $\leq 20 \text{ ha/km}^2$), thereby accommodating the full range of outcomes in terms of spatial clustering. Hereafter, these are referred to as ‘one-at-a-time tests’.

Secondly, we ran simulations where each variable was assigned the value of default, +adjustment, or -adjustment, drawn from a distribution generated by Latin hypercube sampling in the R package *lhs* (Carnell 2022). This method ensures that values are drawn evenly from across the 9-dimensional parameter space without having to test all unique combinations. We chose 150 combinations, and each were applied to both the random and wood-adjacent planting scenarios (5 and 18), with three replicates of each, resulting in a total of 900 simulations per species per adjustment level. Hereafter, these are referred to as ‘LHS tests.’

As with the main results, for both tests we report the predicted increase in total abundance of each species per £100,000 of planting subsidy.

Results

Enrolled scenarios

The predicted increase in woodland bird abundance per unit cost of a planting scheme was negligible except under the scenario in which each 1-km square was planted with 10 ha of clumped woodland. IBM simulations in landscapes with 5 ha of woodland added in clumps in each of sixteen km-squares (scenario 2; Fig. 3) yielded similar increases in bird populations as those with 5 ha planted at random (scenario 1). Ten hectares planted at random in each of forty-six km-squares yielded higher overall increases (scenario 3) than the equivalent five-hectare scenario (scenario 1), but showed no greater benefit per £100k spent (Fig. 3; Table 3). Ten hectares planted in clumps (scenario 4) yielded consistently higher increases in bird populations than the other three enrolled scenarios, both overall and per £100k spent (Fig. 3).

In line with these results, only in scenario 4 (10 ha, clumped) was percentage increase positively correlated with the species’ degree of woodland

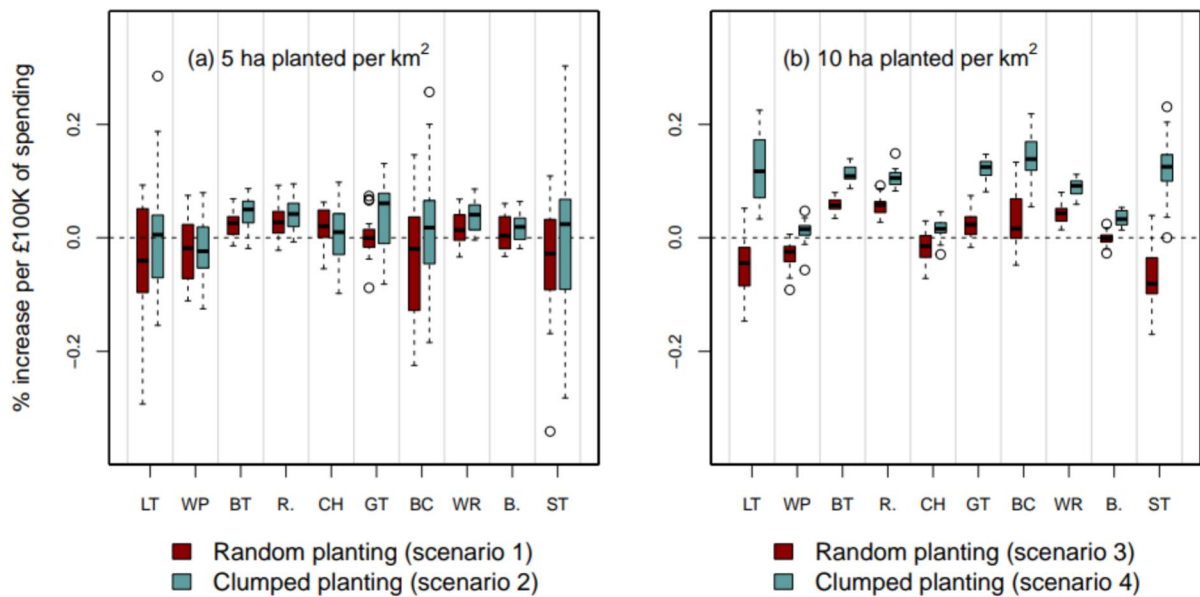


Fig. 3 Percentage increase in bird populations under **a** 5 ha/km² and **b** 10 ha/km² planting in landowner-enrolled parcels, with planting of individual hectares either in a random configuration within each parcel, or a single clump per parcel. Box

