

Adapting genetic algorithms for multifunctional landscape decisions: a theoretical case study on wild bees and farmers in the UK

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Adapting genetic algorithms for multifunctional landscape decisions: A theoretical case study on wild bees and farmers in the UK

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Abstract

1. Spatial modelling approaches to aid land-use decisions which benefit both wildlife and humans are often limited to the comparison of pre-determined landscape scenarios, which may not reflect the true optimum landscape for any end-user. Furthermore, the needs of wildlife are often under-represented when considered alongside human financial interests in these approaches.
2. We develop a method of addressing these gaps using a case-study of wild bees in the UK, an important group whose declines may adversely affect both human economies and surrounding ecosystems. By combining the genetic algorithm NSGA-II with a process-based pollinator model which simulates bee foraging and population dynamics, Poll4pop, we 'evolve' a typical UK agricultural landscape to identify optimum land cover configurations for three different guilds of wild bee. These configurations are compared to those resulting from optimisations for farm income alone, as well as optimisations that seek a compromise between bee populations and farm income objectives.
3. We find that the land cover proportions in landscapes optimised for each bee guild reflect their nesting habitat preferences rather than foraging preferences, highlighting a limiting resource within the study landscape. The spatially explicit nature of these optimised landscapes illustrates how improvement for a given

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target species may be limited by differences between their movement range and the scale of the units being improved. Land cover composition and configuration differ significantly in landscapes optimised for farm income and bee population growth simultaneously and illustrate how human agents are required to compromise much more when the multifaceted nature of biodiversity is recognised and represented by multiple objectives within an optimisation framework. Our methods provide a way to quantify the extent to which real-life landscapes promote or compromise objectives for different landscape end-users.

4. Our investigation suggests that optimisation set-up (decision-unit scales, traditional choice of a single biodiversity metric) can bias outcomes towards human-centric solutions. It also demonstrates the importance of representing the individual requirements of different actors with different landscape-level needs when using genetic algorithms to support biodiversity-inclusive decision-making in multi-functional landscapes.

KEY WORDS

Agroecology, ecological modelling, genetic algorithms, landscape optimisation, land-use decisions, multi-functional landscapes, pollinators, spatial modelling

1 | INTRODUCTION

Human economic activity places significant pressure on global biodiversity, resulting in undesirable trade-offs for both ecosystems and ecosystem services (IPBES, 2019). This is prominent in agricultural contexts (Mattison & Norris, 2005), affecting key groups such as wild bees. These are crucial for maintaining diverse, resilient pollination networks (Hutchinson et al., 2022) and provide significant pollination services to crops (Hutchinson et al., 2021; Rader et al., 2012) and wild flora (Ollerton et al., 2011). However, intensive agricultural practices can cause habitat loss and fragmentation, reducing pollen, nectar and nesting resources for wild bees (Dicks et al., 2021) and causing declines in diversity and abundance (Turley et al., 2022).

With growing global awareness of the societal and economic impacts of biodiversity loss, and political pressure to reverse these declines (e.g. Convention on Biological Diversity, 2022), there is increasing interest in developing 'multi-functional landscapes' that deliver both economic outcomes and sustainable ecosystem service benefits (Boesing et al., 2024). However, significant challenges remain in identifying how habitats in farm-scale landscapes should be arranged to mediate the apparently conflicting goals of humans and wild species such as bees (Gillespie et al., 2022).

Spatial modelling approaches, especially process-based models that predict population dynamics by simulating underlying ecological processes, provide a useful means of assessing land cover configurations for wildlife while accounting for synergistic or conflicting human needs. Numerous such models have been developed to simulate pollinator populations across landscapes, for example Bumble-BEEHAVE (Becher et al., 2018) and Poll4pop (Gardner et al., 2020). These approaches often rely on data from

real landscapes or simply compare sets of pre-defined scenarios (e.g. Graham & Nassauer, 2019; Twiston-Davies et al., 2021), which may not reflect truly 'optimal landscapes' for the target taxa. However, using process-based models in a mathematical optimisation framework may be a novel approach to identifying optimal landscape configurations for multiple ecosystem objectives.

Previous studies (e.g. Elliot et al., 2019) have optimised ecosystem services across landscapes using 'threshold' or 'reference-point' techniques which guide the search using pre-defined criteria often based on decision-maker preferences. However, an optimisation approach which seeks to unconditionally maximise all goals at once can allow us to 'evolve' land cover configurations towards an optimum for all actors with minimal preconceptions about how they should be arranged.

One such method is the genetic algorithm, a metaheuristic optimisation technique that imitates evolutionary principles. Here, a population of 'individuals' defined by bounded parameters is 'evolved' through simulated selection, recombination and mutation towards a solution with maximum 'fitness' according to one or many pre-defined objectives (Mirjalili, 2019). Where there are multiple objectives, the algorithm seeks a solution which simultaneously maximises the scores of several (potentially conflicting) goals by approximating the Pareto front, that is, the set of solutions where no objective can be improved without diminishing the outcome of another (Veldhuizen & Lamont, 1998). These algorithms have rarely been used in the context of landscape decision-making from an ecological perspective (Seppelt et al., 2013) and to our knowledge have never been combined with process-based species models to identify optimal landscapes for species abundance and investigate related trade-offs.

In ecosystem service-focused landscape optimisation approaches (e.g. Desaegher et al., 2021), biodiversity is usually seen as a constraint to the optimisation goals. However, recentring these goals around the abundance or diversity of target species themselves is a novel and useful approach to optimising landscapes for both humans and wildlife. For example, changes in pollinator populations have historically been assessed with focus on market forces and economic indicators (Häussler et al., 2017). However, these metrics rarely fully account for economic benefits offered by wild pollinators, nor the costs of replacing their services with managed pollinators (IPBES, 2016). Holistic, bottom-up approaches to ecosystem management are therefore recommended to ensure long-term sustainable land use (Senapathi et al., 2015), which can be represented using this combined modelling approach.

Furthermore, accounting for the varied forage and nesting preferences of wild bees (IPBES, 2016) is also important when designing land cover configurations that support resilient pollination services. Defining cover types and habitats based on the species-specific services they provide can offer a more detailed view of how individual species or groups respond to land cover changes (Betts et al., 2014). This specificity is often overlooked when general biodiversity metrics are utilised (Chiarucci et al., 2011).

With these considerations in mind, we aimed to investigate the potential benefits of combining a multi-objective optimisation approach with process-based ecological models to inform multi-functional land-use decision-making (The Royal Society, 2023). We utilised a combination of the genetic algorithm NSGA-II (Deb et al., 2002) and Poll4pop, a validated, process-based pollinator abundance and visitation model that simulates bee foraging and population dynamics (Gardner et al., 2020; Häussler et al., 2017; Figure S1), to explore how an agricultural landscape can be 'evolved' to provide theoretical optimum land cover configurations for

- the abundance of one or more guilds of wild bee,
- farm income (a human-centric optimisation) and
- all bee guilds and farm income collectively.

