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RESEARCH ARTICLE

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Quantifying the impacts of management and herbicide resistance on regional plant population dynamics in the face of missing data

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Abstract

1. A key challenge in the management of populations is to quantify the impact of interventions in the face of environmental and phenotypic variability. However, accurate estimation of the effects of management and environment, in large-scale ecological research is often limited by the expense of data collection, the inherent trade-off between quality and quantity, and missing data.
2. In this paper we develop a novel modelling framework, and demographically informed imputation scheme, to comprehensively account for the uncertainty generated by missing population, management, and herbicide resistance data. Using this framework and a large dataset (178 sites over 3 years) on the densities of a destructive arable weed (*Alopecurus myosuroides*) we investigate the effects of environment, management, and evolved herbicide resistance, on weed population dynamics.
3. In this study we quantify the marginal effects of a suite of common management practices, including cropping, cultivation, and herbicide pressure, and evolved herbicide resistance, on weed population dynamics.
4. Using this framework, we provide the first empirically backed demonstration that herbicide resistance is a key driver of population dynamics in arable weeds at regional scales. Whilst cultivation type had minimal impact on weed density, crop rotation, and earlier cultivation and drill dates consistently reduced infestation severity.
5. *Synthesis and applications*: As we demonstrate that high herbicide resistance levels can produce extremely severe weed infestations, monitoring herbicide resistance is a priority for farmers across Western Europe. Furthermore, developing non-chemical control methods is essential to control current weed populations, and prevent further resistance evolution. We recommend that planning interventions that centre on crop rotation and incorporate spring sewing and cultivation

to provide the best reductions in weed densities. More generally, by directly accounting for missing data our framework permits the analysis of management practices with data that would otherwise be severely compromised.

KEYWORDS
Alopecurus myosuroides, blackgrass, demography, density-structured models, herbicide resistance, population ecology, weeds

1 | INTRODUCTION

Understanding and predicting the impact of management on population dynamics of key species is a major focus of ecological research (Mills, 2013; Sakai et al., 2001). The wide spatial distributions of many organisms mean that effective management recommendations must be robust across multiple scales to address many ecological problems (Freckleton et al., 2008; Guerrero et al., 2013; Taylor & Hastings, 2004; Tscharntke et al., 2005). However, broadly distributed populations will experience heterogeneous environments and may display an array of responses to varying environmental conditions and management (Caughlin et al., 2019; Lundberg et al., 2000; Shriver et al., 2019). Additionally, populations under intense management pressure can evolve resistance to interventions (Evans et al., 2015; Heap, 2014; Hicks et al., 2018; Mills, 2017; Moss et al., 2007; Tomasetto et al., 2017) which can further undermine the impact of intended controls. Studies based on a limited number of sites may, therefore, not capture the full range of environmental conditions and phenotypes required to evaluate management strategies (Che-Castaldo et al., 2018; Coutts et al., 2016; Gurevitch et al., 2016). As a result, the collection of data at the metapopulation scale is necessary for accurate prediction of regional scale responses to interventions (Queenborough et al., 2011; Tredennick et al., 2017).

Effective monitoring is key to managing widely distributed populations (Lovett et al., 2007; Schindler & Hilborn, 2015) and well-designed surveillance schemes are required to reveal the drivers of population change. Combined with population models, long-term data enable understanding and predicting population responses to changes in environment and management. However, a major challenge is collecting sufficient data to quantify the full range of variation in space and time. Density-structured methods, which record abundance as discrete density-states, allow rapid measurement of abundance, whilst still permitting insight into site-level population dynamics (Freckleton et al., 2011, 2018; Goodsell et al., 2021; Mieszkowska et al., 2013; Queenborough et al., 2011; Taylor & Hastings, 2004). These methods facilitate the study of population dynamics across a range of environments and phenotypes present in widely distributed populations.

However, a major constraint in the analysis of many ecological surveys is the presence of missing data (Nakagawa & Freckleton, 2008). Missing data are often caused by logistical issues preventing site revisits and the difficulty of collecting data from multiple sources and scales. Incomplete data are problematic for two reasons. First, the loss of data reduces statistical precision through the reduction of sample sizes. Second, the incidence of missing data may be a function of unobserved relationships between variables and patterns of missingness can be non-random in nature. Missing data can therefore increase the bias and uncertainty of estimates of effect size if only complete cases are considered (Nakagawa & Freckleton, 2008, 2011). Imputation can also account for the uncertainty produced by missing data by propagating imputation variability from multiple imputations to subsequent analysis (van Buuren, 2018), which is particularly useful in applied settings where planning effective interventions hinges on a range of possible outcomes (Cressie et al., 2009; Dorrough et al., 2008).

Missing data are particularly problematic for regional-scale studies focussed on management. Populations are often managed across property boundaries by numerous individuals (Epanchin-Niell et al., 2010) with different reporting standards and frequencies, and phenotypic data characterising resistance often require separate experimentation to determine the variability in response to interventions (Comont et al., 2019; Heap, 1994; Hicks et al., 2018). The consequence is that it is often impossible to collect consistent covariate data for all locations where populations have been surveyed. Even small frequencies of missing observations per variable can lead to the loss of large amounts of data. For example, if two variables have missingness rates of only 10%, in the worst case a fifth of cases in a dataset could be affected by data loss. As the number of variables increases, missingness becomes more problematic and is potentially a severe problem in large complex datasets (Nakagawa & Freckleton, 2008). To make robust management recommendations we need methods that facilitate both the rapid collection of data and to provide reliable inference in the face of missing data.

Arable weeds are archetypical examples of populations that are problematic over large spatial extents and require active management. They have severe negative impacts on agricultural economics (Varah et al., 2020), food security (Oerke, 2006; Savary et al., 2019) and biodiversity (Brühl & Zaller, 2019; Relyea et al., 2006), and have rapidly adapted to interventions globally (Heap, 2014). Typically, the management of weeds focuses on integrating several practices (known as integrated weed management or IWM), including herbicide application, physical destruction via cultivation, direct competition with crops, and the timing of interventions with regard to the phenology of the weed (Chauvel et al., 2001; Melander et al., 2005). Despite the need for integrated management strategies, the majority of studies typically focus on testing the impacts of single management interventions under controlled environmental conditions (Buhler, 1999; Chauvel et al., 2001; Harker & O'Donovan, 2013; Melander et al., 2005; Metcalfe et al., 2017, 2018). Several reviews have emphasised variability in responses to interventions between studies and locations (Freckleton et al., 2008; Freckleton & Stephens, 2009; Lutman et al., 2013), and recent work has demonstrated the importance of environmental variability on plant population dynamics, and the need to understand how management outcomes vary under these conditions (Freckleton et al., 2018; Goodsell et al., 2021; Hicks et al., 2021).

Furthermore, many weed populations have a high prevalence of evolved herbicide resistance (Evans et al., 2015; Hicks et al., 2018; Moss et al., 2011; Powles & Yu, 2010). As herbicide resistance can drive increases in abundance, it can result in variations in the demographic parameters of populations through time and across regions. Due to the rapid evolution of resistance, it is therefore extremely important to investigate its impacts. However, research on the impact of herbicide resistance on population dynamics is generally limited in terms of empirical data (Diggle & Neve, 2001; Torra et al., 2008) and no previous analyses have investigated the impact of herbicide resistance on population dynamics at landscape scales. Consequently, it can be difficult to evaluate the success of any set of management practices in an integrated framework.

We tackle the problem of modelling the population dynamics of a damaging arable weed (black-grass, *Alopecurus myosuroides*) in response to management across multiple sites using incomplete data. Black-grass is a particularly problematic weed in western Europe, where over the past 30 years it has evolved target and non-target site resistance to multiple herbicides (Comont et al., 2019; Délye et al., 2010, 2011; Hicks et al., 2018; Kemp et al., 1990; Menchari et al., 2007), and causes severe economic damage (Ahodo et al., 2019; Varah et al., 2020). We include management variables that describe herbicide pressure, cultural control via cultivation and cropping, and the timing of interventions, alongside data on herbicide resistance and soil quality. We develop a novel imputation method that incorporates information about the population dynamics of black-grass to account for the uncertainty and potential biases caused by missing data, allowing us to quantify the roles of different aspects of IWM and evolved herbicide resistance. From these models, we inspect the contribution of sampling and imputation variability on estimated coefficients as well as the effect sizes of different variables. Finally, we simulate different management strategies from our models to evaluate the impact of cropping, herbicide application, and herbicide resistance on population dynamics. We show that in the face of herbicide resistance, which is a key determinant of population dynamics, several cropping practices remain key control methods for black-grass infestations.