extents indicate the inter-quartile range. Whiskers extend to 1.5 times the interquartile range from the box. *LT* long-tailed tit, *WP* woodpigeon, *BT* blue tit, *R* robin, *CF* chaffinch, *GT* great tit, *BC* blackcap, *WR* wren, *B* blackbird, *ST* song thrush

specialisation (i.e. the population increase following woodland planting was greatest for woodland specialists; Fig. 4). No apparent relationship was found between percentage increase and dispersal distance (Fig. S1).

The speed at which population gains from woodland planting were achieved was variable among species, and any consistent gains were always preceded by declines lasting approximately ten years (Fig. 5). These declines should be expected where the land on which the woodland was planted was, on average, more suitable for that species than semi-natural grassland (which is how woodland < 10 years old is characterised in the model). It took between thirteen and sixteen years for these species to recover to pre-planting levels, and 20 to 60 years to approach 100% of the eventual 100-years gain.

Unenrolled scenarios

Across all unenrolled scenarios, clumped and wood-adjacent planting were consistently more beneficial to birds than random planting (Fig. 6; Table 4). The imposition of a limit on the number of hectares planted per km² effectively determined the patch

size of clumped plantings. As the limit was raised, increases in bird populations became more pronounced, up to a limit of 5 or 10ha, depending upon the species. Below this level, wood-adjacent planting was generally of greater benefit than clumped planting (Figs. 6, 7). There was no consistent impact of the ha/km² limit on random or wood-adjacent planting scenarios (Fig. 6).

Sensitivity

Predicted increases in total abundance of each species per £100,000 of planting subsidy were mostly insensitive to adjustments of $\pm 10\%$ in the values of the nine variables. ‘Insensitive’ was defined as the mean for test results lying within one standard deviation of the mean obtained using default variable values (Figs. S4, S5). Exceptions were the lifespan of the robin in the random scenario, one-at-a-time tests, where decreased lifespan augmented the expected increase in abundance (Fig. S4), and the blackcap in both scenarios of the LHS tests, where the outputs were sensitive to adjustment in most variables (Fig. S5).

When values were adjusted $\pm 25\%$, outputs were sensitive to changes in juvenile survival values in two

Table 3 Overall population growth of species under enrolled scenarios

Scenario	Description	Total population growth (%)									
		Long-tailed tit	Woodpigeon	Blue Tit	Robin	Chaffinch	Great Tit	Blackcap	Wren	Blackbird	Song Thrush
1	5 ha, R, 80 ha total	-0.36	-0.18	0.18	0.22	0.13	0.02	-0.3	0.15	0.06	-0.43
2	5 ha, C, 80 ha total	0.08	-0.15	0.32	0.34	0.03	0.3	0.09	0.29	0.15	-0.05
3	10 ha, R, 460 ha total	-0.77	-0.39	1	0.9	-0.47	0.18	0.59	0.78	0.03	-0.81
4	10 ha, C, 460 ha total	2.1	0.18	1.79	1.71	0.14	1.87	2.54	1.35	0.52	1.6

R random planting; C clumped planting

species, clutch size and adult survival in one species each, and $1/b$ in one species in one-at-a-time tests (Fig. S6). In LHS tests, sensitivity was common for several variables for several species (Fig. S7).

When values were adjusted $\pm 50%$, outputs were especially sensitive to changes in adult survival, juvenile survival, and clutch size in one-at-a-time tests (Fig. S8). In LHS tests, outputs were sensitive to changes in almost all variables, in most species (Fig. S9).

