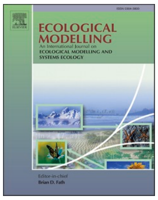
Ecological Modelling 514 (2026) 111489

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Integrating new land cover classes into ecological models to predict their biodiversity impacts

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ARTICLE INFO

Keywords:
Pollinators
Process-based model
Parameter estimation
Biodiversity impacts
Land-use decisions
Silvoarable agroforestry
Bayesian calibration

ABSTRACT

As the need for sustainable agroecosystems gains recognition, new land cover classes are increasingly emerging in temperate landscapes. Process-based ecological models are often the most suitable initial option for predicting the biodiversity outcomes of such novel systems, particularly when implementation and large-scale baseline data remain scarce. However, there are no accepted guidelines for integrating new land covers into these models.

Using UK silvoarable alley-cropping as a case study, we explore how to introduce this emerging land cover into the established process-based pollinator model, poll4pop. We demonstrate several parameterisation approaches, including proxy land covers, field data, expert opinion and Bayesian calibration. We also provide the first field-scale and seasonally-resolved evaluation of poll4pop, using pollinator abundance data collected at three UK silvoarable sites.

Our results show that models using proxy land cover parameters can capture spatial trends in observed bee abundance where suitable proxies exist, but that predictions are improved by integrating field-derived floral cover. Neither bespoke, expert-derived, land cover attractiveness scores nor Bayesian-calibrated scores improved our model fit, although they did reveal valuable insights into model parameter sensitivity. Overall, poll4pop effectively reproduced observed fine-scale spatial variation in bumblebee and spring-flying solitary bee foraging activity in silvoarable systems. However, seasonal differences between communities resulted in reduced model-predictive performance for summer-flying solitary bees.

We demonstrate that poll4pop is suitable for modelling fine-scale pollinator abundance in complex mixed-cropping systems. We also present a practical framework for integrating new land cover classes into process-based models which can guide future modelling of emerging land use systems.

1. Introduction

Growing food demands (van Dijk et al., 2021), and the environmental consequences of conventional intensive agriculture (FAO, 2023; IPCC, 2019), have driven demand for alternative approaches such as organic agriculture, diversified farming, and 'ecological intensification' (Gamage et al., 2023; Jones et al., 2023; Garibaldi et al., 2019; Bommarco et al., 2013). As sustainable land uses are increasingly incentivised, we must find ways to assess their contribution towards environmental goals and identify potential unintended consequences (Staley et al., 2021). This requires continued prediction and monitoring of their biodiversity impacts, which remains challenging over large scales.

Here, we consider agroforestry, an increasingly-incentivised land use under EU and UK policy (EU Cap Network, 2023; DEFRA, 2023), which shows potential for ecological intensification (International Assessment of Agricultural Knowledge, Science, and Technology for Development, 2009; Tsonkova et al., 2012). Specifically, we investigate UK silvoarable 'alley-cropping' systems. In alley-cropping, rows of trees are planted among 'alleys' of interspersed crop. Common tree species include orchard fruits, willow or poplar short rotation coppice, and timber species such as beech or oak (Image et al., 2023; Staton et al., 2024). Generally,

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https://doi.org/10.1016/j.ecolmodel.2026.111489
Received 8 August 2025; Received in revised form 7 January 2026; Accepted 7 January 2026

understories are sown with wildflower or grass mixes or kept bare through mulching and herbicide (Burgess et al., 2003; Staton et al., 2021). While alley-cropping is not widely practised in the UK (den Herder et al., 2017), the current goal is for 10 % of UK arable land to be converted to silvoarable agroforestry by 2050 (Department for Energy Security and Net Zero, 2023; Woodland Trust, 2022) to support net-zero and biodiversity targets.

Such emerging regenerative land uses are especially important for wild pollinators - particularly bees - which are a key conservation priority at both national and global scales (DEFRA, 2014; FAO, 2018; Potts et al., 2024) due to their crucial role in food production and evidence of declines in the temperate zone and beyond (Potts et al., 2016; Zattara & Aizen, 2021). Accordingly, predicting how novel or previously-rare land management approaches will affect wild pollinator populations (Image et al., 2023) in advance of their widespread implementation is crucial. This can help to inform future policy, guide management recommendations, identify implications for different pollinator groups and support multifunctional landscape optimisation procedures (Knight et al., 2024). However, empirical investigations regarding emerging land classes are often limited by a lack of available survey sites and pre-existing data (Kletty et al., 2023). In this case, computational approaches are useful, and may aid proactive, rather than reactive, decision-making (Wintle et al., 2011).

Process-based models are particularly useful for simulating biodiversity responses in new land cover classes which lack sufficient baseline data to support correlative species distribution models (Briscoe et al., 2019). These predict species abundance by drawing on a wide range of knowledge sources to mechanistically simulate ecological processes (Gardner et al., 2024; Zurell et al., 2022). Many such models exist, including ALMass (Topping et al., 2003), inVEST® (Natural Capital Project, 2005), the wider *4pop family (Gardner et al., 2024), and individual-based models such as Bumble-BEEHAVE (Becher et al., 2018) and RangeShifter (Bocedi et al., 2021). These all rely on land cover input data and all face similar choices when incorporating a new land cover type. Although the specific parameterisation requirements will vary among models, the underlying challenge remains the same: how should we derive the required parameters for the new land cover type? Parameters could come from various sources, including expert opinion, published estimates, existing or newly-collected data, or model calibration (Kopec et al., 2010; Koh et al., 2016). It may be unclear which option to choose when considering emerging land cover types: for example, there may be few experts with prior experience of the systems, limited pre-existing data, or few established survey sites from which to collect new data. Therefore, it is important to assess which parameterisation methods maximise current model performance whilst considering feasibility, efficiency, pragmatism, and future robustness.

Using UK silvoarable alley-cropping as a case study, we demonstrate how to incorporate a novel land cover class into an existing process-based model to assess biodiversity impacts. Our model, poll4pop, is a validated, spatially-explicit framework for predicting relative abundance of wild bees across landscapes (Gardner et al., 2020) and has already been used to evaluate diverse land-use interventions (e.g., Blaydes et al., 2022; Gardner et al., 2021; Image et al., 2022). Currently, alley-cropping is not parameterised within poll4pop nor represented in major UK and European land cover datasets (Morton et al., 2024; European Union's Copernicus Land Monitoring Service information 2020). Its composite structure - trees, understory, crop, and their varied management - makes representation in such models difficult (Laub et al., 2025). Previous studies have addressed this by simplifying system configuration or substituting already-parameterised land classes into models (e.g., using orchards to approximate fruit alley-cropping; Graham & Nassauer, 2019; Image et al., 2023). However, such substitutions may misrepresent alley-cropping configuration at scales relevant to pollinators, and may not accurately represent the structural and habitat resources provided to pollinators, thereby affecting predictions (Iles et al., 2018; Krimmer et al., 2019).

In our investigation, we develop the first representation of orchard-fruit silvoarable alley-cropping systems - an expanding, policy-relevant land cover in the UK - within the poll4pop model. In so doing, we compare the available methods of parameterising novel land covers within pre-existing, process-based ecological models. We evaluate five approaches: i) assembling proxy parameters from similar, already-parameterised land cover classes; ii) incorporating corrections to these, and other modelled land covers, based on empirical field measurements; iii) gathering more expert opinion to supplement these field measurements; and finally, obtaining parameter values by calibrating to match observed bee abundances, either using iv) informed or v) uninformed priors. We use detailed field data gathered in three UK alley-cropping systems to evaluate the model's overall ability to predict spatial trends in the abundance of bumblebees and solitary bees when system components are mapped at fine resolution (3 m). Subsequently, we recommend land cover parameters for alley-cropping systems in future poll4pop modelling and provide overall recommendations for approaching the introduction of new land cover classes into process-based models in general. Simultaneously, we provide the first sub-field-scale, seasonally-resolved validation exercise of the poll4pop model, evaluating its ability to predict fine-scale spatial variation in foraging abundance of wild bees in complex, heterogeneous land use systems.

2. Materials and methods

2.1. Study area

We surveyed pollinating insects and floral cover monthly between March-August 2023 at three organic farms containing apple (*Malus domestica*) alley-cropping systems in the East Midlands and East of England. This provided empirical data for model parameterisation, calibration and evaluation. All sites featured similar arrangements of apple trees, understories sown with flower mixes, and non-pollinator dependent cereals in their crop alleys. See Tables A1 and A2 for further site information and sample sizes.

