Supplementary Information

The costs of human-induced evolution in an agricultural system

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Supplementary Methods

Estimating the yield penalty

To estimate the relationship between black-grass density and the yield of winter wheat, we use a dataset of 17 fields spanning four years (2014-2017), with recorded black-grass density state for each 20m by 20m grid square (total *n* = 4903 grid squares), and estimates of average yield for each of those grid squares (see Hicks et al 2018[1]). Yield data were obtained from combine harvester records.

Not all fields were planted in winter wheat in every year, thus for some fields we have multiple years of data (maximum = 3 years) and for other fields we have only one year of data. In addition, not all density states were observed in every field due to variability in black-grass status between fields (Supplementary Figure 1). To appropriately deal with this unbalanced structure in our data we used a mixed effects model. To capture any potential non-linear response of yield to black-grass density, while not over-parametrising the model, we treated density state as an ordered categorical variable (where density state 'low' = 0, and 'very high' = 3) and fit the model to a 2[nd] order orthogonal polynomial representation of this ordered density (called D_{p1} and D_{p2}). We fit the mixed effects model

$$y \sim D_{p1} + D_{p2} + (1|\text{year}) + (D_{p1} + D_{p2}|\text{field})$$ *('mixed eff.poly',* Supplementary Figure 1)

where

y is the yield of winter wheat in t ha^{-1};

(1|year) denotes that we fit a random intercept for each year (*i.e.* we assume the effect of density is constant across years within each field);

(D_{p1} + D_{p2}|field) denotes random intercepts and slopes on the 2[nd] polynomial representation of black-grass density (*i.e.* the effect of black-grass density can change between fields).

Residual plots indicate that model assumptions were met (Supplementary Figure 2). The data do not support less-constrained models that would allow slopes on black-grass density to vary between years within each field: singularity tests on the covariance matrices of these models suggest they are over-fit to our dataset, returning *yes* in each case.

This random effect model provides an estimate of the marginal effect of black-grass density on winter wheat yield, conditional on the effect of field and year (Supplementary Table 1), giving us the appropriate average effect of black-grass density on yield across years and fields (Figure 1a, main text).

Average winter wheat yield at low and medium black-grass densities was just over 9 t ha^{-1}. This decreased to 8.5 t ha^{-1} at high densities and 6.9 t ha^{-1} very high densities (Supplementary Table 2). There is a high degree of uncertainty around these average yields due to the large amount of variability between fields (Supplementary Figure 1). High and very high density states were only observed together in ten of the 17 fields. At these density states, we see wide variation in the effect of black-grass: most fields show a modest effect, declining by 1-2 t ha^{-1} at very high densities. However, two fields (6 and 8) show a very big effect of black-grass with very high densities causing yield reductions of 38% and 69% respectively. This wide variation is consistent with empirical studies of the effect of black-grass on yield[2–9]. Because of the high variability between fields we ran a sensitivity analysis on the yield loss function, described later in this document.

The resulting yield penalties are given in Supplementary Table 1. At medium density, the model-estimated yield loss was -1.1%; however, of the 14 fields for which both the reference state (low density) and the medium density state were observed, 9 had negative estimates and 5 had positive estimates and the 95% confidence intervals on the medium density state include 0. This suggests that there is no mean effect on yield at medium densities.

To test the effect that the modelling approach had on the yield estimates, we also fitted two fixed effects models equivalent to the mixed effects models, except that they do not estimate the marginal effect of black-grass density across fields and years. We again fit a model to a second order polynomial representation of black-grass density state. We term this the fixed effects polynomial model:

$y \sim D_{p1} + D_{p2} + \text{year} + D_{p1}\text{:field} + D_{p2}\text{:field}$ (*'fixed eff.poly',* Supplementary Figure 1)

We also fit a fixed effect model where density state was represented as a categorical variable:

$y \sim D + \text{year} + D\text{:field}$ (*'fixed eff.cat',* Supplementary Figure 1)

We compare the yield estimates on a field-by-field basis, for each year, for all three models (Supplementary Figure 1). We use the same parametric bootstrap process as for the mixed effects model to estimate 95% confidence intervals on the yield estimates from these other two models. For each field in each year we see that the mixed effects model and the two fixed effects models have very similar estimated yields (Supplementary Figure 1): we are therefore confident of the robustness of the yield penalties estimated using a mixed modelling framework. Because of the structure in our data it was not appropriate to estimate density effects for an 'average' field using either of the fixed effects models.