Discussion

We modelled bird population responses to a set of woodland creation scenarios, accounting for varying opportunity costs associated with planting on existing farmland, as well as the ecological effects of the spatial configuration of individual woodlands. Our method allowed species-specific habitat preference data—including our previous modelling work demonstrating relationships between occupancy and the characteristics of individual woodland patches—to be incorporated in an individual-based dispersal and settlement model that simulates annual increments of demography and movement in response to contemporaneous maturation of planted woodlands. The use of an economic model to determine the location of new woodland planting gives our scenarios further real-world relevance, since it incorporates the spatially varying trade-offs associated with land-use change, whereby land managers typically sacrifice agricultural returns to engage in woodland planting (which, in turn, may offer a set of financial benefits over time). This is a development of a wider body of work, which uses comparable ecological economic models to investigate the effects of economic incentives on the conservation of other habitats (such as grassland: Watzold et al. 2016; Simpson et al. 2023) and which explores a wider set of economic incentives than the simple flat rate subsidy modelled here (e.g. Dreschler 2017; Bareille et al. 2023). Note that for woodland creation, we need to consider longer time scales of species response than is typically the case for grassland restoration.

In keeping with long-established area-diversity relationships in the ecological literature (MacArthur and Wilson 1967), our results indicate that the spatial configuration of woodland planting will have