2.2. Pollinator and flora sampling

During each survey visit, we recorded foraging bumblebee and solitary bee abundance along nine 50 m transects at each site - three in each of the tree rows, crop alleys, and field edges (Fig. A1). Two additional transects were established at Site 1 to capture an area of flowering clover ley (full details in A.1.1). After each transect walk, we estimated overall and species-specific percentage cover of flowering plants in three 0.5 × 0.5 m quadrats placed at the beginning, middle and end of each transect.

We also collected pollinator community data to assess potential changes in the observed bee species and trait composition between seasons, and resulting differences in model performance. On each site visit, a total of 16 pan traps were left for 6-8 hours (Potts et al., 2021), with specimens later identified to species level (further details in A.1.2). These data were not used in model parameterisation, as the highly attractive nature of pan traps creates estimation biases, particularly for abundance (Potts et al., 2024, 2025).

2.3. Land cover mapping

Land cover and crop cover rasters surrounding each survey site (10 × 10 km; 3 m resolution) were obtained from UK Centre for Ecology and Hydrology Land Cover, Land Cover Plus, and UK Woody Linear Feature spatial data (UKCEH, 2016, 2021, 2023). From these, arable field margin and woodland boundary edge feature maps were subsequently generated, following Gardner et al., 2020.

Additionally, we mapped all habitats at each survey site in the field and plotted them in QGIS (QGIS.org, 2025) in accordance with typical configurations at our field sites. Separate rasters were exported at 3 m resolution for (i) ‘general’ habitat (e.g., field margins, scrub, ditches), (ii) silvoarable understories, and (iii) silvoarable fruit trees, to allow different parameter assignments.

2.4. Poll4pop model description

Poll4pop is described in full in Häussler et al. (2017), which includes the mathematical formulae, and Gardner et al. (2020). Here, we provide a concise summary of the input and output data, and the foraging, dispersal and population growth simulation processes.

2.4.1. Input land cover data

Poll4pop requires a rasterised land cover map (e.g., with pixel values indicating the locations of cereal, woodland, etc.) and edge feature maps as inputs. Edge features are those generally smaller than the pixel resolution - e.g., hedgerows, arable margins - and are assigned to a proportion of the land cover pixel they occupy according to the ‘edge-feature-width’ parameters defined by the modeller. These rasters are typically generated from remote-sensed data, but we also augment these in this study to include more detailed, manually digitised features present at our survey sites (see 2.3).

2.4.2. Land cover parameters

Three parameters are assigned to each land cover class to simulate how pollinator groups may use them:

1) Floral cover (0-100): the amount of floral resource it provides, varying seasonally (i.e., spring or summer).
2) Foraging attractiveness (0-20): its attractiveness as a foraging resource to each pollinator guild.
3) Nesting attractiveness (0-1): its attractiveness as a nesting location to each pollinator guild.

Values for these three sets of scores have previously been assigned using expert opinion to 35 common European land classes for four bee guilds: ground-nesting bumblebees, tree-nesting bumblebees, ground-nesting solitary bees and cavity-nesting solitary bees (Gardner et al., 2020). Attractiveness parameter scales differ because foraging attractiveness operates in arbitrary units and thus remains on its original, expert-elicited scale, whereas nesting attractiveness is rescaled between 0-1 to enable meaningful multiplication with the input maximum nest density (Gardner et al., 2020; Image et al., 2022).

2.4.3. Other input parameters

The model also takes in parameters specifying maximum nest density, foraging range, dispersal range and population growth for each guild. We use the values given in Gardner et al. (2020), derived from literature data.

2.4.4. Process overview

Using the above information, the model initially generates two outputs: a) a nesting resources map for each guild - derived from the product of the nesting attractiveness score of each land cover, pixel size, and the specified ‘maximum nest density’; and b) seasonal floral resource maps for each guild - derived from the product of the floral cover score for each season and foraging attractiveness score of the land cover type in each pixel.

The model then randomly allocates nests across the landscape using a Poisson distribution defined by the nesting resource value assigned to each pixel. These nests become the source of ‘central-place foraging’, where the typical foraging distance from the nest (i.e., kernel size) is determined by the guild-specific mean foraging distance parameter. The amount of resource gathered by the nest is calculated using attractiveness-weighted distance decay kernels. Thus, the predicted relative abundance of foraging bees visiting a pixel from one nest is a function of the pixel’s proximity to the nest, its floral resource value, and the number of foraging bees sent out from that nest.

The amount of resource gathered is combined with the input growth parameters (e.g., maximum number of workers produced per queen; median and steepness of a lognormal growth function) to determine both the number of workers produced at the end of spring for social guilds (i.e., bumblebees), and reproductive females produced at the end of the active period for all guilds. The model assumes an active period to be one season for solitary bees, and three seasons for bumblebees, typically interpreted as early-spring, late-spring, and summer (Gardner et al., 2021). New reproductive females disperse according to a nesting-attractiveness-weighted distance decay kernel, which limits the number of nests established per pixel in the following time period by the maximum nest density parameter and the amount of nesting resource offered by the pixel.

The model then outputs seasonal heat maps of predicted relative abundance of foraging bees (hereafter ‘predicted foraging abundance’) across the landscape for each specified bee guild by summing the predicted foraging abundance from all nests to each pixel.

2.5. Parameterisation and validation workflow

All modelling and analyses were completed in R version 4.2.2 (R Core Team, 2022). We evaluated five approaches for parameterising two complementary elements of silvoarable alley-cropping systems - trees and understories - in the poll4pop model by assessing the relationship between observed and poll4pop-predicted foraging bee abundance in the 50 m transects conducted at each site. This workflow is summarised in Fig. 1 and parameterisation approaches are described in more detail below. Parameters were assumed to correspond specifically to orchard fruit trees and flower-sown understory types because these were present in all surveyed systems. They were only assigned for bee guilds observed during field surveys, i.e., ground-nesting bumblebees and ground-nesting solitary bees.

2.5.1. Parameterisation approaches

Our five approaches for assigning floral cover, floral attractiveness, and nesting attractiveness scores to the new ‘silvoarable tree’ and ‘silvoarable understory’ land cover types are summarised in Table 1. Here, proxy land cover parameters serve as the baseline method for integrating new land classes into poll4pop. The additional approaches presented are intended as diagnostic refinements. Their purpose is to assess whether proxy values are sufficient, identify which parameters most influence model-data agreement, and determine whether empirical or expert information can meaningfully improve predictions. Each approach is discussed in more detail below.

2.5.1.1. Approach 1: proxy land covers. In Approach 1 we imitated the methodology of previous studies (e.g., Image et al., 2023) by using already-parameterised land covers as proxies for the components of silvoarable systems. Following Image et al., we represented silvoarable fruit trees using ‘orchard’ parameters, with an additional understory represented by ‘unimproved meadow’, chosen due to its high floral cover ranking among poll4pop land covers. Proxy land covers were assumed to be conventionally managed during the original model parameterisation process.

2.5.1.2. Approach 2: field-derived floral cover. Accounting for site-level variation in floral cover may help poll4pop to better simulate variation in observed bee abundance. In Approach 2, we replaced our proxy floral cover scores with scores derived from site-, season- and land cover-specific floral cover data collected in the field (see section 2.2). This was applied to all land covers on which transect surveys were conducted, i.e., not only the newly-parameterised silvoarable understories, but also other elements constituting the silvoarable system, including alley crops, grassy field margins, and the area of clover ley at Site 1.