Scaling up cost of resistance (C_R) in winter wheat

For winter wheat, scaling up involved the following steps:

1. Winter wheat area by region and for England was obtained from DEFRA (2014 figures).
2. We calculated an average black-grass density state for each of the 138 fields surveyed for weed density (Supplementary Figure 3b).
3. We then calculated what proportion of our fields were in low, medium, high and very high density states. We did this for England and for UK government office regions.
4. We used these proportions to calculate the relative winter wheat area in each of the four black-grass density states, both for England and for regions (Supplementary Figure 3c).
5. Using the data from step 2, we calculated the mean per hectare C_R for each density state (Supplementary Figure 3b). We also did this on a regional basis.
6. This per hectare C_R at each density state was then multiplied by the winter wheat area in each density state calculated in step 4. Confidence intervals (95%) were calculated using bootstrapping.

Thus, using the cost of resistance in winter wheat ($C_{R\,ww}$) in the low density winter wheat area in the East Midlands (EM_{low}) as an example:

$$\text{Total } C_{Rww}\, EM_{low}\ (£) = \text{mean } C_{Rww} \text{ in fields with low density state, East Midlands } (£/ha) \times (\text{winter wheat area EM} \times \text{proportion of fields low density in EM})\ (ha) \qquad (1)$$

This was repeated for other density states in a region, then the total costs for the area at each density state were summed to give the total cost in that region. Thus, for the East Midlands:

$$\text{Total } C_{Rww},\ EM\ (£) = \text{total } C_{Rww}\, EM_{low} + \text{total } C_{Rww}\, EM_{medium} + \text{total } C_{Rww}\, EM_{high} + \text{total } C_{Rww}\, EM_{veryhigh} \qquad (2)$$

Scaling up cost of resistance (C_R) over a rotation

The C_R over a rotation was scaled up using a similar method, except that crop areas were not divided into areas of different density states as we have no information about density states in crops other than wheat. The steps for up-scaling rotation costs of resistance were therefore as follows:

1. Crop area by region and for England was obtained from DEFRA (2014 figures).
2. We calculated a mean per hectare C_R for each field, across all the years for which we had data for a field (therefore across all crops).
3. We then calculated a mean per hectare C_R for each region.
4. The mean per hectare C_R was then multiplied by crop area. 95% CIs calculated by bootstrapping.

BGRI-ECOMOD model description and use

Land use or farm management strategies adopted by arable farmers influence the economic outcomes of arable farming systems. Models can be useful to estimate these economic outcomes. Here, a farm- (or field-) level model ("BGRI-ECOMOD") was developed to evaluate the economic consequences of changes in land use or farm management, focusing on Black-grass (*Alopecurus myosuroides*) mitigation strategies. The model was developed based on the assumption that black-grass mitigation strategies influence the economic outcome of the associated crop enterprise. BGRI-ECOMOD performs gross margin analyses by estimating the gross profit (gross margin less operations costs) associated with crop enterprises in different years. The model incorporates the effect of variables such as soil type, sowing date, tillage practices and yield penalties associated with crop sequences. The model also allows the application of yield penalties due to black-grass infestation. The model was developed to allow for the analysis of 13 crops plus set-aside (fallow):

- winter & spring wheat (*Triticum aestivum* L.)
- winter & spring barley (*Hordeum vulgare* L.)
- winter & spring beans (*Vicia faba* L.)
- peas (*Pisum sativum* L.)
- winter & spring oilseed rape (*Brassica napus* L.)
- winter & spring linseed (*Linum usitatissimum* L.)
- sugar beet (*Beta vulgaris* L.)
- ware potatoes (*Solanum tuberosum* L.)

The model was written using the R programming language[10]. Model assumptions are incorporated in the model code. Management data is read into the model from operator-created CSV files, a template of which is provided. The template, and all model parameters, are available at https://github.com/alexavarah/BGRI-ECOMOD.