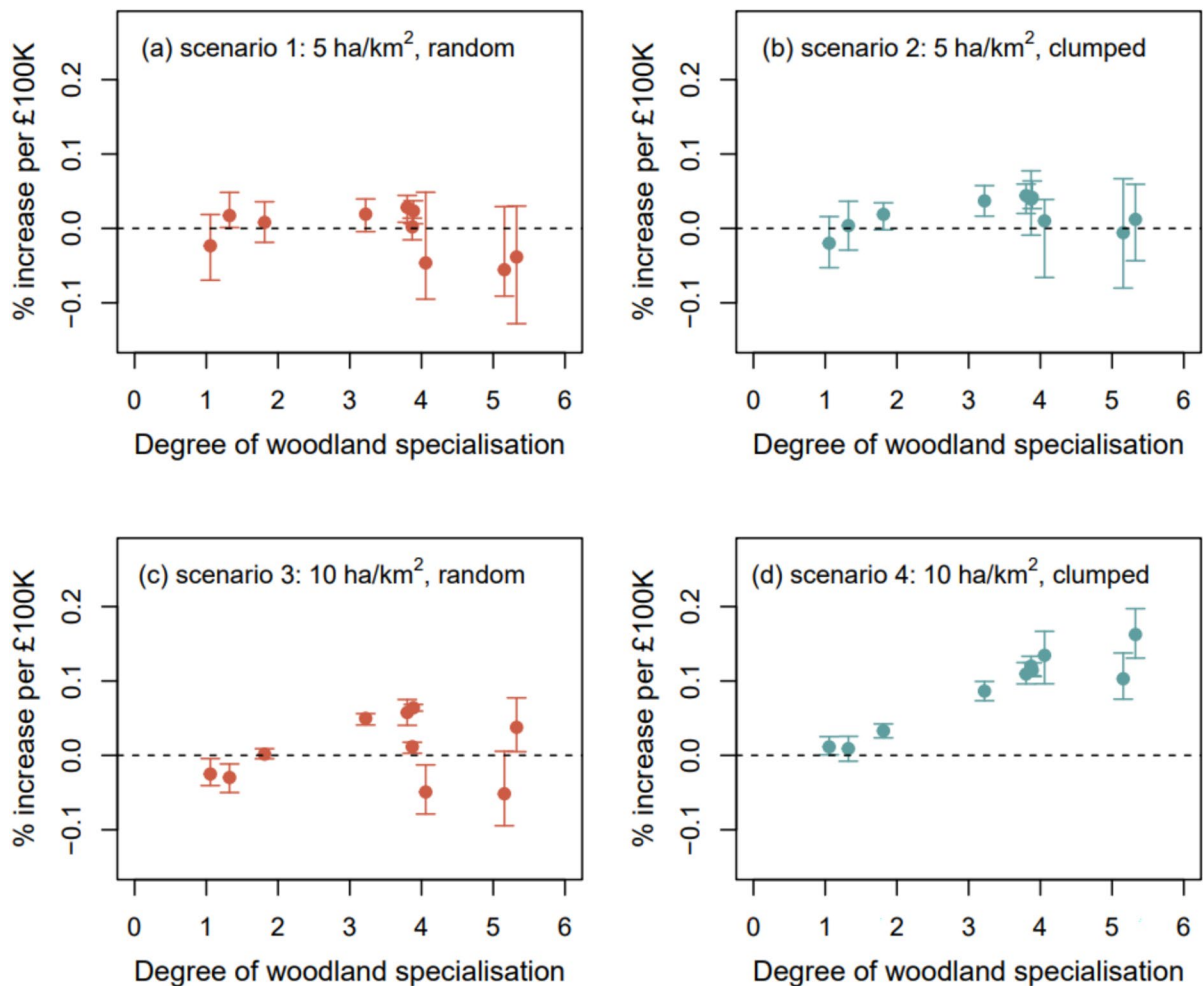


Fig. 4 Percentage increase (per £100k of spending) in populations of ten bird species in scenarios 1–4 against their degree of woodland specialisation. Whiskers indicate the interquar-

tile range of twenty replicates. Points represent (left to right): woodpigeon, chaffinch, blackbird, wren, robin, great tit, blue tit, long-tailed tit, song thrush, blackcap

an important impact on its subsequent biodiversity benefits. A similar study that focussed on the influence of woodland creation on carbon sequestration, recreation, and flood mitigation across England reported comparable impacts of spatial orientation on the delivery of these ecosystem services (Burke et al. 2023). In the present study, planting in random individual hectares consistently resulted in lower population gains for our ten species than planting either in clumps or adjacent to existing woodland. All other things being equal, it would presumably be most economically efficient for an individual landowner to plant in a single clump, so as to minimise costs associated with transportation, access, and

fencing, thereby potentially aligning economic and ecological priorities. Ultimately, however, the spatial arrangement of the cheapest land will likely dictate the default planting arrangement in the absence of further instruction and/or incentive. Economic incentives such as an agglomeration bonus would provide additional incentives for land managers to create new woodland next to existing woodland, or to invest in adjacent rather than scattered blocks of new planting.

The unenrolled scenarios allowed us to further compare the impact of siting new woodlands adjacent to existing woodlands with that of creating discrete blocks (whether clumped or randomly scattered). Wood-adjacent planting consistently out-performed

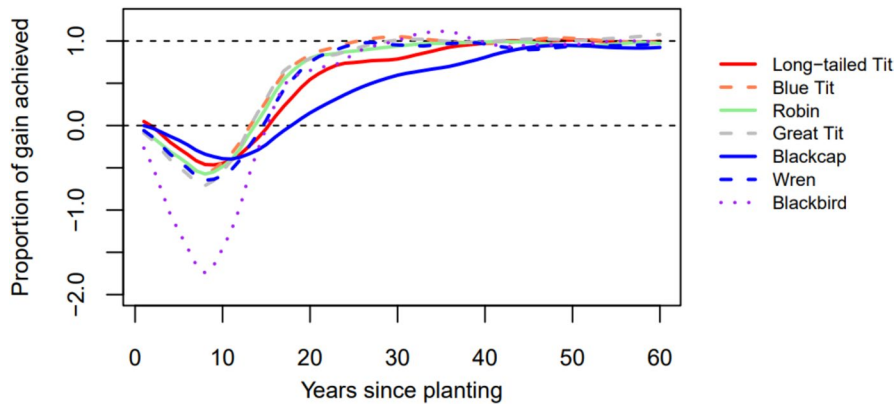


Fig. 5 Population trajectories in scenario 4, for species with a consistent increase in that scenario (omitted: song thrush and woodpigeon). The y-axis represents the amount of gain achieved by year x as a proportion of the total gain achieved

across the full time series. Lines are means from the 20 replicates, smoothed with a loess interpolation, and indicate the proportion of the total gain achieved since planting