FIGURE 1 2020 land cover configuration of the 10×10 km study area, which is situated south-west of Lincoln, UK. The central zone in brighter colours represents the optimised region (radius=2 km), while the remaining fields were not included in the optimisation process, representing a 'fixed' surrounding landscape. See Figure S1 for land cover proportions.

2 | MATERIALS AND METHODS

2.1 | Study landscape

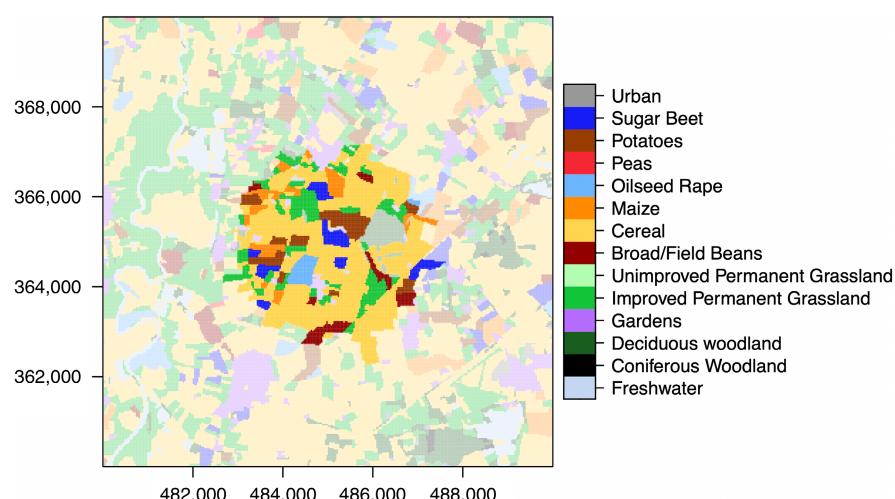
We examined land cover (i.e. the physical material assigned to the land surface of one unit within the landscape) configuration in a representative agricultural landscape with mixed land use. A 10×10 km area was selected corresponding to GB National Grid square SK86, as used by Image et al. (2023) (Figure 1). This represents a typical agriculturally dominated UK landscape which contains pollinator-dependent, mass-flowering crops and potential for woodland creation. The 10 km scale of this landscape was both large enough for the ecological processes simulated by Poll4pop (see Section 2.3.2 for description) and computationally feasible for the optimisation process. Our subsequent optimisations generate simulated landscapes by superimposing different land cover types onto a fixed template of the field boundaries in this grid square.

UK Centre for Ecology and Hydrology Land Cover, Land Cover Plus, and UK Woody Linear Feature spatial data were downloaded from the EDINA Digimap service and converted to raster format at 25 m pixel resolution (UKCEH, 2016, 2020, 2021). Arable field margins and woodland boundary edge features were simulated by respectively rasterising the borders of arable fields and woodlands in the land cover rasters.

2.1.1 | Optimised area

Within the centre of the study landscape, a smaller optimisable area (radius=2000 m) was defined (Figure 1). This radius is larger than the movement ranges of all target guilds (Table S1) and provides enough fields (303) to allow exploration of land cover configuration effects. Within this optimisable area, urban/suburban and semi-natural land cover types were considered fixed since these could not realistically be converted or may be considered protected.

This gives a total area for optimisation of 1360 ha. As mean farm size in the UK is 81 ha, and 101 ha in the East Midlands



(DEFRA, 2022), the optimised area may be considered equivalent to a cluster of farms engaged in collaborative decision-making, surrounded by a larger, fixed landscape that cannot be influenced by the cluster's decision makers.

2.1.2 | Permitted land cover choices

During optimisation, each field within the optimisable area was permitted to adopt one of eight land cover types reflecting those already found within the study landscape: broad/field beans (*Vicia faba*), cereal, coniferous woodland, deciduous woodland, fallow, improved permanent grasslands, oilseed rape (*Brassica napus*; OSR) or unimproved meadow. Cereals were aggregated into a single category because they neither provide floral resources to, nor require pollination services from, bees.

2.2 | Study guilds

We studied three wild bee guilds, all parameterised in the Poll4pop model (Gardner et al., 2020): ground-nesting bumblebees (GNB), tree-nesting bumblebees (TNB) and ground-nesting solitary bees (GNS). According to the model parameters, GNB and TNB have the same movement ranges but different nesting preferences, whereas GNB and GNS have similar nesting preferences but different movement ranges.

2.3 | Genetic algorithm (NSGA-II)

The NSGA-II algorithm is a box-constrained, elitist, non-dominated sorting, genetic algorithm (utilised in this study via the NSGA2R package in R (Tsou, 2022)). This algorithm is conventionally used for multi-objective optimisation where the scores of multiple, conflicting objectives are maximised simultaneously. However, where required the algorithm can be adapted for single-objective optimisations (see *Supporting Information*).

This algorithm was used to evolve a population of landscapes whose 'genomes' are represented by a set of discrete codes corresponding to the type of land cover in each field. Thus, different land cover codes represent so-called 'alleles', sequentially denoting the features of different individuals in the population.

Within the algorithm, the Poll4pop model (see Section 2.3.2) is run on each of these different land cover configurations. The 'fittest' individual landscapes (e.g. the spatial configurations supporting most bees) from each generation are selected as parents for a new generation using non-dominated sorting (i.e. landscapes are ranked higher than others when they are better regarding at least one objective and not worse regarding any other), and then by maximum crowding distance along the Pareto front within these ranks. These undergo recombination (or 'crossover') and produce 'offspring' landscapes which then experience mutation to produce a new, fitter

population of landscapes. This process is then repeated for a number of generations defined according to the needs of the optimisation experiment (Figure 2).

Traditionally, NSGA-II generates values from a bounded continuous scale that represent 'genes' in the population whose fitness will be assessed in each generation. This process was adapted in the landscape optimisation context because the 'genes' are categorical codes representing different land cover types, with no specific logical order or relationship to one another. The new or modified steps of the NSGA2R optimisation process are outlined below.

2.3.1 | Initialising the population

A population of landscapes (each based on the field boundary template of SK86 (Figure 1)) is randomly generated by the genetic algorithm so that the proximate process of natural selection can occur. A 'genome' is defined for each landscape in the initial population by generating a random set of codes corresponding to the eight permitted land cover choices described in Section 2.1.2. These are superimposed onto each field in the optimised section of the landscape (Figure S3).

2.3.2 | Assessing fitness

The fitness function used to assess the success of each bee guild in these optimisations was adapted from the Poll4pop model. Poll4pop is a spatially explicit, process-based model that predicts bee abundance across a given landscape by simulating their central-place foraging, population growth and the dispersal of reproductive females (Gardner et al., 2020; Häussler et al., 2017; Figure S1). In this fitness function, rasterised land cover and edge feature maps are used as inputs. Edge feature rasters for arable margins and woodland boundaries are created based on the composition of each new landscape created in each generation. The model then generates nesting and seasonal floral resource maps for each specified pollinator guild by attributing scores (determined by expert opinion) to each land cover type based on the amount of floral cover, floral attractiveness and nesting attractiveness typically provided.