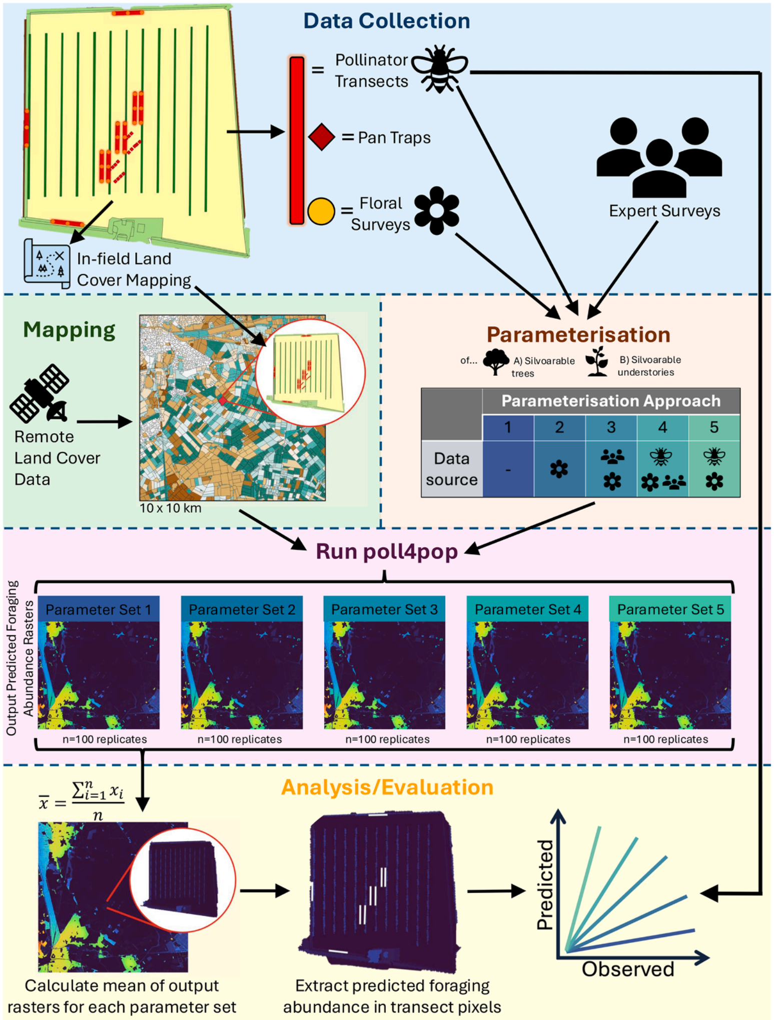

Fig. 1. The process of parameterising and evaluating silvoarable trees and understories as new land cover classes in the poll4pop model, using five proposed parameterisation approaches.

Floral cover for the silvoarable fruit trees was taken from the original poll4pop orchard expert-opinion scores because peak apple bloom (a ~2-week period) occurred and finished between our late-April and late-May field visits. Although peak bloom dates were known, on-site floral-resource measurements would have underestimated cover. The original poll4pop orchard floral-cover parameter is normally weighted 90:10 for early-spring:late-spring (March:mid-April vs. mid-April:May) for bumblebees, but we reversed this weighting to match the observed flowering period at our sites. This ensured the trees' peak flowering was accurately represented in the model, despite floral cover not being derived directly from in-field measurements.

See A.2 for more details. Foraging and nesting attractiveness scores were kept fixed at the proxy values used in Approach 1.

2.5.1.3. Approach 3: bespoke attractiveness scores. Following the original poll4pop procedure, Approach 3 used expert-elicited foraging and nesting attractiveness scores for silvoarable alley-cropping components. Six UK experts in pollinator ecology and agroforestry scored the attractiveness of tree and understory components on a six-point 'none-very high' scale, plus a matching confidence score. These qualitative scores were quantified using the original model protocol (Gardner et al., 2020; Image et al., 2022), and beta distributions were derived for each parameter for input to the model (see Section A.2.2). Field-derived floral-cover scores from Approach 2 were retained because model outputs showed they reduced site-level variation, providing a more stable baseline for comparing parameterisation approaches.

2.5.1.4. Approaches 4 and 5: Bayesian calibration. We replaced the Approximate Bayesian Computation-like routine used by Gardner et al. (2020) in the original model calibration with a fully Bayesian MCMC calibration that samples directly from the posterior, allowing uncertainty from expert opinion and the small number of field sites to be propagated through the model and reducing the risk of site-specific over-tuning (Van Oijen et al., 2005). This was completed using the "BayesianTools" R package (Hartig et al., 2023), with three DEzs chains of length 10,000. Because of run-time limitations, calibration was conducted only for bumblebees, not solitary bees. In Approach 4, informed priors were taken from the expert-derived beta distributions of Approach 3. The likelihood ran poll4pop with candidate parameters then drew from a normal distribution informed by the difference between observed and predicted foraging abundance at exact transect locations, scaled using z-scores and assuming a Gaussian distribution of errors (Van Oijen et al., 2005). Field-derived floral-cover scores from Approach 2 were again used. We added a 'scaling factor' to adjust the Gaussian error width, accounting for systematic variation in observations (Van Oijen, 2008). For comparison, Approach 5 repeated the calibration using uniform, uninformed priors.

After removing a 1,000-iteration burn-in from each chain, convergence was checked visually and using Gelman-Rubin diagnostics (values ≈1 acceptable; >1.1 non-converged; Gelman et al., 2004). Parameter

Table 1
Source of poll4pop floral cover and floral/nesting attractiveness parameters of the new ‘silvoarable tree’ and ‘silvoarable understory’ land classes in each model parameterisation approach. In ‘proxy’ approaches, silvoarable trees are represented by default Poll4pop ‘orchard’ parameters, and the understories are represented by ‘unimproved meadow’ parameters, which were derived from expert opinion in the original model parameterisation (Gardner et al., 2020). Attractiveness parameters were determined separately for ground-nesting bumblebees and ground-nesting solitary bees for each approach.

Parameterisation Approach	Parameter Source		Data Source(s) †
	Floral cover	*Floral/nesting attractiveness*	
1) Proxy Land Covers	Existing poll4pop expert scores for orchards and unimproved meadow	Existing poll4pop expert scores for orchards and unimproved meadow	
2) Field-Derived Floral Cover (Site-Specific)	Field-collected floral cover data	Existing poll4pop expert scores for orchards and unimproved meadow	✿
3) Bespoke Attractiveness Scores	Field-collected floral cover data	Newly-elicited expert scores for silvoarable trees and understories	✿ 👥
4) Bayesian Calibration (Informed)	Field-collected floral cover data	Bayesian calibration using expert-informed priors from Approach 3	✿ 👥 🐝
5) Bayesian Calibration (Uninformed)	Field-collected floral cover data	Bayesian calibration using uninformed priors	✿ 🐝

†Data sources newly collected for this paper to parameterise silvoarable trees and understories in poll4pop, additional to the default parameters of the original model. ✿ = Field-derived floral cover data. 👥 = bespoke, expert-elicited land cover attractiveness scores. 🐝 = In-field pollinator abundance data collected via transects.

correlations ($|r| > 0.7$ flagged as major) were assessed using the summary() function in “BayesianTools”. Final beta parameter distributions for poll4pop were extracted using the “fitdistrplus” package (Delignette-Muller et al., 2025). Section A.2.3 provides further details on the calibration process.

2.5.2. Model evaluation

For each parameter set, poll4pop was run 100 times with a random seed, using parameter sampling (See A.2.2). The model was run on 10 × 10 km landscapes surrounding each study site to fully capture pollinator movement and dispersal ranges. During runs, the field-mapped habitat and silvoarable understory rasters were overlaid on UKCEH 2023 land cover maps, and silvoarable tree rasters were included as a 1 m edge-feature layer. 100 output predicted foraging abundance rasters were output for each parameterisation approach, which we averaged then extracted total predicted abundance in the 3 m^2 pixels matching the exact transect locations for each site, season, and pollinator guild. This enabled a fine-scale, spatio-temporal comparison of spatial trends in observed vs predicted foraging abundance across the sample of transects. We tested trends because poll4pop outputs relative foraging abundance, whereas field data represent absolute counts; direct evaluations of accuracy or reliability is therefore not possible.

In total, 161 transects were assessed: 74 in spring (March-May) and 87 in summer (June-August). For bumblebees, early- and late-spring predicted foraging abundance rasters were summed to produce a total spring prediction. Solitary bees were analysed separately by season because poll4pop treats spring and summer populations as independent (i.e., it does not account for bivoltinism), and because solitary-bee community composition from pan traps differed markedly between seasons. Bumblebees, however, were analysed jointly across seasons since poll4pop simulates a single, continuous population and their functional identity is not expected to vary substantially between spring and summer.

Observed and predicted foraging abundance for each 50 m transect were compared using GLMs (“lme4”; Bates et al., 2025). Spring solitary bees were modelled with a Poisson distribution; bumblebees and summer solitary bees were overdispersed, so negative binomial models were fitted (“MASS”; Ripley et al., 2025). Spatial variables were omitted because poll4pop already accounts for spatial heterogeneity. One weather variable (recorded at the start of each transect) was included per guild, selected via initial correlation checks (see A.3.1 for model variable choices). Model assumptions were checked using “DHARMA” (Hartig et al., 2024).