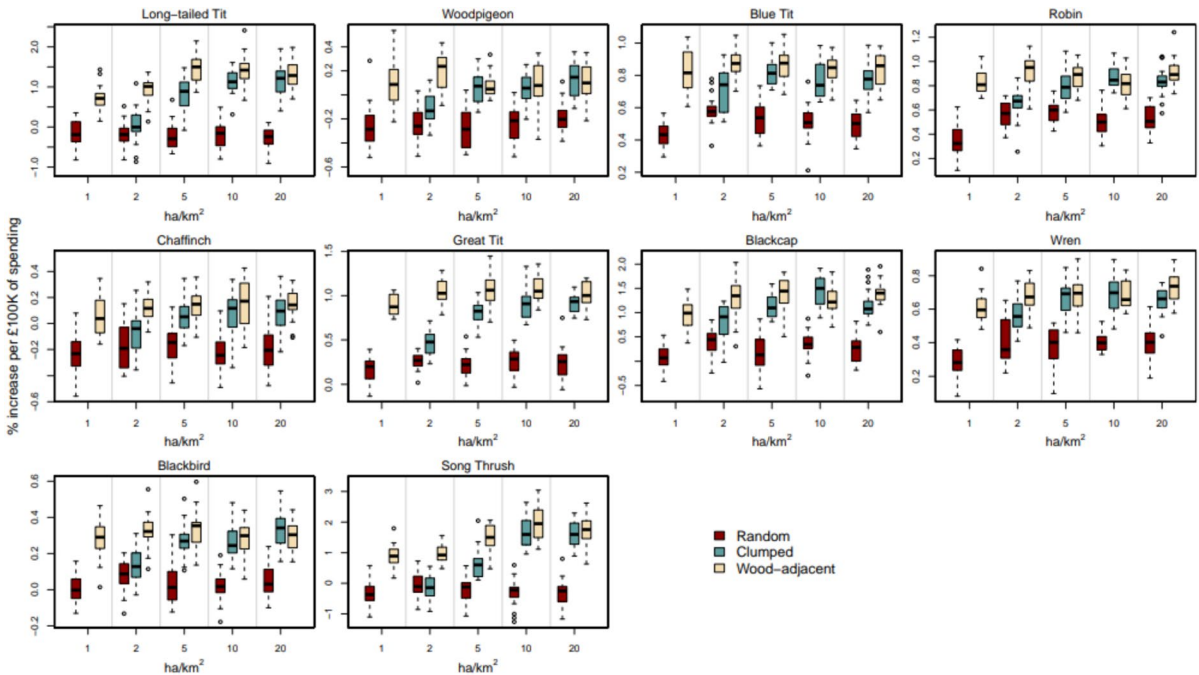


Fig. 6 Percentage increase (per £100k of spending) in bird populations under different levels of woodland planting in any available land (unenrolled scenarios), with planting arranged at random (red bars), in clumps (blue bars), or wood-adjacent (beige bars)

random planting, and was—overall—more beneficial than clumped planting, in agreement with Synes et al. (2020). However, the benefits of wood-adjacent and clumped planting began to converge as the clump size increased to approximately 10 hectares, at which point they were similar for most species (Fig. 7).

The results also suggest that the benefits of large-scale planting could be more modest for individual species than expected. Expansion of the existing woodland area by 2.9% (80 ha, scenarios 1 and 2) produced a maximum population increase of 0.34% (for robin, scenario 2). Even in the most productive