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Estimation of BGRI-ECOMOD outputs

The evaluation of the economic consequences of farm management strategies aimed at black-grass control is based on the gross profit per hectare for each crop enterprise in a year, which is the gross margin less fuel and labour costs. The equations below show how the various model output components were estimated.

$$Output\ (£/ha) = (Crop\ Yield\ (t/ha) - YL) \times Crop\ Price\ (£/t) \tag{3}$$

where YL is yield loss due to delayed sowing, rotational and continuous cropping penalties.

$$\begin{aligned} Fertiliser\ Cost\ (£/ha) \\ &= \big(N\ Fertiliser\ Rate\ (kg/ha) \times N\ Fertiliser\ Price\ (£/kg)\big) \\ &+ \big(P\ Fertiliser\ Rate\ (kg/ha) \times P\ Fertiliser\ Price\ (£/kg)\big) \\ &+ \big(K\ Fertiliser\ Rate\ (kg/ha) \times K\ Fertiliser\ Price\ (£/kg)\big) \end{aligned} \tag{4}$$

$$Seed\ Cost\ (£/ha) = Seed\ Rate\ (kg/ha) \times Seed\ Price\ (£/kg) \tag{5}$$

$$\begin{aligned} Herbicide\ Cost\ (£/ha) = {} & \big(Total\ Application\ Rate\ of\ Other\ Chemicals\ (l/ha) \times \\ & Average\ Price\ of\ Other\ Chemicals\ (l/ha)\big) + \\ & \big(Glyphosate\ Application\ Rate\ (l/ha) \times \\ & Glyphosate\ Price\ (£/l)\big) \end{aligned} \tag{6}$$

$$\begin{aligned} Variable\ Cost\ (£/ha) = {} & Fertiliser\ Cost\ (£/ha) + Seed\ Cost\ (£/ha) + \\ & Herbicide\ Cost\ (£/ha) + Sundry\ Cost\ (£/ha) \end{aligned} \tag{7}$$

where $HerbicideCost$ is the cost of herbicides specifically targeting black-grass (other herbicide costs are incorporated into sundry costs).

$$Gross\ Margin(£/ha) = Output\ (£/ha) - Variable\ Cost\ (£/ha) + Subsidy\ (£/ha) \tag{8}$$

$$Fuel\ Cost\ (£/ha) = Work\ Rate\ (h/ha) \times Fuel\ Consumption\ (l/h) \times Fuel\ Price\ (£/l) \tag{9}$$

$$Labour\ Cost\ (£/ha) = Labour\ Work\ Rate\ (h/ha) \times Hourly\ Labour\ (£/h) \tag{10}$$

$$Operations\ Cost\ (£/ha) = Fuel\ Cost\ (£/ha) + Labour\ Cost\ (£/ha) \tag{11}$$

$$Gross\ Profit\ (£/ha) = Gross\ Margin\ (£/ha) - Operations\ Cost\ (£/ha) \tag{12}$$

$$Rotation\ Probability = \frac{1}{Length\ of\ Rotation} \tag{13}$$

$$Rotation\ Gross\ Profit\ (£/ha) = Gross\ Profit\ (£/ha) \times Rotation\ Probability \tag{14}$$

$$Total\ Rotation\ Gross\ Profit\ (£/ha) = \sum Rotation\ Gross\ Profit_j\ j = 1, \ldots 6 \tag{15}$$

where $Rotation\ Gross\ Profit_j$ is the rotation gross profit of a crop in year j (maximum length of rotation assumed = 6).

Adjustment to crop yields due to rotational and delayed sowing penalties

Delayed sowing and certain crop sequences or rotations are associated with yield penalties (percent yield loss). Adjustments are therefore made to any yield estimated under scenarios of delayed sowing or rotations/crop sequences considered to be sub-optimal. These adjustments are based on a yield response function. The yield loss (*YL*) due to delayed sowing or rotation/crop sequencing is estimated as shown below and deducted from the estimated base yield. For percentage reductions see 'BGRI_ECOMOD_Data.xlsx' at https://github.com/alexavarah/BGRI-ECOMOD. This adjusted yield is then used in estimating the output.

$$YL = Estimated\ Yield\ (t/ha) \times Yield\ Penalty\ (\%) \quad (16)$$

Model flexibility

To ensure flexibility in BGRI-ECOMOD, model input is given in the form of a data frame (created in a CSV file) from which data is automatically extracted and used to estimate the various components of the model outputs. Thus, potential users have the flexibility to change or set the model inputs to any value required. Furthermore, we set the model up so that most model inputs are entered as independent vectors whose length corresponds to the maximum length of rotation (6 years). Thus, the parameters in the first position of each input vector correspond to the management choices made in the first year. This was instead of associating certain model inputs to particular crops, which restricts flexibility. The exception is the machine size vector which is of length five to reflect the main machine types considered in the model.