Starting models were:

Bumblebees: $Observed\ Abundance \sim Predicted\ Abundance * Site + Temperature$

Solitary bees: $Observed\ Abundance \sim Predicted\ Abundance * Site + Wind$

We then performed stepwise regression to remove non-significant terms and obtain the most parsimonious models. Final variables for each guild and parameter set are listed in Table A5. Predictive performance (agreement between spatial trends in observed vs predicted abundance) was evaluated using GLM beta values and significance levels, and model fit was compared using AICc (“MuMIn”; Bartoń, 2024). We also assessed observed-predicted relationships using partial correlations: both variables were regressed against their significant fixed effects, and Spearman’s rank correlation was computed between the resulting residuals.

To investigate why the model performance for solitary bees differed according to season, we compared the foraging range of spring and summer solitary bee species found in pan traps, using a Gamma GLM including site as a fixed effect. Foraging ranges were calculated from intertegular distance using formulae taken from Greenleaf et al. (2007; Roberts, 2025, personal communication).

3. Results

3.1. Approaches 1 & 2: proxy & field-derived floral cover parameter values

There was high site-level variation in the floral cover of surveyed habitats (Fig. 2). The field-derived floral cover parameters differed much more from their poll4pop defaults in summer than in spring. The default floral cover parameter values supplied with the poll4pop model for cereal, grassy field margins and legume ley typically underpredicted the actual floral cover measured in these land cover types in summer, consistent with the fact that the proxy parameters were assigned assuming conventional management, whereas the data for field-derived parameters was collected in organic systems. Conversely, the proxy floral cover parameter values used for silvoarable understories (i.e., those corresponding to unimproved meadow) predominantly overpredicted floral cover at all sites in both seasons. Note that x and y values for silvoarable trees in Fig. 2 are approximately the same for all sites because we retained the default scores for orchards due to absence of replacement floral survey data (see section 2.5.1 for rationale).

3.2. Approach 3: bespoke attractiveness parameter values

Newly-elicited expert scores suggested that the foraging attractiveness of silvoarable trees would be roughly similar to that of orchards (their land cover proxy) for both bumblebees and solitary bees (Fig. 3). This resulted in large overlap in the 95 % confidence interval of the parameter values sampled from each distribution in each poll4pop model run.

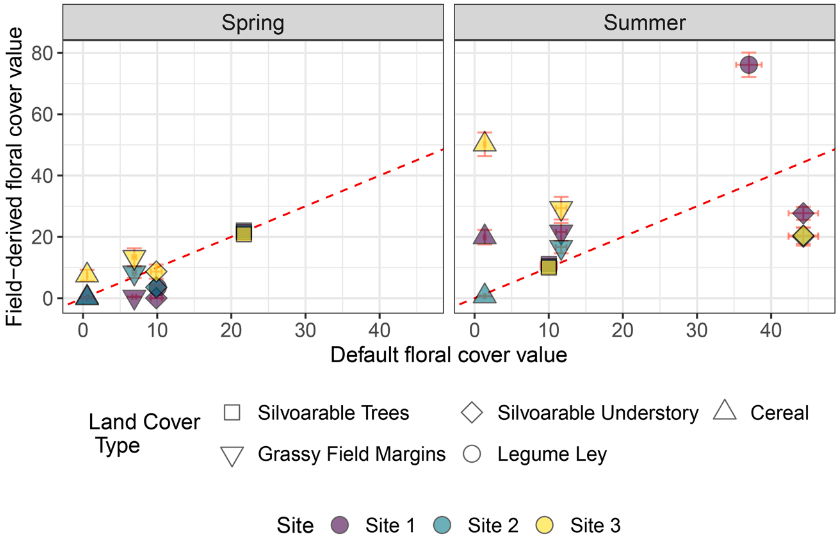

Fig. 2. Comparison of field-derived floral cover parameter values with default poll4pop floral cover parameter values for land covers and proxy land covers at each survey site. The dashed 1:1 line represents equal field-derived and default parameter values. Values above the dashed line signify a land cover with a higher field-derived floral cover value than that of its poll4pop default, and vice versa. Error bars represent standard error. Spring = March, April, May; Summer = June, July, August. Values represent the mean of 100 values sampled from probability distributions associated with each parameter (See A.2.2). Beta distributions were used for the default poll4pop parameters, determined by expert scoring, and zero-inflated beta distributions were used for field-derived parameters, determined by floral quadrat surveys conducted at each field site. Sample sizes for calculation of zero-inflated beta distributions can be found in Table A3. Each probability distribution is defined by the uncertainty on the measured or default score. All floral cover values are bounded between 0-100.

In contrast, the expert score distributions for understory foraging attractiveness, and the nesting attractiveness of both silvoarable components (trees and understory), were less similar to their land cover proxy for both pollinator guilds. The surveyed experts predicted that the foraging attractiveness and nesting attractiveness of silvoarable understories would be higher than their proxy land cover, unimproved meadow, and that the nesting attractiveness of the silvoarable trees would be lower than their proxy, orchards. These subsequently had no overlap in their 95 % confidence intervals.

3.3. *Approaches 4 & 5: Bayesian-calibrated parameter values*

The Gelman-Rubin multivariate diagnostic indicated convergence for all chains in both the informed ($\hat{R}$=1.025) and uninformed calibrations ($\hat{R}$=1.019). There were no major correlations between any parameters, suggesting adequate mixing of chains and independence in posterior sampling.

The marginal posterior distributions were almost identical to their priors for three out of four parameters (foraging and nesting attractiveness of trees; nesting attractiveness of understories) in both the informed and uninformed calibrations (Fig. 4), suggesting limited model sensitivity to these parameters. In contrast, the understory foraging attractiveness posterior deviated substantially from its prior, with a peak density of around 12.5 in the informed calibration and 5.5 in the uninformed calibration - both lower than the expert-informed prior mode of 17. This demonstrates that the empirical bee abundance data used was informative for this parameter during calibration and also suggests that the bespoke expert scores overpredicted understory foraging attractiveness. Trace plots and posterior summary statistics can be found in B.1.

3.4. *Comparing model performance*

Table 2 and Fig. 5 indicate that in every parameterisation approach, there was a significant positive relationship between observed and predicted foraging abundance of bumblebees and of spring solitary bees. This was not true of summer solitary bees for any parameterisation approach. The positive relationship was more statistically significant for bumblebees than for spring solitary bees across all approaches, indicating a stronger correspondence between observed and predicted patterns for bumblebees.

When site-specific floral cover was incorporated compared to when default floral cover scores and proxy land covers were used, model fit (AICc) improved significantly (i.e., decreased by >2) and the positive relationship between observed and predicted abundance (partial correlation) increased and became more significant for bumblebees. Additionally, the interaction between site and predicted foraging abundance became non-significant in our bumblebee GLMs, showing that significant site-level variation in predictive ability was eliminated when site-specific floral cover data were included. Conversely, AICc increased significantly for spring solitary bees when site-level floral cover data was included, and partial correlation decreased.

Integrating bespoke attractiveness scores had no meaningful effect on any metric of model performance for any bee guild in any season compared to using proxy attractiveness scores. Similarly, including attractiveness scores for bumblebees derived from either informed or uninformed Bayesian calibrations had no meaningful effect on any metric of model performance. We highlight that we evaluated model performance using the parameters derived in our Bayesian calibrations with the same data that was used for calibration. This was because all observed data were used in the calibration process due to the small sample size and to maintain consistency with all relevant information at the time of parameterisation (Philips et al., 2004). This had the potential to lead to overfitting, and hence conclusions about model outputs should be approached with caution; however, we present these results to aid discussion of model sensitivity to these parameters and of the Bayesian calibration process.

In summary, using site-specific floral cover improved the model fit and correlation between poll4pop predicted abundance and observed abundance for bumblebees but not for solitary bees (in fact, the reverse was true for spring-flying solitary bees). None of the other approaches led to any additional meaningful improvements.