Table 4 Overall population growth of species under unenrolled scenarios

Scenario	Total population growth (%)										
	Density (ha/km ²) and configuration of planting	Long-tailed tit	Woodpigeon	Blue tit	Robin	Chaffinch	Great tit	Blackcap	Wren	Blackbird	Song thrush
5	1 R	-0.33	-0.62	0.99	0.8	-0.54	0.38	0.2	0.67	0.01	-0.71
6	2 R	-0.39	-0.54	1.35	1.29	-0.43	0.61	0.87	0.94	0.18	-0.13
7	2 C	0.05	-0.26	1.63	1.5	-0.17	1.08	1.89	1.28	0.31	-0.36
8	5 R	-0.51	-0.65	1.22	1.34	-0.39	0.51	0.43	0.9	0.07	-0.46
9	5 C	1.85	0.14	1.88	1.8	0.12	1.86	2.6	1.51	0.64	1.44
10	10 R	-0.46	-0.53	1.18	1.14	-0.48	0.61	0.82	0.94	0.04	-0.73
11	10 C	2.62	0.09	1.78	2	0.17	2.07	3.31	1.56	0.61	3.77
12	20 R	-0.62	-0.44	1.14	1.22	-0.41	0.54	0.57	0.92	0.1	-0.67
13	20 C	2.69	0.3	1.81	1.92	0.18	2.09	2.66	1.5	0.76	3.67
14	1 WA	1.65	0.21	1.91	1.92	0.13	2.05	2.2	1.41	0.65	2.09
15	2 WA	2.12	0.45	2.01	2.09	0.27	2.4	2.96	1.57	0.76	2.22
16	5 WA	3.36	0.19	2.01	2.02	0.31	2.44	3.22	1.57	0.78	3.32
17	10 WA	3.29	0.21	1.9	1.88	0.36	2.46	2.9	1.57	0.64	4.56
18	20 WA	3.03	0.25	1.91	2.09	0.35	2.34	3.18	1.67	0.67	3.94

Abbreviations in second column: R random, C clumped, WA wood-adjacent

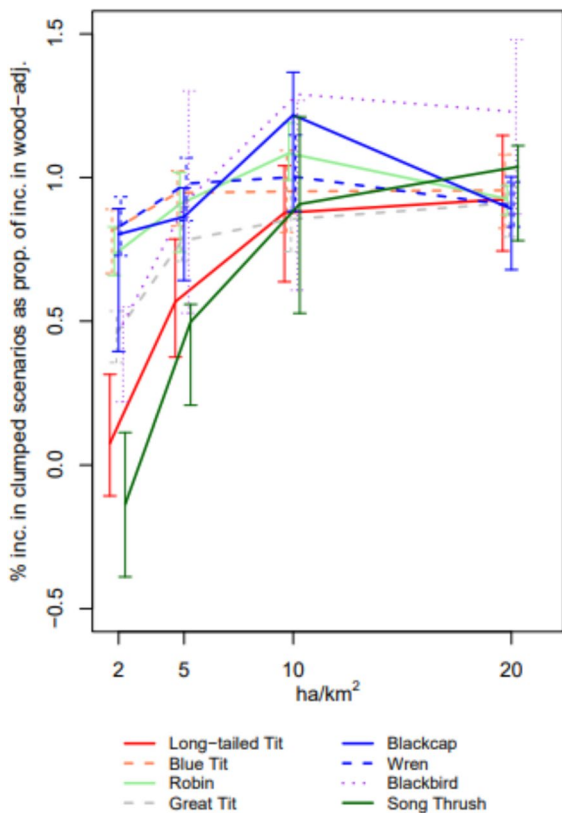


Fig. 7 Population increase in clumped unenrolled scenarios (7, 9, 11, 13) as a proportion of the increase in equivalent wood-adjacent scenarios (15, 16, 17, 18). Hence values of 1 indicate no difference between the pairs of scenarios. Wood-pigeon and chaffinch, which did not show apparent gains in response to any clumped scenarios, are excluded. Points are jittered horizontally to ease interpretation

scenarios, where the stock of woodland in the study area was augmented by 16.8%, and planted adjacent to existing woodland (scenario 17), the species with the largest response (song thrush) only increased by 4.6% over a period of 100 years (Table 4). This is partly explained by our 10 focal species having non-zero densities in non-woodland habitat (i.e. none are absolute woodland specialists, whose populations would be expected to increase more closely in line with woodland area), and partly because not all woodland patches are equally suitable due to variation in patch- and landscape-scale characteristics.