Literature data about the bees' typical movement ranges and life histories are used to simulate their nesting and foraging behaviour in this landscape and thus predict population growth. The bees' movements are simulated at the pixel scale (25 m resolution) using attractiveness-weighted distance decay kernels, meaning the effects of habitat connectivity and landscape heterogeneities on both day-to-day foraging and intergenerational dispersal are accounted for by the model.

From this, a raster of predicted visitation rates of the specified guild to each pixel is generated for each active season. For each guild, a seasonally unbiased 'fitness' score is then calculated by multiplying the total spring and summer floral visitation rates to each pixel. This score represents the abundance of foraging bees in the

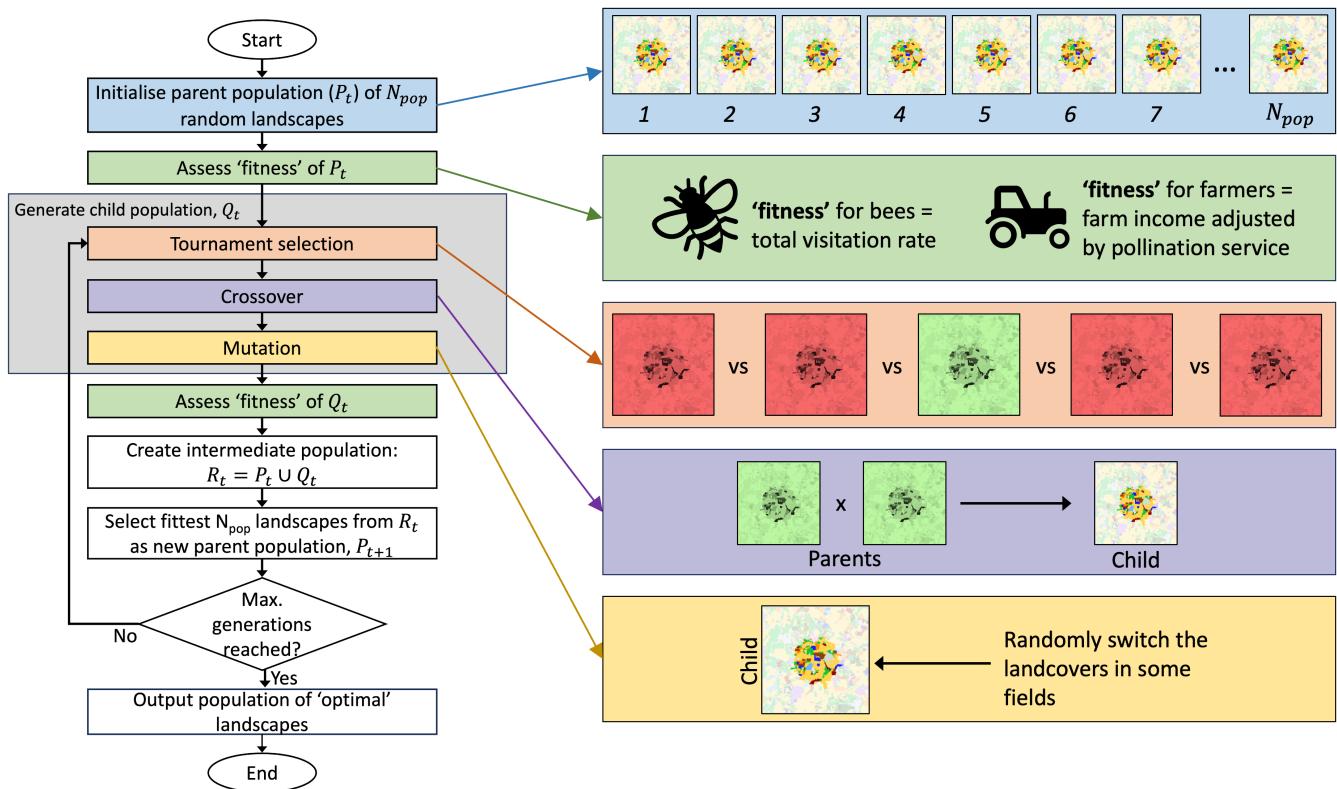


FIGURE 2 Applying the NSGA2R optimisation process in the context of land-use decision-making for wild bee populations and/or farm income. N_{pop} is the number of individual landscapes in the population, as defined by the optimiser.

landscape across both seasons and is used by the genetic algorithm as a fitness measure to compare the suitability of each generated landscape, for each bee guild.

An economic, 'farmer' fitness function was also defined to investigate trade-offs between farm income and bee diversity. This assesses fitness by estimating the total income farmers could receive from each landscape, based on crop price and agri-environment scheme payment rate data for each land cover type (Table 1). Due to omitting production costs and variability in factors such as sale prices, this is not necessarily representative of the true return profile (e.g. gross margin) that a farmer would derive from the theoretical landscape. However, this approach allows us to test trade-offs with a conflicting objective that incorporates some dependence on other objectives, via the crop pollination service modifying oilseed rape and field bean yield.

Yield for these pollinator-dependent crops is assumed to increase with increased visitation (Garratt et al., 2014). Consequently, the yields listed in Table 1 for these crops are assumed to correspond to the mean per-pixel visitation rate for that crop in the real-life landscape. These are adjusted for optimised landscapes by calculating yield adjustment values assuming a linear relationship with visitation rate for field beans, and a curved relationship for oilseed rape (Gardner, 2020, personal communication; see Equations S1/S2). Actual yield values in optimised landscapes are then adjusted according to Equation (1) (see derivation in Supporting Information; Figure S4):

$$Y = Y_0 + (a - a_0), \quad (1)$$

where Y = normalised crop yield (tonnes per ha), Y_0 = national mean crop yield (tonnes per ha), a = yield adjustment values of crop in specified pixel of the optimised landscape (tonnes per ha), a_0 = mean yield adjustment value of the crop in the real-life landscape (tonnes per ha).

Farm incomes are calculated for the whole landscape, to incorporate the additional yield benefits that the optimised area may provide to surrounding farms through promoting increased bee visitation.

Overall, the fitness function outputs one score for each specified objective (Figure S5). In multi-objective optimisations, these scores are not conflated and are treated separately throughout the optimisation process.

2.3.3 | Modifications of original NSGA2R functions

Once tournament selection has created a 'mating pool' of the fittest landscapes in each generation, crossover between pairs of parent landscapes occurs to produce child landscapes with inherited characteristics from both parents. This happens on a gene-by-gene (i.e. field-by-field) basis at a rate determined by a specified crossover probability (e.g. Table S2). The original algorithm, which assumes parameter values are continuous, selects an intermediate 'child' value between the two gene values of the parents. This is not meaningful when the gene values represent discrete, categorical land cover codes. However, some inherent order does

TABLE 1 The calculated theoretical income of each land cover type and their assumed income proxy (AHDB, 2022; DEFRA et al., 2021; Haw, 2017).