2 | MATERIALS AND METHODS

2.1 | Density-structured survey data

Black-grass densities were collected as the focus of a series of on-farm surveys from 2014 to 2016. The data consist of 178 field-level surveys over a network of 70 farms in England (see also Hicks et al., 2018). The density structured method is described in detail in (Freckleton et al., 2011; Queenborough et al., 2011) and involved researchers assigning one of five density states (absent (A), low (L), medium (M), high (H), or very high (V)), to a number of predefined 20 m × 20 m quadrats within each field. Surveys were repeated in subsequent years depending on whether crops in the field allowed sufficient access. For example, fields that were growing non-cereal crops such as oil-seed rape (OSR), were not surveyed and density-states were treated as missing data. All farmers and growers involved in this study consented to be part of a UK Blackgrass research network. Data on blackgrass abundance, agronomic management, and herbicide resistance were collected via a request for any electronically stored management data from field-sites only after receiving written permission from each individual grower.

2.2 | Management data

Management data were collected from farmers either through face-to-face interviews or electronically. These data consisted of sets of variables describing common interventions used to control weed infestations, including herbicide applications, cultivation, cropping strategies, and the timing of controls. This data suffered from high frequencies of missingness due to considerable degrees of non-response to requests for management data and variability in reporting standards between individuals. The groups of derived management variables and explanations on how they potentially impact weed density are displayed in Table 1.

We assessed the impact of several field-level management practices which have varying modes of weed control. Cropping—the sequence of crops planted in a field across successive years—is a key component of control strategies. Crops influence the densities of weeds through competition for nutrients, water and light (Chauvel et al., 2001; Harker & O'Donovan, 2013; Melander et al., 2005), and can also act as a broad proxy for different sets of co-ordinated interventions. We include every combination of crop types observed in the data.

Cultivation involves the preparation of the soil to allow the successful establishment of crops but is also a key component of weed control via physical destruction. We include cultivation as one of four categories, designated here as; 'conventional', 'inversion', 'surface' and 'subsoil', which represent different cultivation intensities. Conventional tillage systems represent a cultivation that penetrates a medium distance into the subsoil, accompanied by additional mechanical disruption of the topsoil (e.g. discs and tines). Inversion involves completely inverting the subsoil and topsoil leading to burial

TABLE 1 Description of management variables and potential effects on weed density.

Variable	Description	Type	Effect
Cropping	Sequence of crops in a transition	Factor (25 categories) **wheat → wheat**, wheat → barley wheat → beans, wheat → beet wheat → cover, wheat → fallow wheat → linseed, wheat → oats wheat → OSR, wheat → peas wheat → potatoes, barley → barley barley → beans, barley → wheat beans → barley, beans → wheat cover → barley, cover → wheat linseed → barley, beet → wheat fallow → wheat, oats → wheat OSR → wheat, peas → wheat potatoes → wheat	A proxy for combined controls, direct competition
Herbicide pressure	No. spray days containing grass-weed or broad-spectrum herbicides	Count	Chemical destruction
Autumn glyphosate	No. of autumn glyphosate spray days (post September 1st)	Count	Chemical destruction/stale seed bed
Cultivation	Cultivation category	Factor (four categories) **Conventional**, inversion, subsoil, surface	Physical destruction, a factor in weed establishment
Soil	Soil category	Factor (4 categories) **Pelosols**, brown soils, ground-water gleys, surface water gleys	Establishment and growth of weeds
Drill season	Drill season	Factor (two categories) **Spring**, winter	Indicator of the period of effective control
Δ drill date	Difference in drill date from seasonal median	Integer ratio	Indicator of the period of effective control
Δ cultivation date	Difference in cultivation date from seasonal median	Integer ratio	Indicator of the period of effective control

Note: Factor levels used as the reference category in model fitting are highlighted in bold.

of anything on the surface (e.g. plough). Surface tillage involves light tillage disturbing the topsoil only (e.g. shallow tines, rollers and direct drilling), while 'subsoiling' represents cultivation of deeper soil, but with little disturbance of the topsoil itself (e.g. mole plough and subsoiler).

Herbicides are a primary component of weed control in intensive arable systems (Harker & O'Donovan, 2013; Lutman et al., 2013), and reduce populations through chemical destruction of mature plants and developing seedlings. Here we derived two measures of herbicidal control; (1) use of the broad-spectrum herbicide glyphosate to control weed seedlings before crop emergence, measured as the total number of applications (i.e. the number of spraying days) of glyphosate after the 1st of September, which includes all applications on false or stale seed beds. (2) The total number of spraying days for grass-weed specific or broad-spectrum herbicides applied between black-grass surveys. These measures have been demonstrated by previous work to provide an accurate measure of herbicide pressure in the absence of more detailed rate information (Comont et al., 2019; Hicks et al., 2018).

A major component of control strategies is the timing of interventions with regard to the growth profile of both the crop and the target weed. Timing management so that they reduce weed numbers without damaging crops is a key concern for farmers. As such we include variables that describe the length of the period in which intense control methods (such as general herbicides and cultivations) can be applied. The drill season denotes the season in which crops were planted (either winter or spring), with spring cropping having the benefit of a longer period in which to apply controls before crops are sewn, as well as partially decoupling the phenology of the crop and weed.

We derived two measures for the relative timings of cultivation and drill date (Δ cultivation and Δ drill, respectively) which represent the difference in cultivation and sewing of crops from the seasonal median date. For example, a negative number represents earlier timing, and a positive number a later timing. This allowed us to investigate the impact of strategies such as delayed cultivation and drilling, often cited as a means to reduce blackgrass population size (Lutman et al., 2013).

We created a coarse soil type variable for each field from the NSRI soil data (Truckell et al., 2009), as soil structure and quality are key determinants of plant growth and dynamics (Hicks et al., 2021; Metcalfe et al., 2018). Each category represents the majority soil type found in the 1 km grid square of the NSRI soil data in which each field was located. The major categories that represent most of our study sites include pelosols, brown soils, surface water gley soils, and ground water gley soils. Each of these major categories has characteristics that could influence weed density.

2.3 | Herbicide resistance data

We used mortality data collected from herbicide sensitivity assays to characterise herbicide resistance. These data were collected from 69 fields in 2014 as part of a larger audit of black-grass abundance and herbicide resistance. These fields are a subset of the fields from which black-grass data were collected. The specifics of seed collection, plant propagation, and resistance assays are detailed in (Hicks et al., 2018). The purpose of the resistance assays was to quantify the levels of herbicide resistance present in the UK black-grass populations at the time of the census. Plants grown from seeds collected across our network of farms were sprayed with one of three herbicide products (Atlantis, Cheetah, and Laser) with application rates chosen to approximate dosages in the field, and mortality was recorded after 3 weeks. We used the field-specific average mortality (henceforth referred to as susceptibility) from the three chemical-specific assays as a proxy for overall herbicide resistance.

2.4 | Density structured models

To estimate the effects of management and herbicide resistance on the probability of observing different density states we parameterised hierarchical ordered category logistic regression models. These models are a suitable choice when the response variable is categorical but has a natural ordering, and is generated by assessments of an underlying continuous variable (Agresti, 2012, p. 180). In our case, they are appropriate as the categorical density states have a natural progression from 'absent' to 'very high' and are generated from subjective assessment of the continuous distribution of weed abundance. Our study focuses on the effects covariate data which are structured at two different scales. Management variables were recorded at the field-scale (i.e. a field in a given year has only one record for each management variable), and density states were recorded at the quadrat level (i.e. in each 20 m × 20 m grid cell). As such we structure the notation for our model as in (3), with field and quadrat level components:

$$\gamma_{jt} = \sum_{m=1}^{M} x_{jmt}\beta_m + \Theta_{j,}$$

$$\eta_{ijt} = \sum_{k=1}^{K} y_{ikt-1}\alpha_k + \gamma_{jt}. \tag{1}$$

The probability of observing category k in quadrat i, within field j, at time t is expressed in terms of a linear predictor, the latent variable η_{ijt} (1). The contribution of field-level variables to the quadrat level linear predictor is expressed by the component γ_{jt}. This is the sum of the products of M field-level explanatory variables $x_{m..M}$ in field j and time t, and the unknown parameters $\beta_{m\ldots M}$. β_m is therefore the coefficient representing the effect of the field-level explanatory variable x_{jmt} on γ_{jt}. To account for spatial variability across landscapes we included a scalar intercept term Θ_j, which represents the field-level random effect on the linear predictor within field j. Values of Θ were drawn from a normal distribution. The quadrat level model is therefore the sum of the field level component, γ_{jt}, and the sum of the products of K density-state indicators $y_{k..K}$ with the unknown parameters $\alpha_{k..K}$. To allow estimation of the probability of transition between density states, models incorporated the effect of source state (i.e. density state of quadrat i at time $t-1$) as indicator variables for covariates $y_{i1} \ldots y_{i5}$, α_k is therefore the coefficient representing the effect of source state k. The constraint $\alpha_1 = 0$ was enforced to ensure identifiability. η_{ijt} is therefore the linear predictor for quadrat i in field j at time t.