3.5. *Seasonal differences observed in solitary bee communities*

The proportion of Andrenidae found in pan traps was much higher in

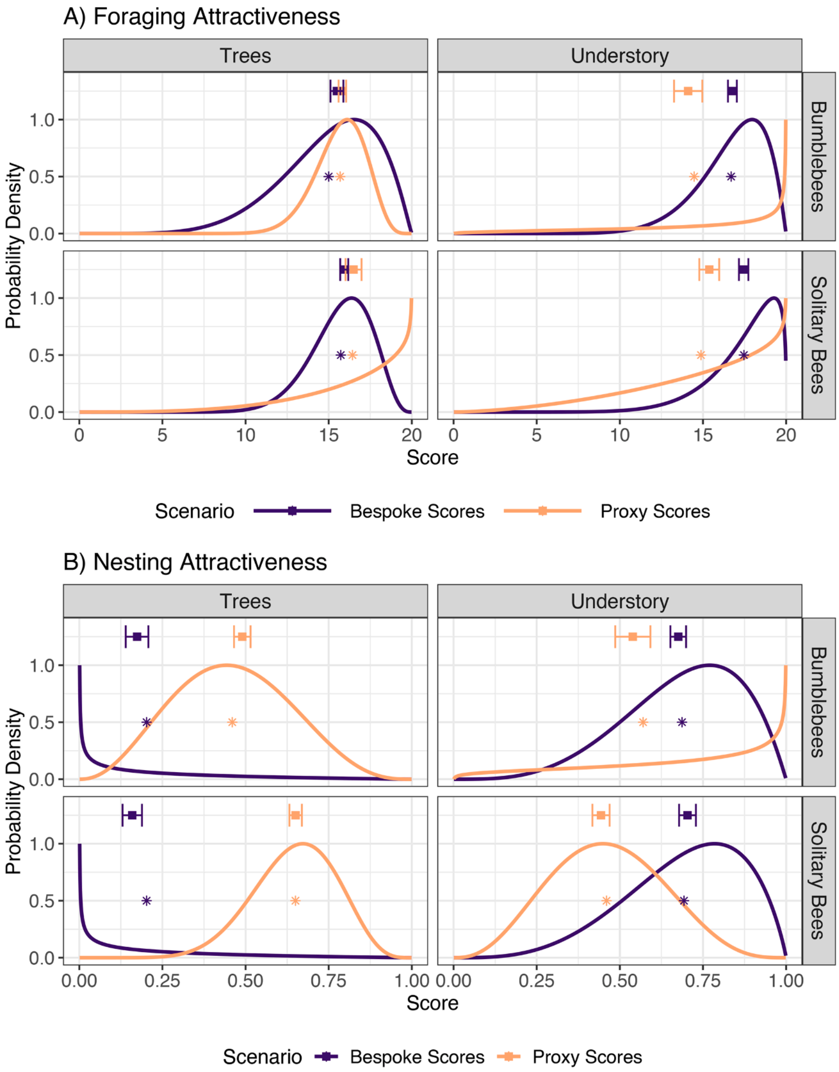

Fig. 3. Beta distributions of attractiveness scores for each parameterisation approach, as determined by expert opinion surveys ($n = 6$). Foraging attractiveness is scored between 0-20 in poll4pop, whereas nesting attractiveness is scored between 0-1. Scores in parameterisation approaches 1 and 2 are the default poll4pop values of their land cover proxies (orchards for silvoarable trees and unimproved meadow for silvoarable understories), whereas scores in parameterisation approach 3 are bespoke, newly-elicited values for the silvoarable components. Stars represent means of the raw expert score distributions. Square points and error bars above show the mean and 95 % confidence interval of the 100 parameter values sampled from each parameter's distribution as used in each of the 100 poll4pop model runs for each parameterisation approach.

spring (56 %) than summer (9 %) at all sites (Fig. 6A), whereas the summer communities were more dominated by smaller Lasioglossum species (18 % in spring and 74 % in summer). The expected foraging range of the solitary bee species found in pan traps in summer was consequently significantly shorter than of those found in spring (Fig. 6B; Gamma GLM; $p < 0.01$, df=66), with no significant influence of site on this effect. We attempted re-running poll4pop simulations for solitary bees with their model-defined foraging range adapted to reflect these differences, but this did not improve model-data agreement for the summer solitary bees (See Fig. B4 and Table B2). Polylectic species dominated in both seasons (Fig. B5). The overall species richness of flowering plants found at transect locations was much higher in summer than spring (Fig. 6C). In particular, more flowering species of Asteraceae were found in Summer at each survey site. Note that bee abundance estimates from pan traps are dependent on local floral density (O'Connor et al., 2019; Potts et al., 2025) and in fact we found no overall difference in solitary bee abundance between spring and summer in our transect observations (Fig. B6).

4. Discussion

4.1. Evaluation of general model performance

By realistically representing silvoarable alley-cropping components (tree rows, understory and crop) in our digital input landscapes, we were able to capture spatial trends in fine-scale foraging abundance of bumblebees and spring-flying solitary bees inside alley-cropping fields using poll4pop, as shown by a significant positive linear relationship between observed and predicted foraging abundance in our GLMs, supported by significant partial correlations for both guilds (Fig. 5; Table 2). This ability to model variation in abundance at fine-scale resolution (i.e., 50 m transects) is particularly important for complex cropping systems with multiple elements such as alley-cropping systems. This is because management options such as tree species, understory management, alley width, etc. can be extremely variable and likely influence the way species use these systems for nesting and foraging. This is also useful when considering other forms of multi-species farming such as relay intercropping or row intercropping, which are gaining popularity alongside recognition of the need for ecological intensification (Amossé et al.,

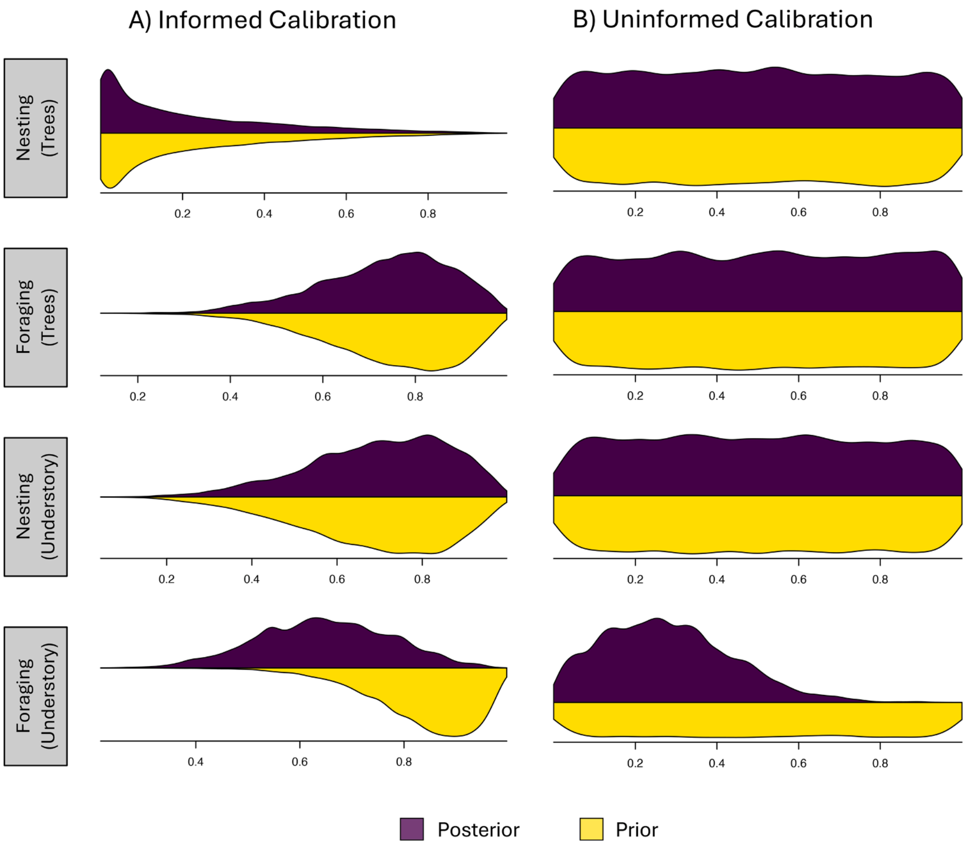

Fig. 4. Posterior and prior distributions for the four poll4pop land cover attractiveness parameters included in A) informed and B) uninformed Bayesian calibrations. Informed priors were beta distributions determined by expert opinion during Parameterisation Approach 3. Uninformed priors were uniform distributions.

2014; Schulz et al., 2020; van Oort et al., 2020).