Land cover type	Yield, \bar{Y} (tonnes per ha)	Price (£ per tonne)	Price (£ per ha per year)	Payment proxy
Oilseed rape	2.7	348.93	NA	AUK Crop income
Field beans	3	204.42	NA	AUK Crop income
Cereal	NA	NA	1117.52	AUK Crop income: wheat
Improved permanent grasslands	NA	NA	496.20	British Hay & Straw Merchant's Association: pick up baled seed hay
Unimproved meadow	NA	NA	511.00	Countrywide Stewardship Scheme: AB1 nectar flower mix
Fallow	NA	NA	522.00	Countrywide Stewardship Scheme payments: AB15 two-year sown legume fallow
Coniferous woodland	NA	NA	45.46	Forestry Commission: carbon and timber returns for lowland conifer on 55-year rotation at £6 per tonne of carbon sequestered (2017)
Deciduous woodland	NA	NA	11.00	Forestry Commission: carbon and timber returns for broadleaved woodland (game/biodiversity) on 100-year rotation at £6 per tonne of carbon sequestered (2017)

Note: Yield per ha and price per tonne are included for pollinator-dependent crops, because these were used in the visitation-rate scaling process described above. All data are taken from 2020 unless otherwise specified. AUK stands for Agriculture in the United Kingdom.

appear among the chosen land cover types when they are ranked by how much fitness each type contributes to the landscape according to the model used in the fitness function. Consequently, when optimising for bee abundance, we modified the crossover function to create a scale of land cover types ranked by an average of the Poll4pop-defined nesting and floral scores for each specified guild of bee (Figure 3c). The algorithm then selects a child value positioned between the two parent land cover types on this scale (Figure S6). This approach would not have been meaningful in optimisations where farm income was included as an objective because the values of various crops were adjusted for each landscape according to bee visitation rates. Therefore, in these circumstances land covers were assigned randomly to fields in the child landscape where the crossover probability was met.

The mutation process serves to maintain genetic diversity within the population of solutions, and to prohibit premature convergence to local optima. We modified the NSGA2R mutation function to account for categorical land cover data by allocating a random land cover to child fields when the specified mutation probability was met (Figure S7).

2.4 | Optimisation experiments

2.4.1 | Optimising landscapes for wild bees

Here, we investigated the differences between landscape solutions for the three bee guilds, optimised both individually and

simultaneously, to explore how the optimisation routine compromises between different habitat and foraging preferences. Single-objective optimisations were executed for the three individual guilds of bee (GNB, TNB and GNS), as well as multi-objective optimisations for all three guilds at once. All guilds were valued equally in the combined objective function.

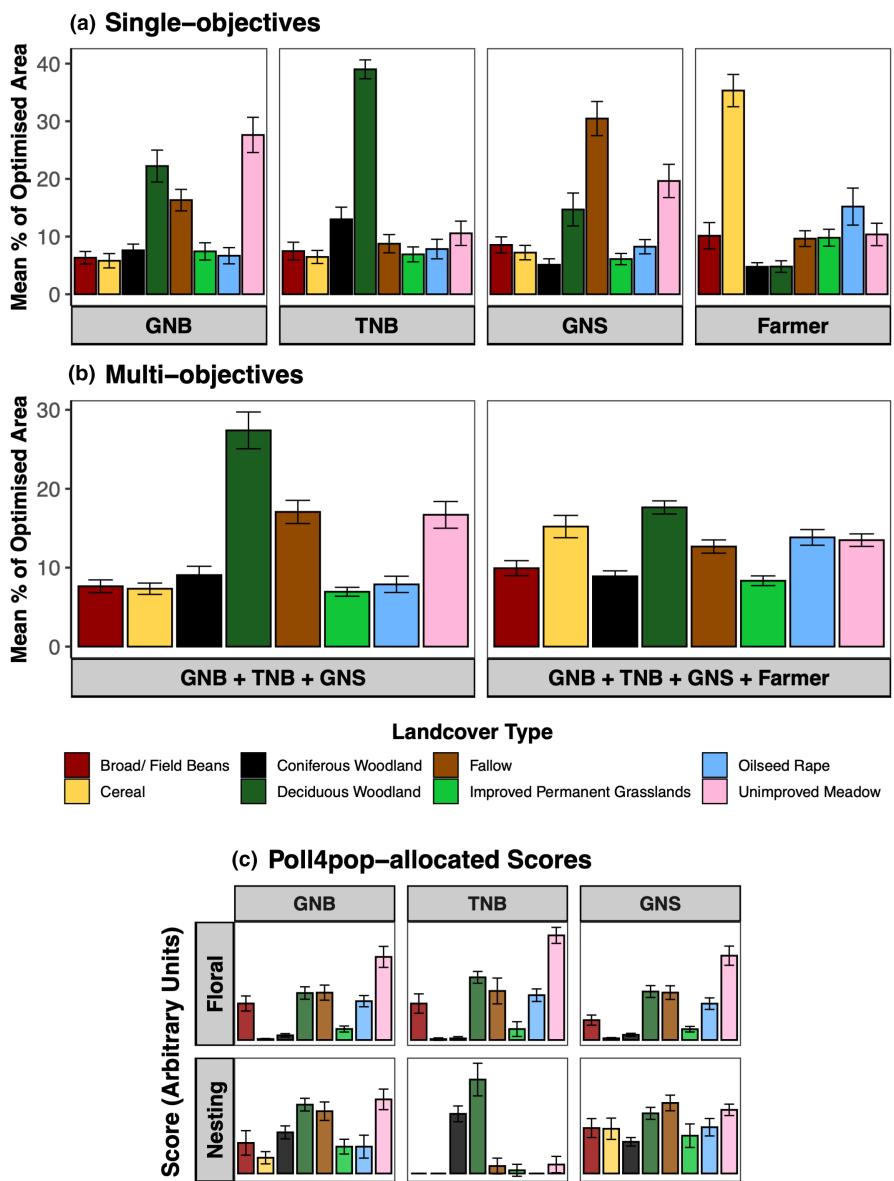
2.4.2 | Optimising landscapes for wild bees and humans

Here, we investigated how introducing a human-based objective to the bee-focused optimisation affects its solution. We first ran single-objective economic optimisations, then multi-objective optimisations with four objectives: maximising total floral visitation rates for each bee guild and maximising the economic income for the farmer. Again, the needs of all four actors were weighted equally.

2.5 | Analyses

Based on preliminary trials, we ran the NSGA2R algorithm with a population of 50 landscapes for 100 generations in each experiment. Other NSGA2R parameters were left at their default values (Figure S8; Table S2). Each experiment was repeated 25 times with different random seeds on the Imperial College High Performance Computing (HPC) cluster to allow exploration of variation among solutions.