The ordering of categories in this model was enforced through a set of $K-1$ 'cut-point' parameters, c_i, where $c_1 < c_2 < \ \ldots c_{K-2} < c_{K-1}$ (Agresti, 2012). For clarity and ease of reading, we drop the t and j subscripts in equations from here on, however, all probabilities are time and field-dependent. We calculated probabilities of observing a given density state, where p_{ik} gives the probability of observing state k at time t, conditional on explanatory variables $x_{m\ldots M}$ at quadrat i within field j:

$$p_{i1} = 1 - logit^{-1}(\eta_i - c_1),$$

$$\vdots$$

$$p_{ik} = logit^{-1}(\eta_i - c_{k-1}) - logit^{-1}(\eta_i - c_k), \tag{2}$$

$$\vdots$$

$$p_{iK} = logit^{-1}(\eta_i - c_{K-1}).$$

We then modelled field-level weed population dynamics using density-structured models (Freckleton et al., 2018; Goodsell et al., 2021).

$$\mathrm{n}_{t+1} = \mathbf{T}\mathrm{n}_t, \tag{3}$$

where n is a vector, of K density states. The elements of n are the observed proportion of a field occupied by each density state at time t, hence observed data are realisations drawn from this distribution and n_{t+1} represents a future density state distribution. $\mathbf{T}$ is a $K \times K$ (where $K=5$) column-stochastic matrix of transition probabilities between states:

$$\mathbf{T} = \begin{pmatrix} p_{11} & \cdots & p_{1K} \\ \vdots & \ddots & \vdots \\ p_{K1} & \cdots & p_{KK} \end{pmatrix}. \quad (4)$$

which describes the population dynamics of the system. We present a general notation for $\mathbf{T}$ without subscripts for ease of reading, but all matrices used in analyses represent transitions at the field scale. The entries of $\mathbf{T}$ are the probabilities estimated in (2), conditional on management and previous density state. As we condition on previous density states (source state) we can reconstruct the probabilities from (2) so that the entries of $\mathbf{T}$ denote the probability of transition from the row state to the column state, that is p_{12} represents the probability of transitioning from state 1 to state 2. Density-structured models are a form of matrix model (Caswell, 2001), and Equation (3) defines a first-order Markov model which can be used to predict future density state distributions. Models estimating transition probabilities were fit using the '*mgcv*' package (version 1.8) (Wood, 2017) in the R programming language R (version 4.13) (R Core Team, 2023). Data and code are available from the Dryad digital repository https://doi.org/10.5061/dryad.9cnp5hqn5 (Goodsell et al., 2023).

2.4.1 | Modelling and imputation of missing data

An integral part of this study was to account for the uncertainty produced by missing data in both the management variables and the biological response (i.e. density-state data). Management data missingness was a consequence of variability in reporting of interventions, whereas density-state missingness was driven by ability to survey fields in non-cereal crops. The dynamics of transitions between density-states are probabilistic in nature, with the distribution of states at time t (conditional on management), determining the distribution at time t_{+1}. We developed an imputation scheme to reflect these dependencies, but also to incorporate the probabilistic nature of density-state transition dynamics inherent in the modelling framework. We divided the imputation into three stages, (i) imputation of management data, (ii) imputation of resistance data, and (iii) imputation of density-state data. In this formulation, the imputed management and resistance data informs the imputation of the missing density-state data.

Management imputation

We imputed missing management data through multiple imputation (MI), implemented through the MICE R package (van Buuren & Groothuis-oudshoorn, 2011). Through MI, the relationships between variables in observed and unobserved cases are used to impute missing data multiple times, with the resultant multiply imputed data used in subsequent analyses. We built imputation models that incorporate information from management variables, average field-scale densities in the present and subsequent years, as well as geographical information (such as latitude, longitude, and soil type), to impute missing data from the variables in Table 1.

We impute missing management observations in the years 2014–2016 using a larger set of management data with observations collected between 2004 and 2016. Variables used in the management imputation (Table S1), were either management variables themselves or were related to management decisions. We include several non-management variables that are important factors for farmers implementing field-scale management but did not include these in the modelling of weed dynamics. Management is often driven by weather and local environmental conditions; hence field identity, year, and geographical location (latitude and longitude) were included as variables to impute missing data. We include information on total herbicide pressure as it is a good indicator of herbicide pressure designed to target black-grass when we lacked specific application date or detailed product information. We also include measures of overall black-grass infestation (mean-density state) in the current and previous years, which are correlated with control effort.

As management factors are influenced by local environmental conditions or the preference of individual farmers, missing values within variables are likely 'clustered' at the field level. In this case, it is useful to impute missing variables hierarchically to account for this structure. In our models we set field-level intercepts for the variables indicated in Figure S3, meaning for each iteration in the MICE algorithm (i.e. each time we impute missing values using the observed values as predictors) we specify field identity as a random intercept to account for field-level associations (van Buuren, 2018). We do not impute missing values for all variables included as predictors, for example, we do not impute mean density state as we only have observations for a handful of years. We used the inbuilt functionality and imputation statistics in the 'MICE' package to inform decisions on predictor structure. After management variables were imputed we derived the variables used in the modelling of black-grass dynamics (Table 1).

Resistance imputation

After management data was imputed, we calculated measures of historical herbicide pressure for fields using our measures of herbicide pressure. Herbicide sensitivity assay data was available for 60 fields out of the 178 that were included in the modelling of weed density. For each field, we take the average of imputed and observed values across all years, for four herbicide variables (Table S2). As herbicide diversity, and application intensity (the number of spraying days), both correlate with the evolution of herbicide resistance (Comont et al., 2019, 2020; Evans et al., 2015; Hicks et al., 2018), we include variables that summarise the historical intensity of herbicides applied to each field. We also include a variable describing the average density state of fields in the years 2014–2016, as infestation severity is an indicator of susceptibility. All variables in Table S2 are used as predictors to impute missing susceptibility values using MICE.

Density state imputation

We use the ideas in Ellner et al. (2016, Chapter 10.5, p. 309) to impute missing density state data. Using this framework, we can impute missing density states for fields with missing observations which are bordered by observed states in previous and subsequent years. This is achieved by calculating the distribution of density states, conditional on the known states and management of a field, on either side of the transition with missing data. We then sample the possible states from this distribution to impute plausible values of the density states. The full specification of this stage of the imputation can be found in Supporting Information. This allows us to fit ordinal regression models using standard ordinal regression modelling software packages such as '*mgcv*'.

We combined the stages of missing data imputation into an iterative multiple imputation scheme (Figure 1). First, missing management data were imputed using MICE, second, we calculated summaries of the historical herbicide pressure for individual fields from the imputed management data. Third, we fitted hierarchical ordinal regressions to parameterise transition matrices and conducted *k*-fold cross-validation to validate model performance. Finally, we used these matrices to impute missing response data for a field with unobserved density states. After each iteration, the density-state distribution for each field with missing states was updated and used as the initial density-state distribution for management data imputation in step one of the next iteration. Imputations were run for $n = 500$ iterations, with the MICE algorithm running for 50 iterations for both management and resistance imputation. We assessed convergence through the summary output plots produced by MICE, as well as assessing the mean density states of imputed fields, and covariate values for management and field-level intercepts. After convergence, we inspected partial autocorrelation coefficients and removed imputed data at the appropriate lags to remove autocorrelation between model estimates in successive time steps to improve computational efficiency. This process left us with 97 datasets which were treated as multiply imputed data and used in model comparison.