There are two possibilities for the type of crop yield data used in the model: (i) it can be estimated based on a response function which takes into account the soil type and N fertiliser rate (kg[N]/ha); (ii) the user can provide crop yield data. The condition below is thus set in the model.

$$Crop\ Yield\ (t/ha) = \begin{cases} actual, if user\ provided \\ estimated, if\ yield\ response function\ is\ used \end{cases}$$

$$YL = \begin{cases} 0\ if\ crop\ yield\ is\ user\ provided \\ \geq 0\ if\ crop\ yield\ is\ estimated \end{cases}$$

There are also options for indicating the tillage methods (*i.e.* ploughing, subsoiling etc.), the number of spraying days, whether there was delayed sowing, the level of black-grass infestation, as well as indicating whether the farmer receives income support payments. In terms of the rotation probability, it is estimated based on the length of rotation set by the user or a value can be set independent of the length of rotation.

There are two scale options for running the model: (i) it can be run for a single field, or (ii) it can be run for multiple fields. To ensure the model generates some results when run for a single field, default data have been incorporated into the model. This default data is not used when running the model for multiple fields. For multiple fields, the model input data must be organised in a CSV file with column headings corresponding to the model inputs. The data in the CSV file is then automatically called into the model. A template of the input file is provided at https://github.com/alexavarah/BGRI-ECOMOD. N.B. the soil data MUST have two decimal places. These are sometimes lost when converting from Excel to CSV.

BGRI-ECOMOD data and data sources

BGRI-ECOMOD was developed to give the user maximum flexibility. As a result, only a limited set of generic values were incorporated into the model. These values include work rates for different farm operations, yield penalties due to the level of black-grass infestation, delayed sowing, crop rotation/ sequences and sundry costs with respect to the crop types defined for the model. All values and data sources for the above-mentioned model parameters, and for the default data, are given in 'BGRI_ECOMOD_Data.xlsx' (see GitHub link above).

How to use BGRI-ECOMOD

Data is called into the model from a user-created CSV file. All model inputs are listed in 'BGRI_ECOMOD_Data.xlsx' at https://github.com/alexavarah/BGRI-ECOMOD. Crop types and tillage methods need to be entered in the input CSV file as specified in the 'Crop & Tillage Labels' sheet of 'BGRI_ECOMOD_Data.xlsx'.

To run the model for multiple fields (lines 4133 – 4153 of the R script):

1. Set the working directory to wherever you have saved the model input data.
2. Allocate a name for the model output file: in the model code provided this is given as 'OUTPUT.csv'. Equate this to *fn* at line 4140.
3. Organise your input data in a CSV file (template provided on GitHub). The name of this file must be equated to *fd* in line 4143 of the code. In the model code provided this is given as 'INPUT.csv'.
4. Set the other parameters at lines 4151-4153:
    - *farm* should be "multiple";
    - *rotlength* should be whatever the rotation length in your data is;
    - *rotprob*: the rotation probability is estimated based on *rotlength*; however, to set rotation probability independent of rotation length, *rotprob* can be set to 1/*x*, where *x* is a user-specified number;
    - *subsidy* indicates whether the farmer is receiving Single Farm Payment ("yes" or "no");
    - *yieldoption* tells the model to run using either measured yield data ("actual"; in which case yield values must be provided in the CSV input file), or estimated yield based on yield response functions ("estimate").

To run the model for a single field (lines 4095 – 4130), *filename* and *farmdata* must be set to NULL and *farm* set to "single". Set the soil index as specified in sheet 'Soil Index & Farm Data' in 'BGRI_ECOMOD_Data.xlsx'. *rotlength* can be specified by the user; if unspecified, the default rotation length is 6, corresponding to the length of the crops vector. If the user wishes to use ECOMOD's default field data, set default="yes" in line 4128; otherwise, to use one's own data, un-comment lines 4103 – 4126, write in your own data, and set default=NULL at line 4128.