FIGURE 3 (a, b) Mean proportions of each land cover in the optimised region of solutions for each set of objectives in (a) single-objective and (b) multi-objective optimisations. GNB, ground-nesting bumblebees; GNS, ground-nesting solitary bees; TNB, tree-nesting bumblebees. Error bars represent standard deviation on land cover proportions for each landscape (Table S3). (c) Expert-allocated nesting and floral resource scores for each land cover and each guild of bee as used in the Poll4pop model/fitness function. Floral scores are the product of allocated floral attractiveness scores and the sum of floral cover scores for each season. Scores are arbitrary and relative; hence, y-axis values are omitted. Error bars represent standard error.



R version 4.1.3 was used for all analyses (R Core Team, 2022). Due to run-time constraints, 6% of optimisations did not complete on the HPC. Of the remaining solutions, analyses were performed on only the highest-ranked landscapes from the final population generated in each trial. Note that the number of high-ranking landscape configurations for each repeat varied due to differing arrangements of the final population along the Pareto Front. Therefore, sample sizes from each optimisation were different; in total, 1978 solution landscapes were included in our analyses (Table S3). Mean patch area of solution landscapes was calculated using the 'landscapemetrics' package in R (Hesselbarth et al., 2019). Interactions between the objectives of the optimisations and land cover proportions of the populations of landscape solutions were assessed using ANOVA.

3 | RESULTS

3.1 | Landscape composition

3.1.1 | Single-objective optimisations

The mean proportion of each land cover within the final optimised area for single-objective optimisations are shown in Figure 3a. These proportions were significantly different across optimisations (ANOVA, $F_{31,2104} = 850.946, p < 0.01$). The dominant predicted land covers were unimproved meadow when optimising for ground-nesting bumblebees (GNB), fallow for ground-nesting solitary bees (GNS), deciduous woodland for tree-nesting bumblebees (TNB) and cereal in optimisations for farm income.

In solutions to single-objective optimisations for each bee guild, we found positive relationships between the mean proportion of each optimised land cover type and both the floral and nesting resource scores allocated to that land cover type in the Poll4pop model (Figure 3c). This correlation was significant in all tests but one and was consistently stronger with nesting score than with floral score (Table 2).

3.1.2 | Multi-objective optimisations

The proportions of each land cover type predicted from the multi-objective optimisations are shown in Figure 3b. These were also significantly different from each other (ANOVA, $F_{15,13672}=483.424$, $p < 0.01$). Deciduous woodland was predicted to be the most abundant land cover in both multi-objective optimisations, however deciduous tree cover was significantly higher when not including the farmer (Tukey HSD, $p < 0.01$). Cereal was the second most prevalent land cover when including the farmer, and significantly greater than all other land cover types apart from deciduous woodland (Tukey HSD, $p < 0.01$). While the proportions of deciduous woodland, fallow and unimproved meadow were significantly lower when the farmer was included compared to the bee-only optimisation, the proportions of beans, cereal, improved grassland and oilseed rape were significantly higher (Tukey HSD, $p < 0.01$).

3.2 | Landscape configuration

The mean land cover patch area within the optimised area was dependent on the objective of the optimisation (ANOVA, $F_{5,1972}=42.031$, $p < 0.01$; Figure 4a). The mean patch area in the TNB solutions was significantly greater than for any other set of objectives (Tukey HSD, $p < 0.01$). Conversely, mean patch area in the solutions for the farmer-inclusive multi-objective optimisations was significantly smaller than for any other set of objectives (Tukey HSD, $p < 0.01$). Examples of these differences are visualised in Figure 4b.

3.3 | Objective fitness

Figure 5 shows that, for each bee guild, the mean fitness (i.e. guild abundance) of solution landscapes was higher in their respective single-objective optimisations compared to the land cover configuration in

the real-life landscape. However, abundances were lower in the single-objective 'farmer' optimisation compared to all other optimisations. Conversely, the fitness (i.e. theoretical income) of solution landscapes for the farmer was slightly lower than in the real-life landscape in all optimisations (this may relate to how anthropocentrically organised the 'real-life' landscape already is; see Section 4.2.3).

When measured across the whole 10 × 10 km grid square, the relative fitness of solutions for TNB was greater than that for GNB in two thirds of optimisations; however, it was always lower than that of GNB when only the optimised region of solution landscapes was considered. Optimal landscape fitness for GNS was always similar (or even reduced) compared to the predicted abundance for the real-life landscape when measured across the whole grid square but was consistently higher in the optimised region.

4 | DISCUSSION

4.1 | Ecological implications

4.1.1 | Habitat composition

The most prevalent land cover types in landscapes optimised for each bee guild separately were consistently those which (according to the specifications of the model) provide the best nesting resources for that guild, rather than floral resources (Figure 3a,c; Table 2). Our outcomes suggest that prioritising nesting habitat is a key factor when attempting to increase wild bee diversity, perhaps because bees are central place foragers and often nest site-limited (Verboven et al., 2014). However, Häussler et al. (2017), using a predecessor of Poll4pop, found late-flowering foraging resources to be the main limiting factor within the landscape, even when nesting resources were reduced by 50%. These contrasting findings highlight the need for more direct investigations regarding the relative importance of different resources for wild bees (Harmon-Threatt, 2020; Requier & Leonhardt, 2020). This demonstrates how the combination of process-based ecological models with genetic algorithms may facilitate better identification of limiting factors in a landscape, which may have previously been overlooked.

Landscapes optimised for ground-nesting solitary bees (GNS) and ground-nesting bumblebees (GNB) were each dominated by deciduous woodland, fallow and unimproved meadow (Figure 3a). Contrastingly, landscapes optimised for tree-nesting bumblebees (TNB) were dominated by deciduous woodland, a valuable nesting