2.4.2 | Imputation validation

We validate our MICE imputation model suitability by checking how successfully our imputation structure returns values of missing observations. We do this by 'amputing' (artificially removing), values of variables from the complete cases. We do this for each incomplete management variable included in the first imputation stage. We also run the same validation exercise using the herbicide susceptibility data, but include missing observations from herbicide variables, as imputing missing mortality data is dependent on constructing historical records of herbicide pressure for individual fields. For each variable, we drop 20% of the total observations in the complete case data and examine the average absolute error (or the 'multiple category area under the curve (mAUC)' (Hand & Till, 2001) for cultivation categories) between imputed values and the observed value for each amputed variable. This exercise allowed us to examine whether the relationships between observed variables provided sufficient information to accurately impute missing values. We run each imputation

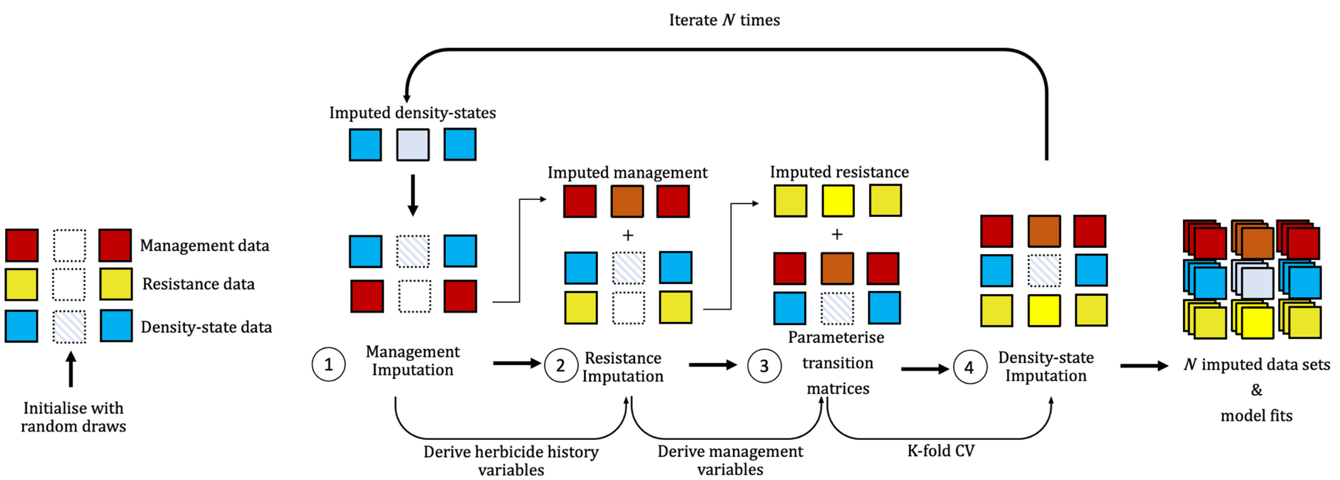

FIGURE 1 A schematic of all the steps involved in imputing missing data and modelling of population dynamics. Initially, missing density state data are replaced with random draws from a uniform distribution. Missing management data are imputed using chained equations implemented in the mice R package (1), using observed variables that influence management decisions. Variables that describe the historical herbicide pressure on individual fields were then derived from the imputed management data, and the resistance metrics were then imputed using these metrics and the mean density of fields in the year in which resistance metrics were measured (2). Variables used to model the effects of management on black-grass dynamics are then derived from the imputed management and resistance data, and used to parameterise field-level transition matrices using ordinal regressions implemented in the 'mgcv' R package (3). *K*-fold cross-validation is conducted after the full model fit to assess predictive performance. Missing density states are then imputed using transition probabilities estimated by the regression models (4). The missing density-state data at step 1 are then updated with the imputed density states, and steps 1–4 are repeated *N* times, the final output is a set of *N* data sets including imputed management, resistance, and density-state data, as well as *N* model fits and *N* results from the *K*-fold cross-validation from step 3.

for a total of 50 iterations for each imputation in 'MICE' and 50 total iterations, of which we use the final 40 to calculate accuracy metrics.

2.4.3 | Model selection

To assess the impact of management on black-grass dynamics we fit models with different sets of predictors and compare predictive accuracy to identify the best-performing model. As we were interested in assessing the relative impact of the effect of different management practices, we fitted a set of models with management variables categorised into 'groups' of related predictor variables (Table 2). These groups were selected to represent a-priori hypotheses about how management affects weed densities, and their relative importance was assessed by removing a group of predictors and calculating the predictive performance of the reduced model. This allowed us to assess the importance of groups of similar management variables (e.g. cultivation, soil and herbicide applications) for predicting black-grass density. Included in the model set is a model with an interaction term between herbicide susceptibility and herbicide pressure, to test for variable herbicide efficacy with increasing resistance. We fitted two additional models, one that includes all management variables, and one that includes none, to provide baselines for comparison. All models contained terms for density-state effects in the previous year, as well as fixed effect terms for year, and a random intercept for field identity.

Assessing model performance

To assess model performance, we performed *K*-fold cross-validation ($k=5$) at each iteration of the imputation. In each fold 1/*K*th of the data is excluded at random, and a model fit to the remainder. Predictive performance was assessed by predicting the unseen data from the fitted model.

We assessed the predictive performance of our models via logarithmic loss, which quantifies classification accuracy by penalising incorrect predictions:

$$LL = -\frac{1}{N}\sum_{i=1}^{N}\sum_{k=1}^{K} y_{ik}\log\left(p_{ik}\right), \tag{5}$$

where N is the number of samples and K is the number of classes. y is an indicator (0,1) whether the classification is correct, and p is the predicted probability of classifying observation i as class k. As classification accuracy increases, log loss approaches 0. Log loss penalises classifiers more severely if they are more confident of an incorrect prediction (Good, 1952).

After model comparison, we selected the 'best' performing model (i.e. the model with the lowest log loss) and accounted for sampling uncertainty in the estimation of coefficients by simulating 1000 values from the posterior probability of each parameter from each imputation. This was implemented using the '*gam.mh()*' function in 'mgcv'. This function simulates parameter values from the likelihood under the assumption of maximum a posteriori probability

TABLE 2 Terms included in each model compared.

Model	Cropping	Cultivation	Soil	Herbicides	Glyphosate	Susceptibility	Δ drill * season	Δ cultivation * season	Susceptibility * herbicides
No cropping		×	×	×	×	×	×	×	
No cultivation	×		×	×	×	×	×	×	
No Soil	×	×		×	×	×	×	×	
No herbicides	×	×	×			×	×	×	
No susceptibility	×	×	×	×	×		×	×	
No timings	×	×	×	×	×	×			
All management	×	×	×	×	×	×	×	×	
Susceptibility * Herbicides	×	×	×	×	×	×	×	×	×

Note: Terms separated with an * denote the inclusion of both the main effects and interaction between the variables. Field and year terms were included in all models as random and fixed effects respectively.

(i.e. a Bayesian model with uniform priors on all parameters). We then inspected the coefficient values and contributions of the imputation and sampling uncertainty.

2.5 | Sensitivity analysis

To understand the field-scale consequences of management strategies in more tangible terms, we conducted a sensitivity analysis for a range of different strategies under the model. We simulate dynamics using two-step periodic models to examine the sensitivity of weed densities to changes in management across 2 years:

$$n_{t+1} = \mathbf{T}^{m1} n_t,$$

$$n_{t+2} = \mathbf{T}^{m2} n_{t+1}, \tag{6}$$

where $\mathbf{T}^{m1}$ and $\mathbf{T}^{m2}$ represent the transition matrices modelling the set of managements for each step in the projection. We parameterised matrices for each strategy for each of the 97 models selected after imputation and project from an initial density-state distribution where all states are 'low' density. We summarised results by taking the mean density state of all quadrats within a field after each simulation, as this provided a simple summary of whether fields increased or decreased in density. We projected strategies across the range of variation we observed in the management variables (Table S3), as well as every soil type, cultivation, and rotation. For each simulation, non-focal variables were kept constant: with, spray days = 0, autumn glyphosate = 0, susceptibility = 100, soil-type = pelosol, cultivation = conventional, drill season = winter, Δ cultivation = 0, Δ drill = 0, and cropping = wheat → wheat → wheat. The year transition was kept constant, and we simulated strategies using the average field-level effect. This analysis provides the ability to examine the effects of varying management on expected future density states.

3 | RESULTS

The management data used for modelling weed dynamics consisted of 33% complete cases, whilst 34% of observations were missing all management data except cropping, but still had complete records for soil and geographical variables (Figure 2). The final third of the data comprises varied missingness patterns, with high missing frequencies from timing variables. Density state data suffered missingness for approximately 34% of fields in 2015 (Figure S1), most missing observations were in non-cereal crops, primarily OSR. The patterns of missing in the full set of management data (2004–2016, display similar missing patterns (Figure S1)).