BGRI-ECOMOD evaluation

We evaluated model estimates of yield (see Methods and Supplementary Figure 4) and model estimated gross margins. Using Farm Business Survey[11] (FBS) cereal farm data, we extracted the gross margins from crops (*i.e.* from agriculture) and the gross margin from Single Farm Payment (SFP). This was done for each government office region. These crop and SFP gross margins were added together to give one gross margin (agriculture and basic payment) per cereal farm. For each Government Office Region, we then calculated mean gross margin and 95% confidence intervals.

We compared ECOMOD model estimates with FBS-derived regional gross margins 2014. In both FBS and ECOMOD, gross margin is estimated per crop enterprise; however, ECOMOD also incorporates fuel and labour costs associated with each crop enterprise (*i.e.* gross margin minus crop-specific operations costs). The difference was not expected to put ECOMOD estimates outside the range of FBS estimates, and this was found to be true. A second consideration was that we used crop prices from NIX 2014 in the ECOMOD input data. These prices proved to be optimistic in their predictions of farmgate prices. We therefore expected our estimates of gross margin to be higher than those from FBS data; nevertheless, the values estimated by ECOMOD fall within the 95% CI range of FBS values for each region (Supplementary Table 4).

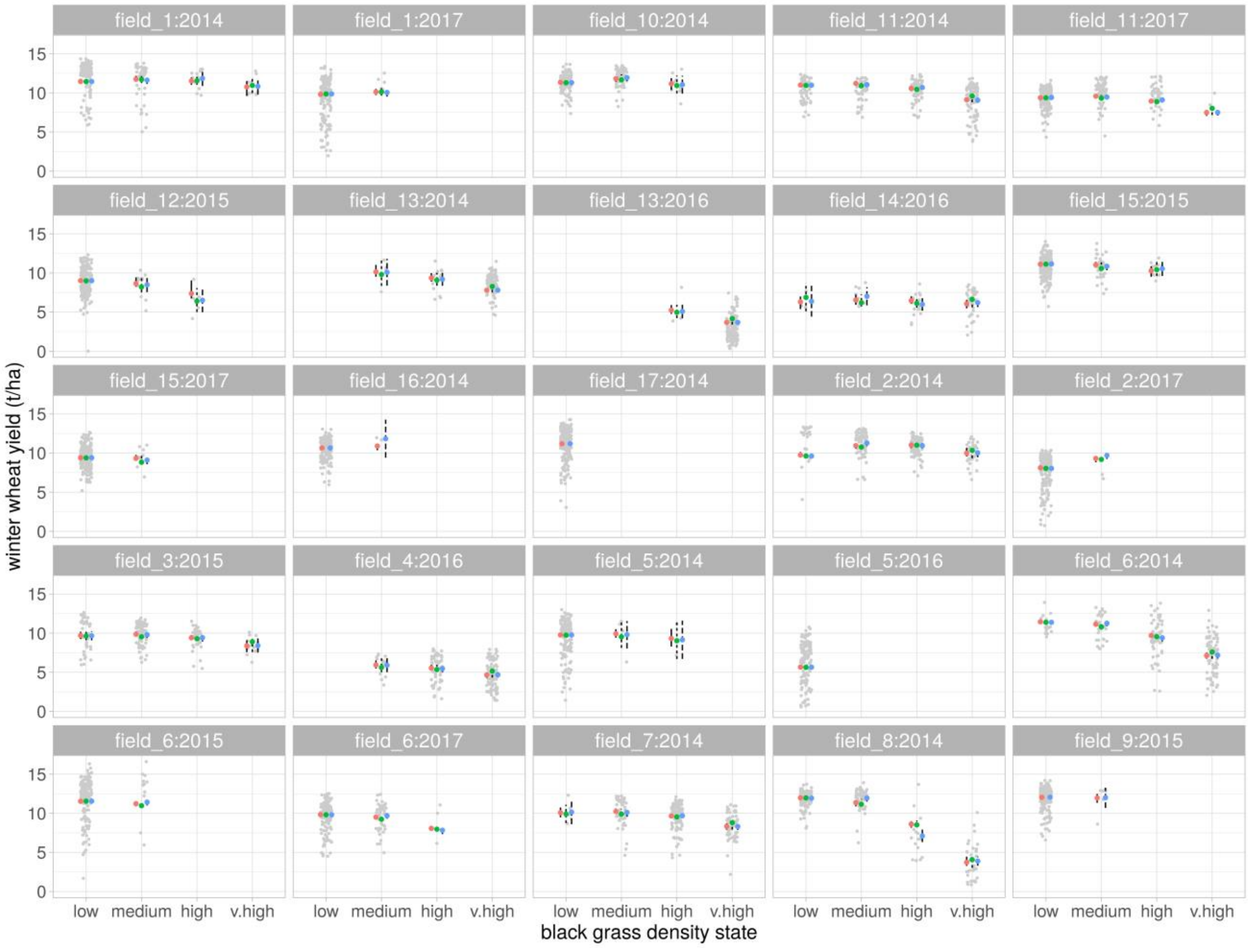
Sensitivity analysis – yield penalty

We applied a yield penalty to winter wheat crops to account for the competition effect due to different densities of black-grass. However, the effect on yield – especially at high and very high density states – was very variable, resulting in uncertainty in the yield penalties applied. We carried out a sensitivity analysis to assess the effect of this lack of certainty. The limits used in this sensitivity