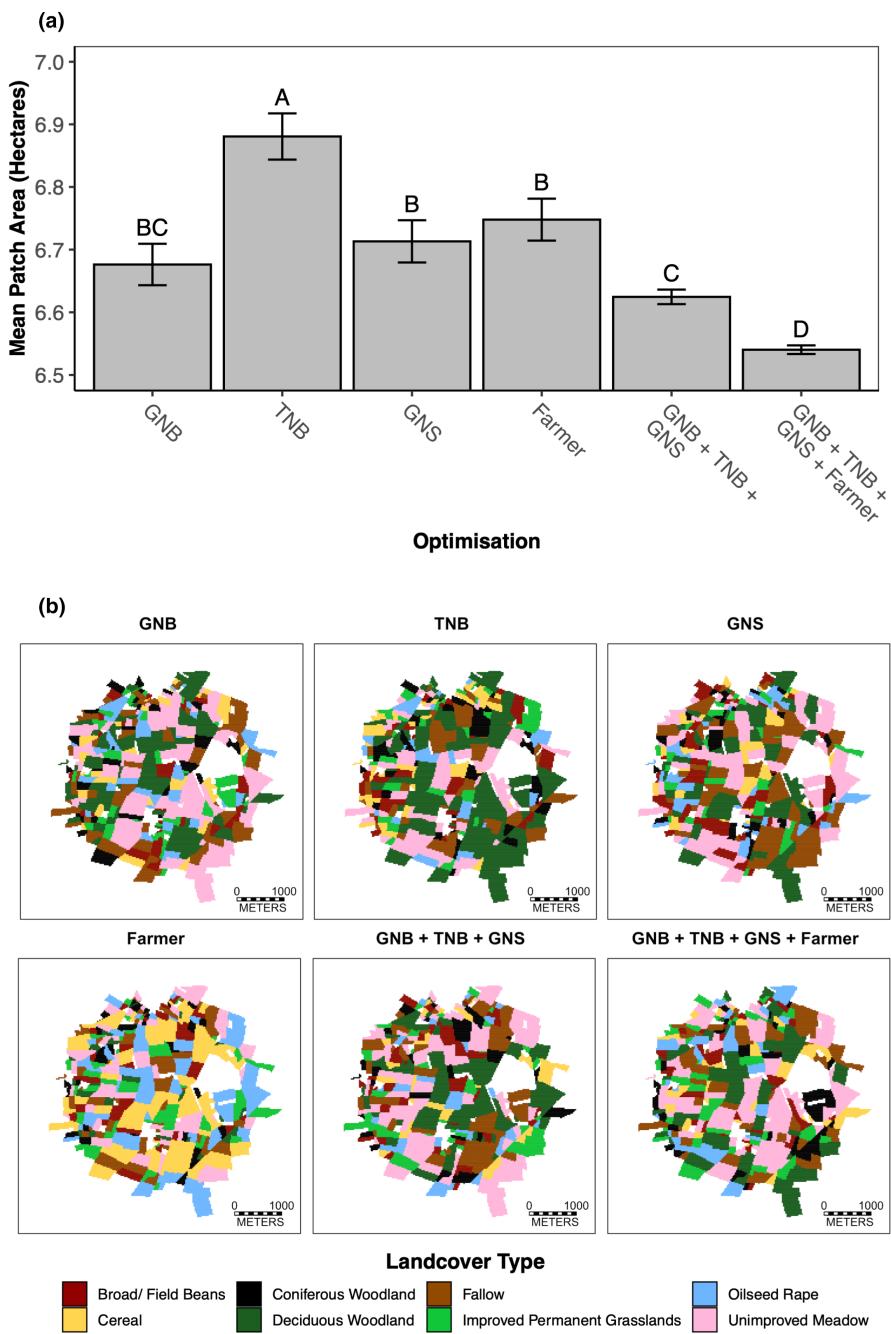
TABLE 2 Spearman's rank correlations between Poll4pop-allocated floral or nesting scores for each optimised land cover type for each bee guild, and the respective mean proportions of the same land cover types in solutions of single-objective optimisations for each guild.

Poll4pop score	Ground-nesting bumblebees	Tree-nesting bumblebees	Ground-nesting solitary bees
Floral	0.762*	0.595	0.833*
Nesting	0.922**	0.878**	0.976**

Note: N=8 in all tests.

* $p < 0.05$. ** $p < 0.01$.

FIGURE 4 (a) Mean patch area in optimised solutions for each set of objectives. Error bars represent standard error on patch area for each landscape as specified in Table S3. A greater patch area equates to a less fragmented landscape. Optimisation types with the same letter exhibit no significant difference from each other (TukeyHSD, $p < 0.05$). (b) Predicted land cover distributions in optimised landscapes that exhibited the most similar land cover proportions to the mean of all solution landscapes for each set of objectives (as shown in Figure 3a,b). GNB, ground-nesting bumblebees; GNS, ground-nesting solitary bees; TNB, tree-nesting bumblebees. Note that all simulations were run at 25 m pixel resolution across the whole 10 × 10 km landscape.



and forage habitat for TNB (Liczner & Colla, 2019; Figure 3c). This illustrates that landscape optimisation for the benefit of one taxon may cause habitat loss and fragmentation for another (Holzkämper et al., 2006; Figure 3c).

Landscapes optimised only for farm income were dominated by cereal, which provides the greatest farm income but minimal resources for bees (Figure 3c). This was very different to patterns of optimised land cover distribution for any single bee guild.

Similarly, the average composition of landscapes optimised for all three bee guilds simultaneously differed significantly when the farmer was also included (Figure 3b), demonstrating this conflict between human-centric and wildlife-centric objectives. Although seminatural (deciduous woodland/ unimproved meadow) and

regenerative habitats (fallow) were prevalent in landscapes optimised for all three bee guilds and the farmer simultaneously, providing some compromise for maintaining both bee populations and farm income (Evans et al., 2018), no solutions completely resolved this trade-off. Both farm income and bee abundance in these compromise landscapes were consistently lower than in landscapes optimised for each objective separately (Figure 5).

4.1.2 | Habitat configuration

The spatially explicit nature of our optimised landscapes allows exploration of both the key effects of configuration on bee

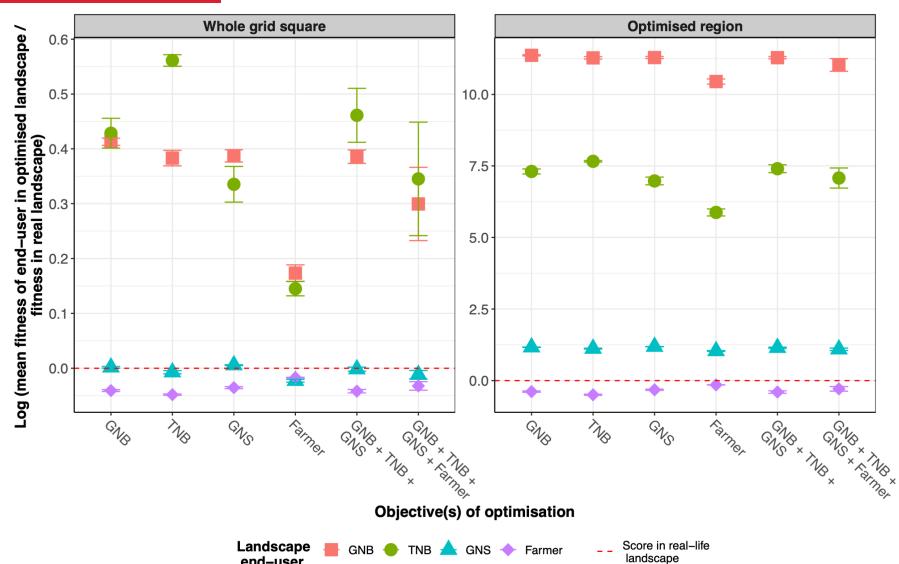


FIGURE 5 Relative fitness of solution landscapes generated by each optimisation experiment compared to the fitness predicted for the real-life landscape for ground-nesting bumblebees (GNB), tree-nesting bumblebees (TNB), ground-nesting solitary bees (GNS) and farmers across the whole grid square (left) and the optimised region of the grid square (right). Fitness was normalised by dividing mean fitness of solution landscapes for each end-user by its predicted fitness for the real-life landscape. Note log scale. Points below zero denote lower fitness than the real-life landscape and vice versa. Error bars show standard deviations. See Table S3 for sample sizes.