In contrast, none of the poll4pop parameterisations we tested were successful at predicting spatial trends in abundance of summer solitary bee species in these systems. Whilst there are 25 species of bumblebee in the UK, there are more than 100 species of ground-nesting solitary bees, over 50 of which are key crop pollinators (Falk, 2015; Hutchinson et al., 2021). Therefore, condensing this large and varied group into one set of model parameters may result in overgeneralisations which decrease model predictive ability. Furthermore, differences in guild species composition between seasons may affect modelling outcomes (Gardner et al., 2020). Whilst parameterising species-level or finer guild models would require new expert scorings and plant-species-level habitat maps beyond the scope of this study, we ran a post-hoc trial in which we calculated a shorter mean foraging range based on size of the solitary bee species found in summer compared to spring at each site (Fig. 6B). However, re-running the model whilst accounting for this shorter foraging range did not improve model performance for solitary bees in summer (Fig. B4), suggesting that this was not the mechanism behind decreased model predictive ability in this season.

Another potential explanation is that small-bodied bees are generally more difficult to detect on transects, so they may be under-represented in the observational data used to check model predictions (Hutchinson et al., 2022). This human error is difficult to correct for: pan traps overcome the detection problem but they are unreliable for assessing abundance due to the influence of surrounding floral availability on catches (O'Connor et al., 2019; Potts et al., 2025). Alternatively, the seasonal mismatch may reflect differences in the composition and distribution of floral resource abundance among elements of the system. In spring, a single dominant resource - apple blossom - provides a concentrated and spatially distinct foraging target (Fig. 2: Silvoarable Trees). This aligns with the higher proportion of Andrenids recorded in spring, which are key apple pollinators (Burns & Stanley, 2022), and may explain the higher model performance observed in this season. In summer, however, floral resources are more abundant, species-rich, and distributed among the system in the understories, crops, and field margins (Fig. 2; Fig. 6C). This diffuse and taxonomically-mixed floral community is harder for the model to represent accurately. If only a subset of these flowers is actually useable to summer solitary bees - particularly species with specialist dietary or morphological requirements (Garibaldi et al., 2015) - then the model may overestimate the value of habitats containing many irrelevant flowers, or underestimate habitats containing fewer but more suitable resources. This provides a potential explanation for reduced predictive performance in summer.

Our results demonstrate the importance of evaluating model performance in novel systems against real-world data. They also offer the first seasonally-resolved evaluation of the poll4pop model, showing the value of considering how the communities of modelled taxa may differ throughout the year in relation to the resources available. Future work could address the underperformance for summer-flying solitaries by parameterising these to the genus- rather than guild-level, or alternatively by specified functional groups, with the choice of groupings refined by the study intention, e.g., key crop pollinators or species of conservation interest. We suggest that the solitary bee parameters determined in this study are assumed to represent typical or common Andrenidae species, which were the most predominant genus found in spring, when model predictive performance was highest. Overall, our results show that poll4pop is nonetheless suitable for annual-level modelling of UK crop pollination service at fine scales because many UK pollinator-dependent crops flower in spring - e.g., apples, oilseed rape, field beans - when the model best captured spatial trends in solitary bee abundance. Furthermore, bumblebees, which were well predicted across both seasons, are often the main recorded pollinator in UK summer-flowering, pollinator-dependent crops (Hutchinson et al.,

Table 2

Outcomes of generalised linear models (GLMs) assessing the relationship between observed and predicted foraging abundance of bumblebees and solitary bees in each parameterisation approach, after stepwise regression. Negative binomial GLMs were used for bumblebees and summer solitary bees, and Poisson GLMs were used for spring solitary bees. Number of transects: $n_{spring}=74$ and $n_{summer}=87$. An AICc value of two lower than another in the same pollinator group indicates significantly-improved model fit, i.e., the predicted abundance fits the observed abundance better. Partial correlation was used when more than one model term was significant (see methods), otherwise a regular Spearman's Rank correlation test was conducted. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Pollinator	Parameterisation Approach	Data Source(s) ‡	Significant Model Terms				AICc	(Partial) Correlat-ion
			Predicted Foraging Abundance (V)	*Site (S)*	*Temp (bumble-bees) or Wind (solitary bees)*	*S*V*		
Bumblebees (Spring and Summer)	1) Proxy Land Covers	-	0.02 ± 0.005***	**	***	**	355.95	0.25**
	2) Field-derived Floral Cover (Site-specific)	✿	0.01 ± 0.003***	**	***		352.60	0.43***
	3) Bespoke Attractiveness Scores	✿ 👥	0.01 ± 0.003***	**	***		352.60	0.42***
	4) Bayesian Calibration (Informed Prior)	✿ 👥 🐝	0.01 ± 0.003***	**	***		352.14	0.45***
	5) Bayesian Calibration (Uninformed Prior)	✿ 🐝	0.01 ± 0.003***	**	***		352.24	0.52***
Solitary Bees † (Spring)	1) Proxy Land Covers	-	3.29 ± 2 *	**	*		146.67	0.27*
	2) Field-derived Floral Cover (Site-specific)	✿	5.85 ± 2 *	**			149.31	0.20*
	3) Bespoke Attractiveness Scores	✿ 👥	5.89 ± 2 *	**			149.12	0.20*
Solitary Bees (Summer) †	1) Proxy Land Covers	-	0.00± 0.7				203.93	0.14*
	2) Field-derived Floral Cover (Site-specific)	✿	-0.30 ± 0.7				203.78	0.10*
	3) Bespoke Attractiveness Scores	✿ 👥	-0.28 ± 0.7				203.80	0.10*

†Bayesian approaches not tested for solitary bees due to run-time constraints.

‡Data sources newly collected for this paper in order to parameterise silvoarable trees and understories in poll4pop, additional to the default parameters of the original model. ✿= Field-derived floral cover data. 👥 = bespoke, expert-elicited land cover attractiveness scores. 🐝 = In-field pollinator abundance data collected via transects.

2021).

4.2. Assessment of parameterisation approaches

4.2.1. Field-derived floral cover scores

Model predictive ability improved significantly for bumblebees when including field-measurement-derived floral cover scores compared to using the default expert-derived scores of proxy land covers (hereafter proxy scores), showing that using field-data for parameterisation can be a valuable step when modelling at the field scale (Fig. 5; Table 2). The underprediction of field-derived floral cover by proxy land cover scores was also consistent with the fact that the proxy land cover parameters were originally assigned for conventional systems, whereas all three survey sites used in this study were organically managed. Therefore, more flowering resources (weeds) would be expected in the latter. Such in-field assessment of resource availability may help to account for different management choices at the parameterisation stage for new land covers. This is especially true when considering systems such as alley cropping, whose management approaches may vary widely between sites, e.g., differences in tree selection or sown understory mixes (Table A1). Our results reflect this, revealing high variation in floral cover between land cover types and between sites (Fig. 2).

In contrast, model predictive performance decreased for solitary bees in spring when field-derived scores were included instead of proxy scores (Table 2). As discussed in Section 4.1, this could be because, when taking floral measurements in the field, we did not consider that the habitat preferences of solitary bees in each season may differ. Therefore, we suggest that including field-level floral measurements during parameterisation may be most useful either when considering generalist groups of taxa, or groups whose floral specialisms are concordant (in which case only the cover of specific floral species should be measured). Note that including field-derived floral cover scores made no meaningful difference to model performance for solitary bees in summer compared to using proxy scores.

While collecting field-level floral cover data for every site is not feasible for large-scale or scenario-based applications, our results show that such data are nevertheless valuable during the parameterisation stage for two reasons. First, site-specific floral cover enabled us to reduce site-level variation and thereby establish a clearer baseline of model-data correspondence from which other, more generalisable parameters (e.g., foraging and nesting attractiveness) could be derived and/or evaluated. This diagnostic use of field-derived data can be helpful in any model where key parameters are expected to vary substantially across sites. Second, the comparison between proxy and field-derived floral cover scores provides insight into how reliance on proxies may influence model performance at broader scales. For example, proxies consistently underrepresented floral cover in certain habitats at our study sites (Fig. 2), which was associated with lower correspondence between predicted and observed abundance for bumblebees (Fig. 5). Such comparisons help identify where proxy parameters are robust and where they may introduce systematic biases.