analysis (Supplementary Table 10) do not come solely from our data as, despite it being the most spatially explicit dataset available, it remains a limited dataset of 17 fields. We are therefore uncertain about the limits estimated solely from our data; thus, we started with limits obtained from our data and then used the literature to assess whether these limits were wide enough.

We used our model to estimate the percentage reduction in yield at each density state in each field. We then used the confidence intervals around those estimates to inform the likely limits in our sensitivity analysis (Supplementary Table 10). We excluded fields 4 and 13 from this process as the low density reference state was not observed (see Supplementary Figure 1).

We observe most variability in the high and very high density classes. In our data, yield loss ranges from 13% – 68.9% at very high densities of black-grass (Supplementary Table 10). In empirical studies in the UK (Supplementary Table 3), high black-grass densities reduced wheat yield by 13%[2], and very high black-grass densities reduced wheat yield by 29-32%[2], 13-35%[3], 9-19%[4] and, in an unpublished trial quoted in a more recent paper, 47%[8]. A study in Greece found that very high black-grass densities caused wheat yield reductions ranging from 10 to 30%[5]. In Poland yield was 53-61% lower in untreated plots compared to treated plots[9], and they also quote an earlier UK study where moderate black-grass populations reduced wheat yield by 45%. In a 2003 UK study which collated data from a series of competition trials of winter wheat and black-grass[7], maximum yield losses of 60 – 70% were seen at very high black-grass densities (that study, like ours, also showed a great deal of variation in yield loss). We are therefore confident that, at the very high density state, limits of 0-70% are sufficiently extreme.