abundance (Gillespie et al., 2022) and the effects of managing for multiple species groups alongside humans. We found lower patch area (i.e. higher landscape fragmentation) in landscapes optimised for farmers and bees simultaneously than any other set of objectives. However, in individually optimised landscapes, both wild bees and farmers benefitted from less fragmented landscapes (Figure 4a,b). This could be because there are few land cover options in our model that are optimally beneficial for both bees and humans. Therefore, meeting multiple objectives requires more landscape heterogeneity and, consequently, smaller patch sizes. This supports the work of Memmah et al. (2015), who showed that attempting to assign land covers to prescribed land parcels in a way that meets every objective may result in solutions that are not optimal for any objective.

GNS have a much smaller foraging range than the bumblebee guilds and hence require greater density of habitat patches in the landscapes they traverse (Gathmann & Tscharntke, 2002). However, the expectation of smaller patch size for GNS was not reflected in our results (Figure 4a,b). One explanation could be because the minimum patch size was constrained by field sizes in the real-life landscape (mean field size in the optimised region = 4.5 ha), which are potentially already greater than the optimum patch size for GNS (foraging kernel = 191 m in Poll4pop). This is supported by the smaller increase in predicted abundance for GNS than for TNB or GNB in their individually optimised landscapes (Figure 5), perhaps because many land covers were beneficial for all three guilds, but the existing field sizes were innately more suitable to GNB and TNB movement ranges. This further highlights the potential trade-offs in managing for multiple guilds that may previously have been perceived to have similar needs.

4.2 | Modelling implications

4.2.1 | Representing the needs of individual groups

The needs of non-human species are often conflated into simplified 'biodiversity' metrics in landscape optimisations, (e.g. Juutinen et al., 2019)—that is, a single objective. In contrast, the outcomes of our experiments are driven by several individually represented groups of species that all contribute towards biodiversity but have different habitat preferences. This approach provides more detailed insights into the requirements of different taxa and the challenges of reaching acceptable compromises between the needs of humans and individual species groups, or even simply between different species groups (e.g. Figure S9).

In the farmer-inclusive multi-objective optimisation, one human objective was outnumbered by three bee objectives, whereas in similar experiments, a single biodiversity objective is often outnumbered by multiple anthropocentric ecosystem service metrics (e.g. Verhagen et al., 2018). Our alternative set-up allows exploration of how much the bee guilds are required to compromise when the landscape is also used for income, rather than the reverse. Accordingly, in the farmer-inclusive multi-objective optimisation, the average visitation rate of each bee guild still increased throughout the generations of the optimisation process (compared to the random starting landscape), indicating improved landscape suitability for bees. In contrast, farm income generally decreased (Figure S10). This information, that is the relationship between theoretical income loss to the farmer and quantified improvement of wild bee populations, could be used to help determine acceptable thresholds of compromise (and, thus, compensation for economic loss), which account not

just for farm income foregone but also the amount of biodiversity improvement desired.

Additionally, our results capture differences in the ways taxa with different ecologies are likely to experience changes to the landscape. For example, unlike the other two guilds, the predicted abundance of GNS in optimised landscapes is only higher than the real-life landscape when the optimised region is considered alone, and not when calculated across the whole grid square (Figure 5). This is perhaps because their smaller foraging range reduces beneficial spill over of populations from the optimised region into the surrounding landscape. Similarly, compared to the original landscape, TNB abundance sometimes improved more than GNB abundance when measured across the whole grid square, but always less when measured across only the optimised region. This could be due to lack of woodlands causing TNB nest limitation in the real-life landscape. The algorithm thus tends to create a nesting hotspot (i.e. more trees; Figure 3a) in the optimised region, enhancing the landscape-level population by relying on TNB having access to foraging resources outside the optimised region. However, when the fitness of the surrounding landscape was not included, the necessary balance of resources was not available and hence the TNB underperformed compared to the GNB. This highlights the need to consider individual traits—for example foraging ranges—of species or groups throughout the optimisation process (Lima & Zollner, 1996).

Overall, we show that using multiple objectives to represent the multifaceted nature of biodiversity produces (a) less anthropo-biased landscape solutions, and (b) more detail about how landscape changes may affect the various species in question. This alternative approach—a computational equivalent of ‘multi-species placemaking’ (Olsen, 2022)—may help identify discrepancies and acceptable balances between the wide-ranging needs of wildlife and human stakeholders. Future land cover optimisations should consider the balance between multiple ecocentric and anthropocentric objectives, and how this may affect their landscape solutions.

4.2.2 | Realism of solutions

Due to the simplifications and assumptions inherent in any ecological modelling or optimisation procedure, some aspects of our optimised landscapes may not be entirely realistic. For example, in this set of experiments, we did not consider crop management practices such as rotation or blocking, which may temporally and spatially constrain aspects of the landscape. However, our approach is not designed to predict exact land cover configurations that should be implemented. Rather, it should be used as a supportive tool in the decision-making process by finding multiple high-quality landscape solutions in a reasonable computational timeframe (Memmah et al., 2015). This allows identification of patterns and similarities from different solutions, which can be used to inform decision-making. Furthermore, the attractiveness and feasibility of landscape configurations is often subjective and difficult to formulate within the algorithm. Therefore, an

iterative approach between expert opinion and optimisation procedures may be advisable, allowing stakeholders to engage with a representative range of solutions (Stewart et al., 2004).

In every modelling exercise, there is a balance to be found between realism and simplification. For example, allowing completely random allocation of land cover types to fields within the chosen area is unlikely to comply with how farmers typically choose to configure their fields. However, we allowed this here because the resulting landscapes provide novel insights into how different habitat configurations could enhance pollinator numbers. Future experiments could improve realism by adjusting and constraining which land cover types can be introduced on a field-by-field basis via the lower and upper bounds parameters (e.g. Verhagen et al., 2018). Similarly, linear and sub-field features (e.g. uncultivated arable margins, hedgerows) remained fixed in our experiments. Since farmers may be more willing to alter these features (as changes are less likely to affect overall farm income), future optimisation experiments should include aspects such as the width or type of field boundary features that could be established.

Despite the fact that our optimisation approach was relatively unbiased, the results of our optimisations were still constrained by the spatial arrangement of existing fields—that is, field sizes were assumed to remain constant. Therefore, despite the equal consideration of bee and human needs in the optimisation process, there is still human-driven subversion of true optima for bees. While using the existing field sizes and shapes of the real landscape is a realistic constraint on decision making, it also bypasses a rare opportunity to explore optimal landscapes for bees outside of human-defined environments. Optimising landscapes with no limits on field size or location is an avenue for further investigation, which would also provide a more detailed outlook on landscape configuration, potentially revealing more insight into aspects such as optimal habitat patch size for each guild of bee.