To explore generalisability, we tested a post hoc floral-cover parameterisation using the mean of our field-derived values for each land cover across sites (Fig. B4). Its performance was comparable to that of the proxy approach (Table B2). This suggests that, given the wide variation in floral cover across our sites, proxy parameters currently provide a reasonable starting point for representing silvoarable alley-cropping systems, when a general (rather than site-specific) metric is

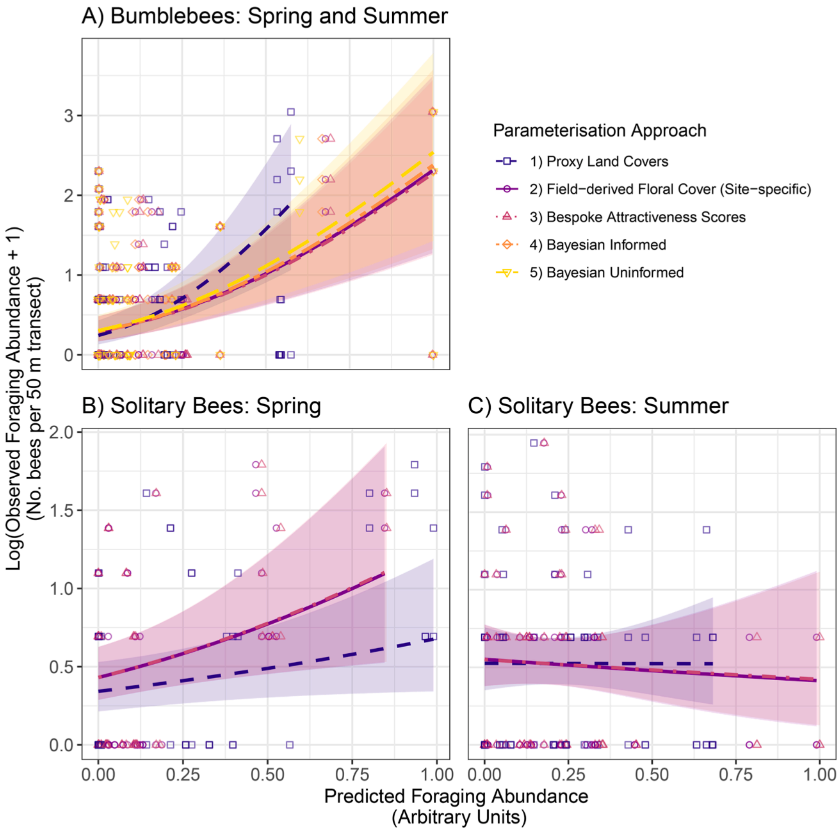

Fig. 5. Observed vs poll4pop-predicted relative abundance of foraging bumblebees and solitary bees in transects at all three UK silvoarable survey sites in 2023. Solitary bee results are considered separately for spring and summer because the poll4pop model assumes the summer-flying solitary bee populations are independent of the spring-flying populations (i.e., representing different species with later flight periods), whereas bumblebee populations are treated as the same colonies being continuously active across multiple seasons. Number of transects: $n_{spring}=74$ and $n_{summer}=87$. Bayesian approaches were only conducted for bumblebees, not solitary bees, due to run-time constraints. Predicted foraging abundances (x-axis) were rescaled to 0–1 within each panel to remove arbitrary between-guild differences arising from guild-specific parameters within the model. Fitted curves represent the GLMs described in Section 2.5.2 and Table A5. Error shading around regression lines represents 95 % confidence intervals.

required. Further monitoring of floral cover across more sites would help to determine whether variability in floral cover reduces as these systems become more commonly implemented and standard approaches begin to emerge. This could potentially enable more widely representative floral cover field measurements to be calculated in future.

4.2.2. Bespoke, newly-elicited attractiveness scores

Using bespoke foraging and nesting attractiveness scores for silvoarable trees and understories, newly elicited via an expert opinion survey, did not affect poll4pop model performance compared to using proxy attractiveness scores (Fig. 5; Table 2). This might be due to similarities in the parameter distributions of proxy and bespoke foraging attractiveness scores for each land cover (Fig. 3). Although the quantitative values of the different parameter sets may be different for each land cover, their relative ranking among other land cover types in the surveyed fields did not change drastically (Table B3). Therefore, both parameterisations might represent a roughly equally attractive resource to the simulated bee populations, relative to the surrounding landscape. Indeed, the location of pollen resources, alongside their quality, has been shown to be a key contributing factor to increased bee abundance (Ganser et al., 2021).

Although including bespoke attractiveness scores seemed to have no effect on model performance in our study, this was a valuable exploration of the extent to which experts might need to be engaged when parameterising new and lesser-studied land cover classes. Expert-score elicitation may be more necessary when proxies that appropriately represent the resources offered by a new land use do not already exist within the model being parameterised. Furthermore, gathering these bespoke scores served a second purpose of ensuring expert-informed probability distributions were available for use as informed priors in a Bayesian calibration of parameters, thereby providing a starting point for posterior parameter likelihood distributions that can be updated as more data surrounding pollinator abundance in alley-cropping systems becomes available (Arhonditsis et al., 2007).

4.2.3. Bayesian-calibrated attractiveness scores

The results of our calibrations suggest limited model sensitivity and possibly parameter redundancy for three out of four of the calibrated parameters, given the model structure and available observational data (Fig. 4). Only the silvoarable understory foraging attractiveness parameter showed notable deviation from its prior, indicating both stronger empirical support and an overestimation by experts. These findings may reflect inherent ecological characteristics of these land covers, and related survey limitations. Tree-related parameters may have had minimal influence because the apple tree flowering period is brief (~ two weeks) and poorly aligned with our observational data collection period (~ six months). Moreover, tree nesting attractiveness likely had little effect in this context as the model was calibrated solely for ground-nesting species. In contrast, understories provide foraging resources throughout the pollinator active season (Staton et al., 2021) and thus likely influenced observed bee abundance more directly. Furthermore, the metric used for evaluation was predicted relative foraging abundance, which is strongly influenced by the foraging attractiveness of the land cover. It is likely that field data on nest densities would need to be collected and compared to the poll4pop-predicted nest densities to provide sufficient power for

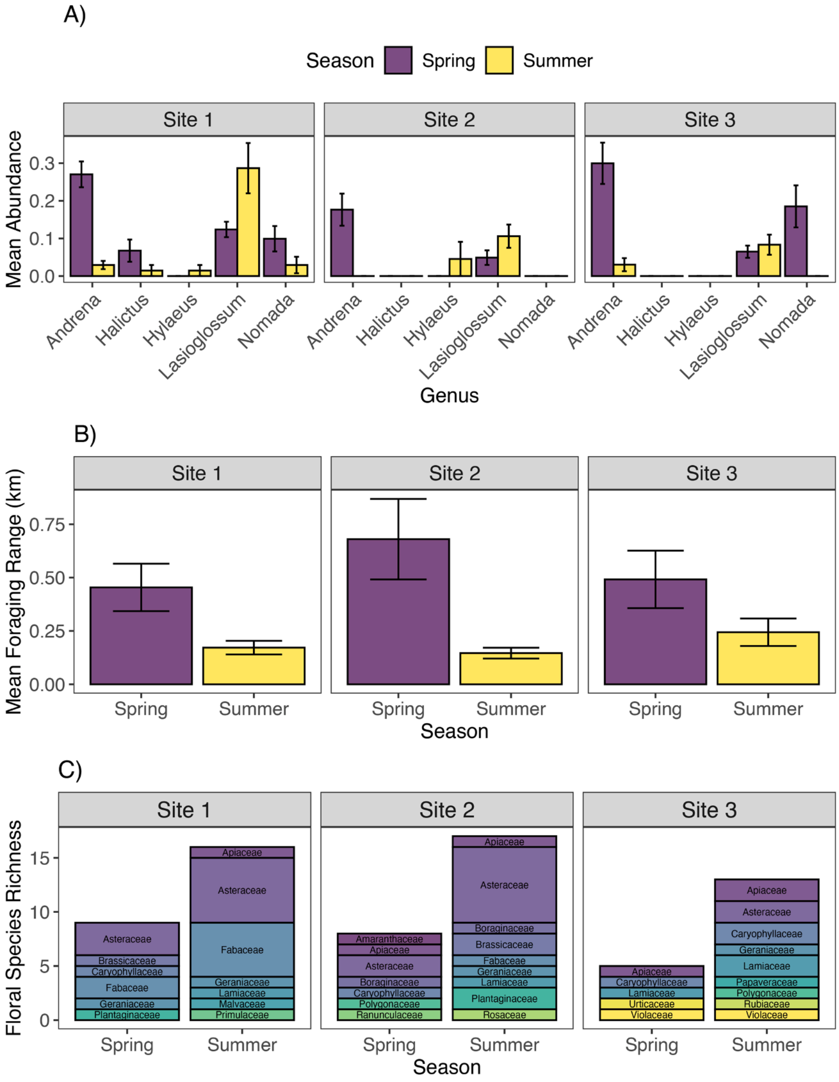

Fig. 6. A) Mean abundance of solitary bee genera found in pan trap samples in spring and summer at three UK silvoarable survey sites in 2023. N_{bees}=509. B) Mean foraging range of solitary bee species found in pan traps in spring and summer, calculated from intertegular distance using formulae taken from Greenleaf et al. (2007.) C) Overall species richness of plant families found on transects in silvoarable understories, crops, and grassy field margins in spring and summer at three UK silvoarable survey sites in 2023. Error bars represent standard error in all cases.

effective calibration of the nesting attractiveness parameters. However, such field data is challenging to collect (Tsiolis et al., 2022).