Supplementary Figures



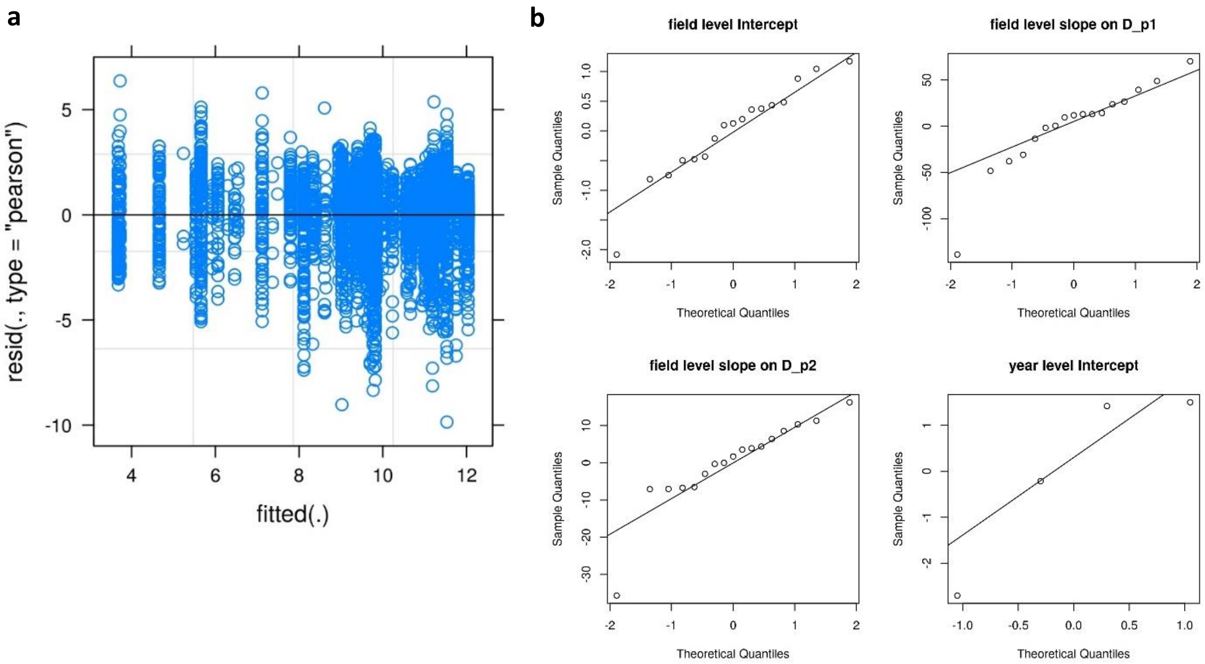
Supplementary Figure 1 | Observed winter wheat yield and black-grass density state of each 20m by 20m grid square (grey points, jittered to aid visualisation) from 17 fields across 4 years (2014-2017). Dashed lines show 95% confidence intervals on model-estimated yield, generated through 10,000 parametric bootstrap samples (some confidence intervals are narrow enough to be obscured by the point). Coloured points show the estimated wheat yield from three different models:

• 'mixed eff.poly' = a mixed effects model that treated black-grass density state as an ordered categorical variable and used a 2nd order orthogonal polynomial representation of density (this model was also used to estimate average yields conditional on field and year effects, and these estimates informed the yield penalty used in ECOMOD);

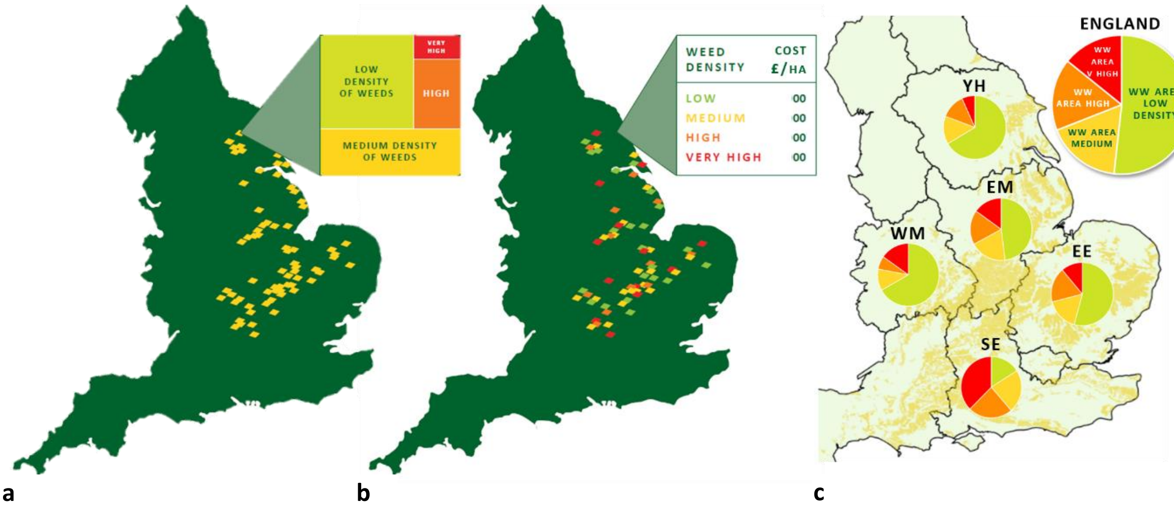
• 'fixed eff.poly' = a fixed effects model where black-grass density state was treated as an ordered categorical variable and the model was fit to a 2nd order orthogonal polynomial representation of density class;

• 'fixed eff.cat' = a second fixed effects model where black-grass density state was treated as a categorical variable.