Imputation accuracy for management variables removed from the complete cases was high and exhibited only small biases (Figure 3) when compared to the values contained in the data. Cultivation dates were, on average imputed to have values 0.25 days earlier than the true observations, whilst drill dates were half a day later. Herbicide variables (glyphosate and number of spray days), had high accuracy and little bias and susceptibility imputations were on average 5% lower than their respective true values. Cultivation categories however had high mean mAUC scores, demonstrating relatively poor discrimination between categories. This suggests the sets of variables and the structure of the imputation models we chose for imputing missing values were appropriate, and provide plausible values for missing data.

3.1 | Model selection

Including management in models of weed density considerably improves predictive performance as models without management variables perform the worst (Figure 4). The most important management variable is cropping, as removing cropping from the model produces significant decreases in performance (LL = 0.786). Other models were difficult to distinguish between, but removing cultivation, timing, resistance and herbicide variables reduced predictive performance on average. There was no evidence of an interaction between herbicide pressure and susceptibility increasing model performance (LL = 0.783). As it was hard to distinguish between management models, we selected the model containing all management for subsequent analyses.

3.2 | Coefficient estimates

Previous weed densities had the largest effect on current weed density, and higher-density states had large positive effects on weed density (Figure 5, 2nd panel). Interannual effects were also key determinants, as the year effect in 2015 was higher than in 2014 (Figure 5, 3rd panel). Cultivation categories had negligible effects on weed density. Effect sizes for surface, subsoil, and inversion cultivations all had large amounts of uncertainty introduced by the imputation (Figure 5, 4th panel). Herbicide variables had much lower uncertainty and smaller effect sizes. Autumn glyphosate applications had a small negative effect on weed density, whilst increasing overall herbicide intensity was associated with small positive effects on density. The susceptibility coefficient had a relatively large negative value, meaning high susceptibility (low resistance), was associated with lower densities (Figure 5, 5th panel). As the range of levels of susceptibility in populations is high this coefficient will have a large impact on weed density and evolved resistance (low susceptibility) and is therefore a major driver of black-grass population dynamics.

Soil groups all had positive effects compared to the reference category (pelosols) (Figure 5, 6th panel). Soil groups also had larger uncertainty introduced when sampling variability as accounted for. This is also the case for rotation (Figure 5, 8th panel), and numerous low sample size categories exhibited high sampling and imputation variability. However, the effect of each crop on weed density was often more pronounced and most cropping categories had large negative coefficients compared to cropping continuous wheat crops. Notably

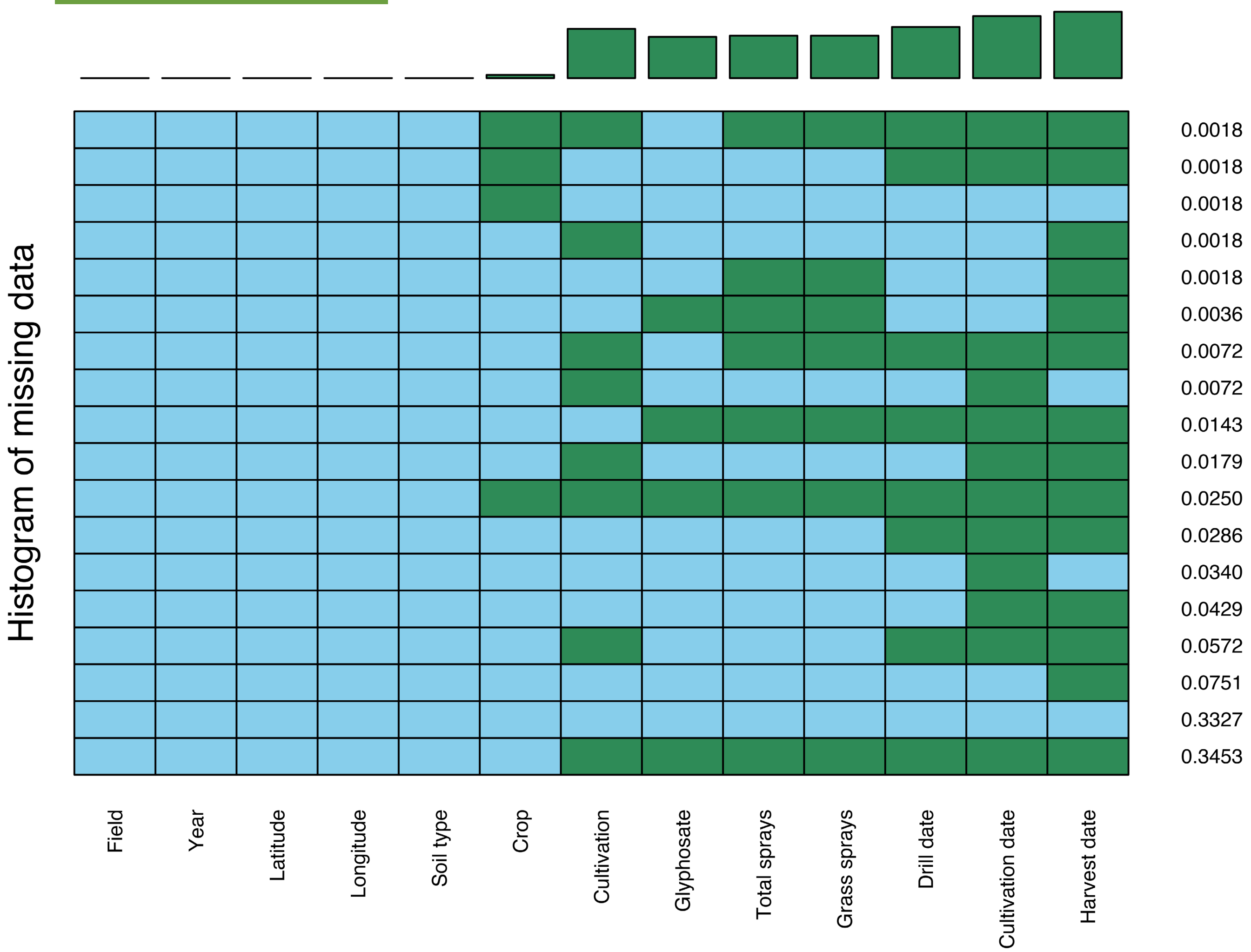

FIGURE 2 Patterns of missingness for variables used in the imputation of missing data between 2014 and 2016. A bar plot of missingness frequencies is displayed above each variable, and indicates the relative proportion of cases where each variable was missing in the full management data. Patterns of missingness (right panel), indicate the relationship between missingness between different variables. Blue indicates cases where cases were observed, and green indicates where a case was missing. Numbers on the right of the figure indicate the total proportion of the data for which the pattern was observed.

cropping barley and sugar beet produced consistent reductions, whilst rotating to beans, oats and OSR generally increased densities.

Timing coefficients (Figure 5, 7th panel) were all associated with large amounts of imputation uncertainty, but all coefficients have noticeable effects on weed density. Drilling in winter produces higher blackgrass densities than drilling in Spring, whilst later drill and cultivation timings will reduce densities further. The interaction coefficients for both drill and cultivation timings with drill season are both positive, meaning that delays to drilling and cultivation in spring result in larger decreases than in winter.

3.3 | Sensitivity analysis

Variability in the effect of management introduced by sampling or the imputation was reflected in the sensitivity analysis, which examined the impact of management on weed density using two-step population projections (Figure 6). For example, different cultivations had negligible impacts on weed density (Figure 6, 1st panel), and only fields with majority of pelosol soils had differentiable weed densities compared to the other three categories. Spring cultivation and drilling provide considerable decreases in density compared to the equivalent management in winter (Figure 6, 2nd panel). However, delayed cultivation and drilling in winter, provide little improvement in control, whilst delayed spring management decreases densities even further than spring drilling and cultivation alone.