The extent to which the outcomes here will be applicable to other taxa is variable. As a very general rule, for animals that exist at high densities and travel very short distances each day (such as many

invertebrates), a 1-ha woodland patch will be large enough to maintain a viable population (unlike for many birds) (see Synes et al. 2020, which examined the theoretical responses of 8 trait-based species to various woodland creation scenarios). Since these taxa are also likely to be relatively poor dispersers (Neumann et al. 2017), a large number of small woodlands scattered across a landscape could be more beneficial for them than a small number of larger (and necessarily more widely spaced) woodlands, thus potentially reversing the trend seen here for birds. The same, to a lesser extent, may be true of rodents such as mice and voles. However, it is also true that the presence and abundance woodland birds, many of which are close to the top of the food chain, reflect the state of lower trophic levels. Since our models are based on empirical data of bird populations in woodlands of different sizes in the study area, our results may still provide an indication of the fuller biodiversity implications for different planting scenarios.

Models vs reality

It is always worth remembering George Box's adage, "all models are wrong, but some are useful" (Box and Draper 1987) when interpreting the outputs of simulation models. Accordingly, some of the results presented here are merely the logical outcomes of model architecture, rather than of biological processes, and in this sense are 'wrong'. A relatively trivial limitation of the model comes in the form of the false precision of some of the outputs. For example, we use model-derived, species-specific relationships between occupancy in woodland patches and those patches' characteristics (such as age, structure, size, coverage of woodland in the surrounding landscape, etc.), and whilst those model estimates are necessarily approximations derived from noisy, empirical datasets, we employ them in a deterministic manner that takes no account of that variance, or of cumulative uncertainty across all the statistical models in our framework.

More importantly, perhaps, the way that we have formulated our IBM, such that patches of contiguous habitat are considered as discrete units, arguably misrepresents the functioning of habitat mosaics. Our ten species are woodland birds (with varying degrees of specialisation), for whom this formulation is largely appropriate, but for some species (such as woodpigeon), to characterise a patch of arable farmland and

an adjacent patch of woodland as two separate sets of territories in which individuals conduct their breeding seasons is incorrect. The same individuals will employ both patches, one largely for feeding, and the other largely for roosting and nesting.

What matters for the purposes of this study is whether such issues should fundamentally affect the interpretation of the results. Here, we suggest that for the more generalist species, such as woodpigeon and chaffinch, predictions of the relative impacts of different scenarios may be less reliable than for woodland specialists such as blackcap and song thrush, where the discrete-patch model is more realistic. Given that creating woodland for biodiversity is, by definition, implemented for the benefit of woodland species, the core messages of the study ought to remain valid: (1) clumps of woodland are more cost-effective for woodland bird conservation than are randomly scattered small patches amounting to the same overall area; (2) regional-level benefits, even where measured as gains per unit cost, may be invisible beneath some (considerable) threshold of investment; (3) siting new woodland adjacent to existing patches only performs better than planting discrete clumps below a certain clump size (10 ha for most species in these models, but real-world results are likely to be different, and context-dependent). Our findings support Bateman et al. (2024) who show that a flat-rate subsidy for woodland creation, in which enrolment is determined according to the economic circumstances of landowners, is less cost-effective than more targeted policies (e.g. those that specify the spatial arrangement of new plantations).

The sensitivity tests should give cause for trust in the parameterisation of our models, especially for those variables whose values are somewhat arbitrary—namely the emigration, dispersal, and long-distance dispersal probabilities (which take defaults suggested by the RangeShifter authors). Under minor perturbation ($\pm 10\%$ adjustment) outputs were insensitive to changes from default variable values in almost all cases; in only one species (blackcap) was there reason to suppose that the outputs could be heavily dependent upon the specific values of the defaults. In one important way, this is the species for which one might wish to pay least attention in any case; as a long-distance migrant, its patterns of breeding season patch-occupation are probably

not determined in the same way as for resident species, and the overall model structure may not be appropriate.

Moderate adjustments ($\pm 25\%$) revealed sensitivity only to demographic variables in the one-at-a-time tests, and only in three of twelve species. In these models, the demographic variables are those with the most empirical support, hence are most likely to be correctly parameterised. Sensitivity was more widespread in LHS tests, which may be more realistic, but in five species the outputs were insensitive to all changes. Only when variable defaults were adjusted by 50% were outputs sensitive more often than not, and we argue that this constitutes an overly stringent test of the models.