Whilst limited conclusions can be drawn from model evaluation using these parameters because we used the same observed data for both calibration and evaluation, we note here that they resulted in no meaningful improvement in model predictive ability compared to using proxy parameters, consistent with our results when using bespoke, expert-derived attractiveness parameters (Fig. 5; Table 2). This may relate to the lack of sensitivity shown during the calibration to three of four of the attractiveness parameters. Thus, whilst our calibrations did not yield different results to other parameterisation approaches, they did reveal insights into model sensitivity to our new land cover parameters. This aids assessment of whether either expert priors or empirical data are informative when generating parameters for new land cover classes. Furthermore, as more survey sites and data become available, these can be used to update the posterior distributions of parameters output by the Bayesian calibration, whilst using the previous posteriors as informed priors. This can be a particularly effective method of finding and updating parameters for emerging land covers such as silvoarable alley-cropping in the UK, which do not have many baseline data or established survey sites to draw upon initially.

4.3. *Caveats & future work*

Our simulations were run at a 3 m resolution in order to compare observed and predicted foraging abundance at a fine scale whilst capturing the spatial configuration of the alley-cropping components. However, this level of resolution would likely be too computationally expensive to maintain when modelling areas significantly larger than our 10 × 10 km study landscapes with standard computing resources. This could be addressed by running the model at a coarser resolution and including the silvoarable tree rows as edge features in the model inputs, alongside the silvoarable trees. In this case, the model will assume the tree rows only occupy a specified proportion of the pixels in which they are present. This may reduce the correspondence between observed abundance and predicted visitation at the field scale, but would still be sufficient to capture relevant patterns for regional- or national-scale applications.

As alley-cropping systems can vary widely in their configurations and management, the parameters determined in this paper are either reflective of the specific systems surveyed (in the case of the field-derived parameters) or somewhat generalist (in the case of the bespoke, newly-elicited expert parameters). Whilst we only studied three sites due to limited availability, we stress that systems with different configurations of silvoarable elements can be incorporated into the model by realistically representing their configuration in input maps, since poll4pop accounts for these elements of context dependence through its spatially-explicit nature. Furthermore, if the composition of the modelled silvoarable elements varies significantly from our sites, our results suggest that spatial variation in abundance can be captured by finding suitable proxy land covers. If the time and resources are available, representing the field-level floral cover of systems should be prioritised to achieve the best model predictions, since we found this had the largest influence on predictive ability and enabled poll4pop to reproduce the observed between-site differences, thereby reducing the need to artificially control for these in the model-data comparisons. This is especially relevant in studies, like ours, which seek to parameterise a new land cover using data collected in organically-managed field sites, but where the land cover could also fall under conventional management, thereby creating discrepancies in the floral availability provided by in-crop weeds (Milberg et al., 2025). This may be common when considering emerging regenerative and/or agroecological land uses, whose pioneering practitioners are often progressive and may already carry out sustainable land management practices such as organic agriculture.

Whilst our method of carrying out multiple model runs, each sampling parameters from their uncertainty distributions, accounted for uncertainty in the underlying parameter values of the poll4pop model, there are other sources of uncertainty that this did not capture. This includes potential observation error in field measurements, the small number of survey sites visited, and simplified assumptions of pollinator behaviour in the poll4pop model. Observation and measurement error of empirical abundance data could be accounted for in studies using mean observed values to validate model predictions by weighting each survey measurement by the inverse of its standard error, however this was not possible in our study because we treated each transect as a separate datapoint. Future work could also focus on increasing the number of study sites as they become available, and conducting long-term monitoring in silvoarable alley-cropping systems to generate larger datasets for refining parameter estimates and thus improving the representation of these systems at the landscape level. Beyond this, incorporating Bayesian calibration with iterative updates as new data become available could help to address some of this uncertainty.

5. Conclusions

We have integrated the spatial representation of silvoarable alley-cropping systems into the process-based poll4pop model and demonstrated its ability to capture spatial variation in bumblebee and spring-flying solitary bee foraging abundance in these systems. We have also provided the first within-year, sub-field scale, seasonally-resolved validation of poll4pop, demonstrating its capabilities in the fine-scale simulations of pollinator populations in novel or emerging agroecosystems. Based on our results, we suggest that future studies using poll4pop to predict pollinator abundance in silvoarable alley-cropping systems can use proxy parameters to represent floral cover parameters but should supplement with field data if possible, and bespoke expert-derived attractiveness scores as a generic parameter set for initial landscape-level modelling (available in Table B4). These results facilitate future investigations of how pollination service and ecosystem function in our UK farmed landscapes may change if, as encouraged, high proportions of silvoarable alley-cropping are implemented in the near future (Department for Energy Security and Net Zero, 2023), thereby better informing policy and practice in agrifood systems.

For others attempting to introduce novel land cover class parameterisations into existing process-based models, we make the following recommendations, which may be progressed through as increasing amounts of knowledge/data become available:

- Proxy land cover parameters, if suitable options are available, can produce reasonable model predictions for novel landcover classes. These may be the only option available for very newly implemented land covers.
- Bespoke expert opinion may be elicited, as the land cover begins to be implemented and initial studies and field experience begin to be gathered. These may be especially suitable when large-scale field data collection is still impractical.
- Field-measured values may be preferred for parameters that are hard for experts to estimate and/or likely to vary widely in different situations (as was the case for floral cover in our study), in which case initiating dedicated small-scale studies to gather this parameterisation information is valuable.
- Site-level variation in implementation is high for novel landcover classes for which a community of practice is still developing. Identifying influential parameters (in our case, floral cover) for which it is possible to gather field data is beneficial for removing site-level variation, potentially making the calibration and/or evaluation of other parameters more accurate/feasible.
- Bayesian calibration is a time-intensive approach to finding parameters, and the results depend on the context of the calibration data. We showed it valuable for revealing potential overestimation by expert opinion parameters but it is likely to be more powerful at later stages when implementation and data-providing field studies of the novel landcover are more widespread and can be used to improve on priors based on previous expert opinion.

Code and data availability

All reproducible code and processed data are available at: https://doi.org/10.5281/zenodo.17715001. Poll4pop model code is freely available to download from https://github.com/yclough/poll4pop (https://doi.org/10.5281/zenodo.4001015, Gardner et al., 2020b).

CRediT authorship contribution statement

Ellen Knight: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tom D. Breeze:** Writing – review & editing, Supervision, Conceptualization. **Robbie D. Girling:** Writing – review & editing, Supervision, Conceptualization. **Alexa Varah:** Writing – review & editing, Supervision, Data curation, Conceptualization. **Michael P.D. Garratt:** Writing – review & editing, Data curation. **Louise A. Hutchinson:** Writing – review & editing, Data curation. **Simon G. Potts:** Writing – review & editing, Data curation. **Jo Smith:** Writing – review & editing, Data curation. **Tom Staton:** Writing – review & editing, Data curation. **Emma Gardner:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the NERC Scenario DTP (grant number NE/S007261/1). We thank the farmers at our survey sites for their extended cooperation and enthusiasm, Sarah Ashby for her assistance with field work, and Deepa Senapathi and David Cameron for their valued advice.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2026.111489.

Data availability

A link to the code/data repository (Zenodo) has been made available in the manuscript (Section 6: Code and Data Availability)

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