Increased glyphosate pressure produces a small difference in weed density between years (Figure 6, 5th panel). Systems with high-intensity herbicide pressure were associated with slightly higher weed densities than low or medium-intensity systems, although also with considerable variability in outcome (Figure 6, 6th panel). Susceptibility to herbicide pressure, however, shows considerable differences between populations with low and high susceptibility. Populations with high prior susceptibility (90%–75% mortality) to herbicides demonstrate low increases in between-year density, whilst populations with low susceptibility (25%–10% mortality), can

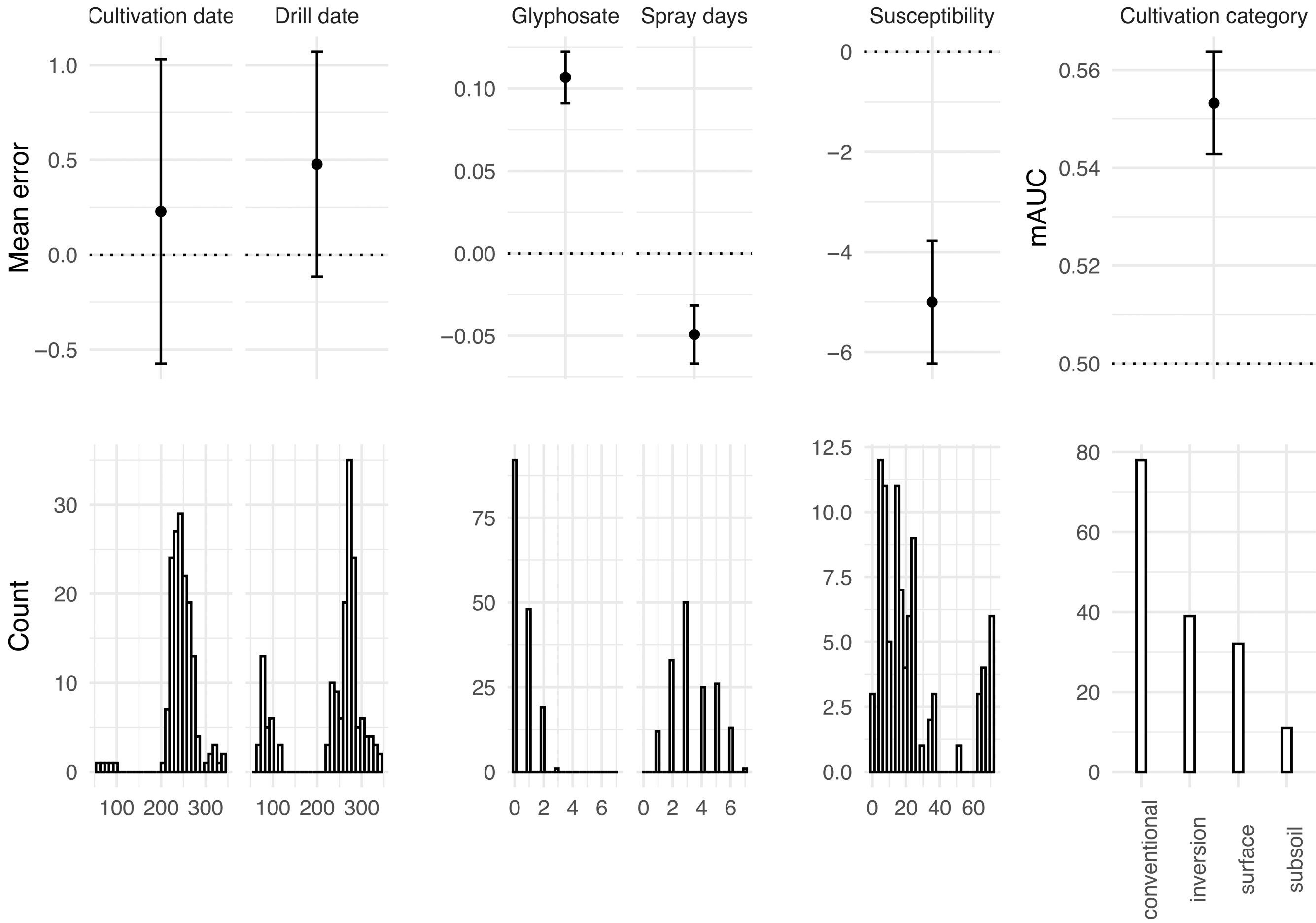

FIGURE 3 The top row illustrates the imputation error for management variables included in the modelling of black-grass density-states. Continuous variable error uses the average absolute error, and categorical variables use a multiple category 'area under the curve' (mAUC). Errors are the average error over 50 total iterations of the imputation cycle. Horizontal dashed lines represent the value at which there is 0 error for continuous variables and the value at which mAUC represents no better than random guessing for categorical variables. The lower row contains histograms that illustrate the distribution of the observed values in each variable.

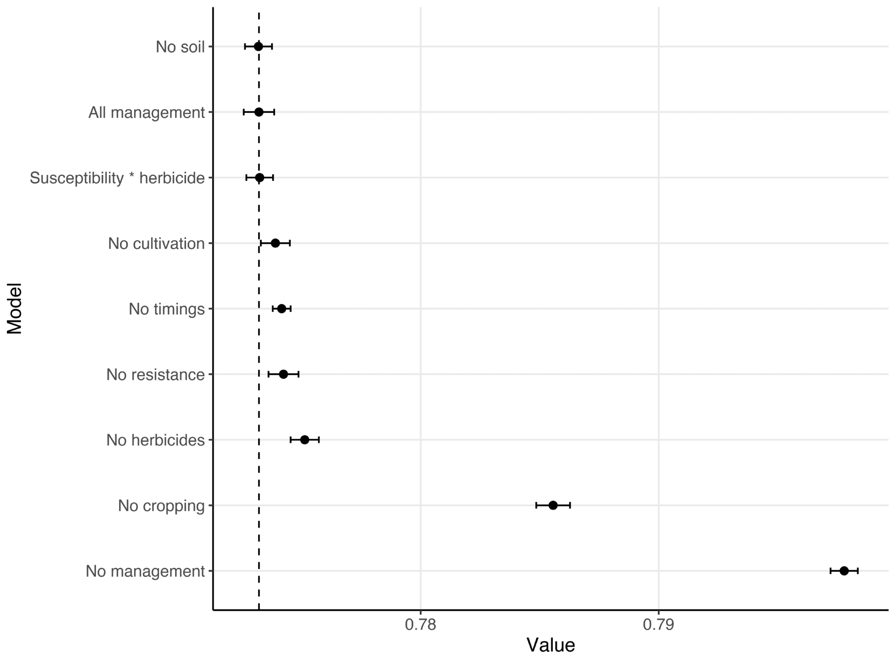

FIGURE 4 Log loss scores for models with groups of management variables excluded. The model with 'No management', only included terms for initial density, year, and a field-level intercept term. Points represent the mean value for each model, and bars are 95% quantile intervals. The dashed vertical line represents the mean log loss for the model with all management variables included. The model including an interaction term between herbicide and resistance is labelled 'Susceptibility * herbicide'.