Managing expectations

The results here also reinforce empirical observations of the time-lags associated with woodland creation (Watts et al. 2020; Hughes et al. 2023). Beneficial outcomes may not only take several decades to fully materialise, but could also be preceded by net medium-term declines of the very species likely to be viewed as indicators of success. One of the assumptions in our models—which constitutes a way in which they are ‘wrong’—is that newly planted woodlands are effectively identical to semi-natural grassland from the perspective of woodland birds. This isn’t literally true, but it is a better solution than (a) assuming that woodland matures instantaneously, or (b) extrapolating the age-occupancy relationship beyond the existing data (which would probably overestimate the speed at which woodland develops), and as such remains a key component of the modelling process.

Even after establishment, many woodland resources are exceptionally slow to develop. In a study of temperate woodland maturation in south-eastern Australia, Vesik et al. (2008) estimated that large tree-boughs and hollows had only a 30% likelihood of developing in any given woodland site within its first 100 years. In Missouri, USA, herbivorous insect density per unit leaf area continued to increase with estimated woodland age up to 300 years (Jeffries et al. 2006), and Fuentes-Montemayor et al. (2022) argue that in the UK, it takes between 80 and 160 years for woodland creation sites to develop

certain vegetation attributes similar to those of mature ancient woodlands.

We have tried to take such latency effects into account, but our model results could still be optimistic, given that they implicitly assume that all planted woodlands will develop along the lines of the sites used to generate the model parameters (WrEN sites), yet this is not necessarily the case. By definition, the WrEN sites are successfully established woodlands, which constitute some unknown proportion of the sum of planted woodlands. It should be assumed instead that at least some of the woodlands planted by subsidy schemes will fail to establish successfully. Results presented here may equally apply to woodlands created through natural colonisation, as opposed to the planted sites used for the WrEN project. However, we lack a comparator dataset of ecological outcomes derived from naturally colonised sites, so here restrict our interpretation to planted woodlands.

We have also assumed that the only costs associated with woodland creation are the opportunity costs of foregone agricultural profits, along with planting costs, but ongoing management (especially deer control in the UK) is likely to be required if new woodlands are to be maximally beneficial to wildlife.

Conclusions

Woodland creation is a key component of biodiversity restoration and ecosystem service delivery plans across the globe, but there is little empirical data available to guide strategic decision-making. We constructed individual-based demography, dispersal, and settlement models for a suite of UK birds, and applied them to a real-world landscape modified by illustrative planting schemes informed by an economic agent-based model that simulates the response of land managers to financial incentives. The outputs, presented in terms of ‘extra’ birds per unit cost of planting, revealed important differences between scenarios.

We particularly wish to emphasise two lessons from the study. Firstly, not all woodland creation schemes are constructed equally; the cost-effectiveness of new woodland, in terms of subsequent benefits to biodiversity (in this case birds), is strongly determined by its spatial configuration. Planting

alongside existing woodland is likely to be vastly more effective than planting either in isolated patches or in small clumps. The advantage of wood-adjacent over clumped planting disappears only as clumps exceed 5–10ha.

Secondly, short-term biodiversity targets (and specifically those related to woodland birds) are unlikely to be well served by woodland creation. This is not to belittle the value of this activity; indeed, a different suite of species should benefit from the conversion of intensive grassland or arable land to the sort of scrub vegetation that will precede mature woodland. Our results and conclusions apply most specifically to woodland specialists, where we emphasise that the benefits of woodland planting are likely to take decades or longer to materialise, and that the restoration of existing, degraded woodland might be more immediately productive. Even over longer timescales, modest increases in tree cover will likely result in less-than-modest increases in woodland bird numbers (though benefits will be greatest for woodland specialists, which are arguably not well represented in our study). This result further emphasises the benefit of protecting what woodland already exists, rather than assuming that losses of current woodland can be readily offset by new planting.

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Data availability Code used to produce all results and figures is provided in the supplementary materials. Data used in this code is available from the authors upon reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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