4.2.3 | Model limitations

Although not all experiments completely converged, the plateauing improvements in fitness displayed in Figure S10 suggest the solutions may be approaching optima. However, we note that algorithm stagnation and true optima can be hard to distinguish without much longer run-times than was feasible for our pilot study. The resulting landscapes nevertheless provide useful insights into synergies and trade-offs between objectives. Our bee-centric results appear to be ecologically realistic, and the mean predicted abundance of each guild was higher in their individually optimised landscapes compared to the real-life landscape (Figure 5). The lack of complete convergence may explain why the predicted income of landscapes optimised for farmers alone remained fractionally lower than the real-life landscape. This suggests that these solutions are converging towards a composition similar to the real landscape, which is essentially already optimised for farm income (Figure S2). Allowing each optimisation to run for more generations may provide more

certainty and more understanding of optimal spatial configurations within the landscape. In future studies, a more detailed sensitivity analysis (e.g. Pinel et al., 2012) could be conducted to determine initial parameters such as population size and ensure global optima can be reached in the allotted optimisation timeframe. Further exploration is also required into the effects of modifying the crossover/mutation functions of the genetic algorithm on the step-size of the algorithm in the parameter search space.

The scalability of our approach may be limited in terms of introducing more objectives. Separating solutions by Pareto dominance has been shown to become less viable when more than three objectives are used in one optimisation, thereby decreasing the search efficiency of the algorithm (Ishibuchi et al., 2008). This could explain the high number of rank 1 solutions resulting from our optimisations including all four objectives (Table S3). However, we still deem these results worthy of analysis because Figure S10 suggests our solutions may be approaching optima. Similarly, introducing more parameters (e.g. more land cover choices), or increasing the optimised area, could also reduce efficiency. Therefore, with the current available data, our approach may be most useful at a small scale. Our solutions may not apply to the whole landscape but could instead represent 'biodiversity islands' where parcels of land may be dedicated to improving wild bee populations.

We quantified the uncertainties associated with our results by repeating each experiment 25 times with different random seeds, producing a population of 50 distinct optimised landscapes each time. There are also stochastic elements in the Poll4pop model used to calculate fitness, for example nest allocation according to a Poisson distribution (Gardner et al., 2020). Therefore, no two sets of landscape solutions generated from optimisations with the same objectives should ever be the same. However, we did not account for uncertainty in the underlying parameters of the Poll4pop model (e.g. expert-determined nesting/floral attractiveness of land cover classes). This could be achieved in future studies by drawing randomly from these parameters' certainty distributions in each optimisation run (e.g. Image et al., 2022). Future work in progress proposes a methodology for integrating uncertainties in optimisation procedures with uncertainties in complex process-based models (Petrovskii et al., 2024, manuscript in preparation).

5 | CONCLUSIONS

We have demonstrated how a process-based ecological model can be combined with a genetic algorithm to identify optimum land cover composition and configurations that account for both the habitat preferences and movement ranges of different taxa. This suggests there is potential to apply these methods to other scenarios using alternative process-based species models (e.g. Rangeshiftr; Malchow et al., 2021). Such approaches could support more effective conservation land-use decision-making by more holistically representing how different taxa use and experience landscapes. This case study also highlights two key considerations for future work applying

similar techniques to other landscapes or ecological scenarios. First, using process-based models that simulate species' behaviour, and examining which resources the optimisation then prioritises, can help to identify which resources are likely to be limiting to populations and why. Second, our results suggest that optimisations should give more consideration to the number of anthropocentric objectives versus the number of ecocentric objectives used, given the strong effect this has on the final 'optimal' land cover solutions.

AUTHOR CONTRIBUTIONS

Emma Gardner and Ellen Knight codesigned the project. Ellen Knight adapted the algorithm, ran the optimisations, analysed the data and wrote the manuscript. Emma Gardner and Robbie D. Girling supervised the project. Colin G. Johnson and Shengxiang Yang provided technical support and advice on optimisation algorithms. Mike Image provided advice on use and interpretation of Poll4pop. Andrew Lovett and Tom D. Breeze provided advice on economic considerations. Heiko Baltzer, Tom D. Breeze, Julia Brettschneider, Emma Gardner, Robbie D. Girling, Alex Hagen-Zanker, Mike Image, Ellen Knight, Andrew Lovett, Sergei Petrovskii, Alexa Varah and Mick Whelan contributed to critically revising the manuscript. Christopher Lee gave critical input into context and implications for landscape decision-making.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14424>.

DATA AVAILABILITY STATEMENT

All data and code available via <https://doi.org/10.5281/zenodo.13646914> (Knight et al., 2024).

STATEMENT ON INCLUSION

Our study investigated a modelling approach regarding theoretical landscapes, and as such no local data collection or stakeholder engagement took place. However, the range of authors from different backgrounds provided a diverse set of viewpoints, which may represent the perspectives of various stakeholders in our theoretical scenarios.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Overview of the Poll4pop model, which was parameterised and validated for four bee guilds in the UK by Gardner et al. (2020): Ground-nesting bumblebees, tree-nesting bumblebees, ground-nesting solitary bees and cavity-nesting solitary bees.

Figure S2: Landcover proportions of the original 10 × 10 km SK86 grid square used as reference landscape in our optimisation experiments.

Figure S3: Landscape initialisation process.

Figure S4: Visualisation of the derivation of Equation (1).

Figure S5: Visualisation of how the fitness function calculates scores for each objective, using the output 10 × 10 km rasters with 25 m pixel resolution.

Figure S6: The crossover process, which occurs for each field if a specified crossover probability (default value = 0.7) is met.

Figure S7: Summary of the crossover and mutation process. Landcovers in the lefthand table are ranked by an average of Poll4pop-defined nesting and floral scores for each guild of bee.

Figure S8: To ensure the choice of population size and generations parameters was sensible, preliminary investigations were executed in which multi-objective optimisations with different combinations of population size and maximum number of generations were run.

Figure S9: (A) Normalised objective fitness scores for final landscapes of multi-objective optimisations including only bees. (B)

Normalised objective fitness scores for final landscapes of multi-objective optimisations including bees and the farmer.

Figure S10: Evolution of mean fitness score for each objective in each generation, separated by the type of optimisation being carried out.

Table S1: Mean of foraging kernels of bee guilds used in the optimisation process, as defined by the Poll4pop model (Gardner et al., 2020).

Table S2: Values and of origins of subjective NSGA2R algorithm parameters, as used in all optimisation experiments.

Table S3: Number of completed optimisations and final population landscapes analysed for each objective (i.e. 'end-user' of the optimised landscape) and radius.

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