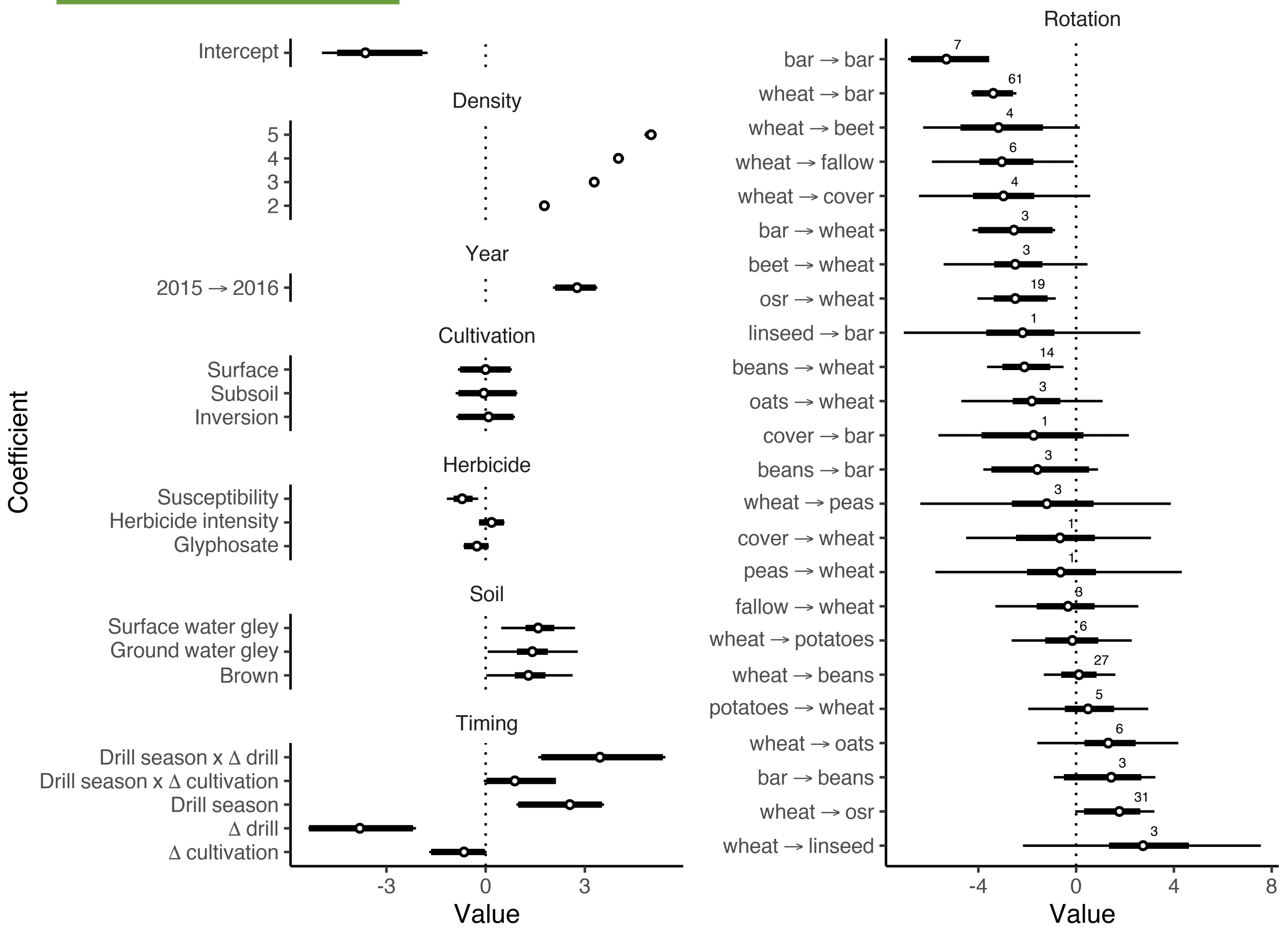

FIGURE 5 Distributions of management variable coefficients estimated from scaled covariate data from the model including all management variables. Distributions represent imputation and sampling error and are calculated from 1000 sets of coefficients sampled from the posterior estimates of models fitted from 97 imputed datasets. Thick bars are the 90% quantile interval for the uncertainty in coefficient estimates introduced by imputation, thin bars are the 90% quantile interval for the combined imputation and sampling uncertainty. Terms separated by an arrow represent the effect of those terms during the transition from 1 year to the next. Numbers next to each rotation represent the number of fields observed in each category. Density state, cultivation, soil, and rotational variables were estimated with respect to a reference level, which were 'Absent', 'Conventional', 'Pelosols' and 'Wheat → Wheat', respectively.

exhibit cases where fields are predicted to have fields that consist mostly of high or very high-density states (Figure 6, 7th panel).

Rotational strategies also provided clear differences in weed control (Figure 7). Rotations containing barley and beet produce low-density populations with little variability. Beans and OSR, provide slightly higher densities, with higher variability in outcome. Wheat and OSR, result in higher density weed populations, averaging on around 5% of quadrats increasing in density, this is accompanied by high variability in outcome, with some populations displaying over 10% of quadrats increasing in density to high or very-high-density states.

4 | DISCUSSION

We have presented a framework for incorporating management, environmental, and herbicide resistance covariate data into empirically backed models of population dynamics, whilst accounting for the uncertainty produced by missing data. To our knowledge, this study is the first of its kind to use data of this scale and variety to model population dynamics, and the first to link the effect of herbicide resistance on regional-scale weed dynamics using extensive empirical data. This study is unique in terms of scale and the number of populations, meaning the estimates of management and environment are likely generalisable across a wide spatial extent. Consequently, this study represents an important step towards the goal of quantifying the drivers of population dynamics at the scales which are relevant for robust management over environmental and biotic gradients.

We highlight two major challenges facing the management of populations. First, we demonstrate considerable variability in responses to management, highlighting the need to collect data that span the range of environmental conditions over which organisms exist. Second, owing to the frequently incomplete nature of large-scale surveys, analysis must be integrated with methods to deal with the bias and uncertainty caused by missing data.

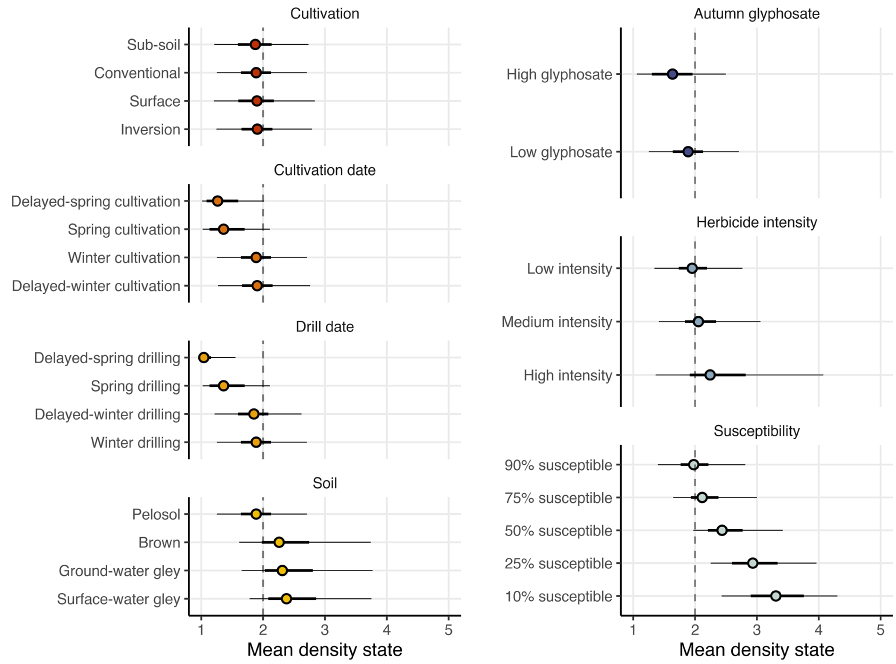

FIGURE 6 Sensitivity analysis of the impact of different management variables on weed density, including cultivation, soil type, herbicide pressure, timings, and herbicide susceptibility. The figure displays the results of a two-step density-state projection to assess the sensitivity of weed densities in response to varying management conditions. Points are the mean density state across the simulated field, and thick and thin bars are 50% and 90% quantile intervals respectively. Intervals represent the combined uncertainty introduced by the imputation of missing data and sampling uncertainty simultaneously. Dashed vertical lines represent the initial mean density of the field before simulating management strategies.

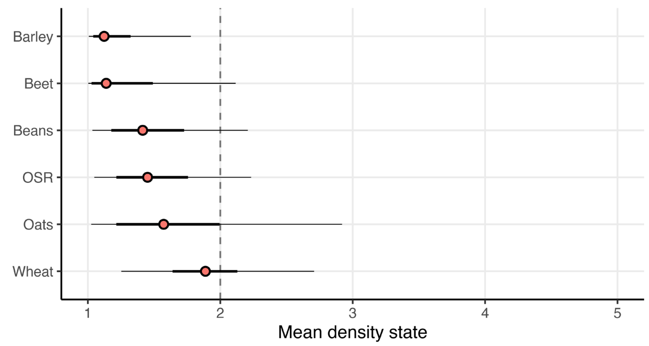

FIGURE 7 Sensitivity analysis of the impact of different rotations on weed density. Points are the mean density state across the simulated field, and thick and thin bars are 50% and 90% quantile intervals respectively. Intervals represent the combined uncertainty introduced by the imputation of missing data and sampling uncertainty simultaneously. The dashed vertical line represents the initial mean density of the field before simulating rotational strategies.

4.1 | Impact of management on weed control

A large suite of techniques has been developed to control black-grass populations (reviewed in Lutman et al., 2013). It can be difficult to untangle and measure the effectiveness of such interventions in reducing weed population sizes, with models providing an efficient way to interrogate data (Freckleton et al., 2018). We applied this approach to quantify weed responses to a suite of common interventions used to control black-grass population size. Although we demonstrate that many controls have modest effects on population growth, our analysis provides a thorough quantification of the impact and uncertainty associated with managing weed populations. This study provides a useful baseline for farmers to plan strategies to minimise the damage done by one of Europe's most pervasive pests.

In our analyses, the most effective option for reducing weed population variables is cropping, which is consistent with several previous quantitative studies of black-grass control (Goodsell et al., 2021; Lutman et al., 2013). Whilst cultivation and herbicide applications have noticeable but smaller effects on weed density compared to cropping, rotations are often collinear with particular management strategies (Figures S5 and S6). A potential consequence is that much of the variation in weed density produced by managements such as herbicides, cultivations, and timings could be aliased by crop rotation. For example, a common strategy for black-grass control is a spring barley or sugar-beet rotation, which involves later drill dates to time herbicide application with the phenology of the weed, and allow more intensive cultivations (Chauvel et al., 2001). Similarly, Freckleton et al. (2018) show that different practices are applied to fields with high and low densities of weeds, which can mask effects.

Counter-intuitively, increased herbicide pressure was associated with slightly higher weed densities, albeit with considerable uncertainty. This is a pattern also reported by Champion et al. (2003) in another large-scale survey. A likely explanation is that post-emergence herbicide application, unlike most other managements, is adjusted depending on the weed densities observed within a field by the farmer. In this case, we would expect to see higher applications associated with higher densities, as the decision to apply high herbicide pressure is made after initial densities are measured. This may also explain the lack of evidence for any meaningful interaction between herbicide pressure and susceptibility, as there would be few cases where highly susceptible populations will require multiple treatments. This pattern highlights a major limitation for many applied ecological studies, where complex causal relationships exist between response and explanatory variables (Grace, 2016; Hooper et al., 2005). The consequence is that precise causal relationships are difficult to unpick in the framework we present, and any results should be considered carefully. In our case, the estimates of the effect of herbicide pressure are logically not the true causal effect.

Similarly, precise resolution of the effect of herbicide resistance may also be hindered by growers changing management strategies in response to evolved resistance. Specialised methods designed to determine causal relationships between explanatory and response variables have been used in applied ecological studies (Butsic et al., 2017; Dee et al., 2023; Grace, 2021), integrating them into a framework that also accounts for missing data and environmental heterogeneity is challenging but a worthwhile avenue for future research.

Glyphosate intensity shows the expected relationship, with higher intensities resulting in lower weed densities. As delayed drilling and cultivation in spring provide consistent reductions in density, this suggests that farmers are relying heavily on glyphosate in combination with spring drilling to see continued control of weed populations. Unfortunately, due to the increasing rate of evolved resistance to chemical controls (Comont et al., 2019), continued reliance on herbicides is not sustainable. Our analyses conclusively demonstrate how populations with high susceptibility to herbicides have much lower population growth rates than fields with low susceptibility to chemical controls. Whilst studies of population dynamics have often relied on simulations with the effect of resistance being assumed or based on limited empirical data (Diggle & Neve, 2001; Osipitan et al., 2019; Richter et al., 2002), ours is the first application of extensive empirical data, to quantify the impact of resistance on future weed population sizes. A key focus for farmers will be to assess resistance levels to properly gauge how infestations will change over time. It is important to note that we treat resistance as static over the course of the study period, when in reality it is likely to increase over time. Although the evolution of resistance can be rapid (Mohammad et al., 2022; Neve & Powles, 2005a, 2005b) over the time period of our study (2 years) the magnitude of these changes is likely to be limited (Comont et al., 2019; Davies & Neve, 2017; Hicks et al., 2018).

Evaluating alternative weed controls is increasingly important to circumvent the problems caused by evolved herbicide resistance, as well as safeguard herbicide efficacy for the future (Bagavathiannan et al., 2019). Here, we have not been able to provide conclusive evidence that common non-chemical control options, namely cultivation, have meaningful impacts on weed density over regional scales. This may be due to the coarse measure we used (Colbach et al., 2005; García De León et al., 2014; Lutman et al., 2013; Weber et al., 2017), in combination with variability introduced by environmental dependencies and missing data. To further resolve the impact of cultivation, it will be necessary to gather more consistent and detailed information on measures of cultivation intensity, such as tillage depth and frequency.

4.1.1 | Regional scale population dynamics

This work corroborates previous regional scale studies that find these systems characterised by high variability at the field level and marginal effects of management on population growth rate (Freckleton et al., 2018; Goodsell et al., 2021). In an applied setting, assessing population dynamics across the full geographic extent of an organism is extremely important, as without accounting for the variability in population dynamics at local scales, it becomes difficult to design robust strategies for all locations at which organisms occur (Caughlin et al., 2019; DeMarche et al., 2019). We accounted for environmental variability through hierarchical modelling of field-level effects and included a coarse variable to account for soil composition. However, there are several climatic variables which are important drivers of plant abundance and distribution and should be considered for future efforts (Colbach et al., 2006; Freckleton & Watkinson, 1998; Hicks et al., 2021; Lima et al., 2012; Peters et al., 2014; Tredennick et al., 2016). There is also considerable potential for interactions between the environment and management to affect population dynamics (Paniw et al., 2017; Tye et al., 2016). For example, the effect of weather could have drastic impact on the efficacy of herbicide applications. It's been demonstrated that temperature and humidity directly impact herbicide efficacy on application (Johnson & Young, 2002) and growing conditions can affect how vulnerable weeds are to applications (Riethmuller-Haage et al., 2007). Future assessments of management on regional-scale plant population dynamics should include more comprehensive environmental drivers and interactions with management.

4.2 | Imputation of missing data

Imputing missing observations was an essential step to allow evaluation of the impact of management on weed density across the appropriate scale. Excluding missing data would have reduced the dataset to a fraction of its original size and severely reduced the power of our analyses. Across all three data sets (management, resistance, and density states), we had complete management and resistance data for only 15% (13,678 out of a possible 86,680) of cases. Moreover, of this 15% of data, only 13 fields had observations in concurrent years necessary for evaluation of the impact of management, further reducing the size of the data down to only 7191 observations of weed density. Multiple imputation of missing data allowed us to leverage a much larger data set than otherwise possible. The bespoke approach we take here provides additional value; by leveraging the target of our analyses, a density-structured model of dynamics, we can incorporate our understanding of dynamics to provide information about missing drivers. This approach is also transferable to other common systems where dynamics are modelled as Markovian systems, for example, matrix or integral projection models. Our population-model-based multiple imputation approach holds considerable value for future studies in applied ecology, firstly as a tool to account for bias and uncertainty in incomplete data, but also to leverage the full value of data collected to understand the population dynamics of pests or species of conservation concern (Conde et al., 2019).

To conclude, our study provides an important advance towards managing populations over large scales and with high frequencies of missing management data. We provide estimates of the effect of common management practices on weed density that may allow farmers to plan effective interventions, using cropping and the timing of interventions to reduce weed numbers. Importantly we highlight that evolved resistance to herbicides is strongly associated with high population growth across regions, demonstrating the need to develop non-chemical options as well as safeguard the future efficacy of chemical control. It is also important that we begin to develop more thorough models of the effect of environmental variables on weed density to better inform management. Overall, our study has demonstrated that understanding the impact of management drivers on regional-scale plant dynamics involves overcoming multiple challenges. Primarily being able to identify the effect of interventions in the context of high variability introduced by imperfect data collection and high environmental variability. We demonstrate the impact of this variability on predicting plant dynamics over large spatial scales and highlight the need for effective planning of data collection from managers and for plant abundances.

AUTHOR CONTRIBUTIONS

Robert M. Goodsell, Dylan Z. Childs, David Comont, and Robert P. Freckleton, devised the concept and analytical components of the study. Robert M. Goodsell carried out the analysis and wrote the manuscript. David Comont, Helen Hicks and Richard Hull provided agronomical and ecological expertise whilst writing the manuscript. Helen Hicks, James Lambert, Richard Hull, Laura Crook and David Comont collected the blackgrass density, management, and herbicide resistance data. Paulo Fraccaro and Katharina Reusch provided editorial support during writing.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflicts of interests.

DATA AVAILABILITY STATEMENT

Data and code available via the Data Dryad Digital repository (Goodsell et al., 2023): https://doi.org/10.5061/dryad.9cnp5hqn5.

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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: Patterns of missingness for variables used in the imputation of missing data.

Figure S2: The predictor structure used in the imputation of management data.

Table S1: The variables included in the imputation of missing management data.

Table S2: Variables included in the imputation of missing susceptibility data.

Table S3: Simulation parameters for projections of weed density under varying herbicides intensity, glyphosate applications, susceptibility to herbicides, and changes in timing of drilling and cultivation.

Figure S3: The proportion of 2015 fields in each crop that had observed (A) or unobserved (B) density states.

Figure S4: The mean value of glyphosate, total spray days, cultivation date, and drill date for each crop observed in our management data.

Figure S5: The proportion of each crop observed across each soil group (upper panel), and cultivation (lower panel).

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