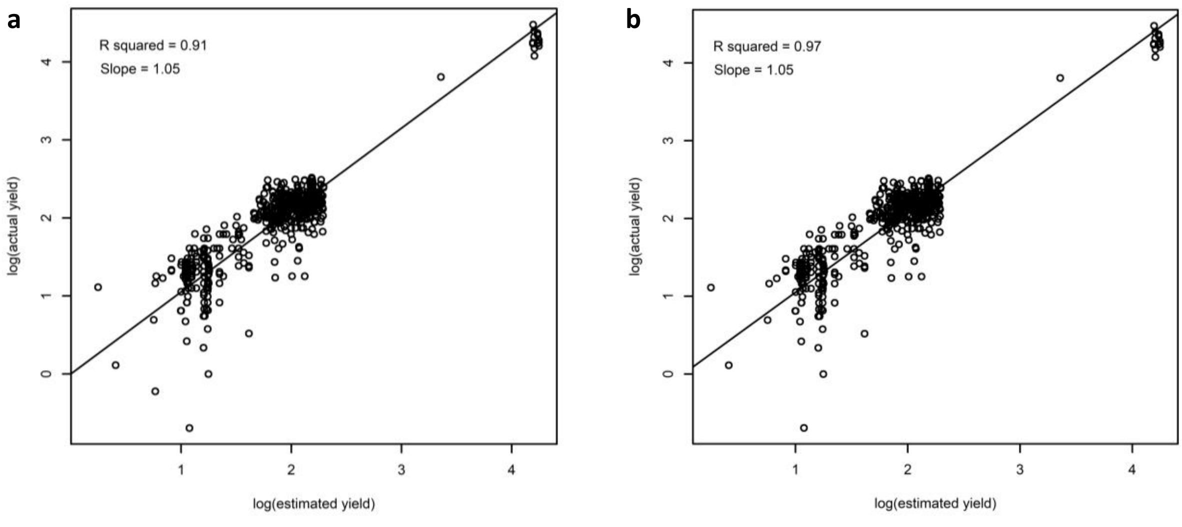
Because of the structure in these data it was not appropriate to estimate average density effects using the fixed effects models.



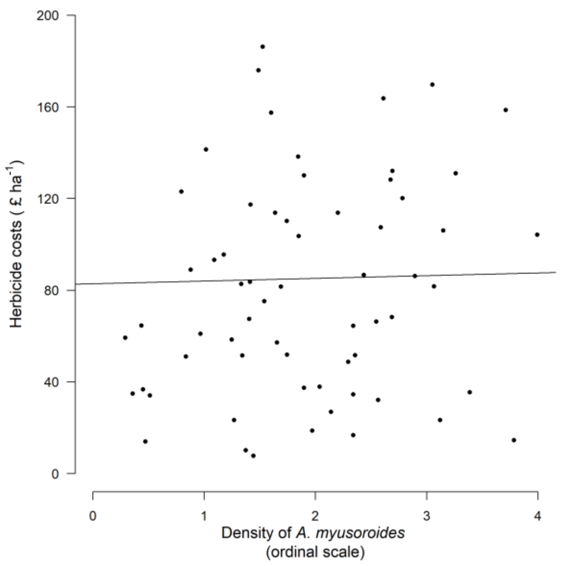
Supplementary Figure 2 | Model check plots for model 'mixed eff.poly'. a, residual plot; b, random effect distribution, where D_p1 and D_p2 are the first- and second-order polynomial representations of the ordinal density state variable.



Supplementary Figure 3 | Methods used to estimate field- and national-scale cost of resistance and yield loss in winter wheat crops. **a,** We used the proportion of each density state within a field to estimate a weighted mean cost (or yield loss) by running empirical field management data through ECOMOD. We did this for each field (*n* fields = 66) and each year (*n* max = 10). For each field we then calculated a mean cost of infestation (C_I) and yield loss due to infestation (YL_I) over all the years for which we had data. The frequency of resistance to mesosulfuron in each field was used to calculate the proportion of C_I and YL_I that were due to resistant plants. This gave a cost of resistance (C_R) and a yield loss due to resistance (YL_R). **b,** Each field was then ascribed a mean density state to allow calculation of the mean C_R and YL_R per density state (here, colours are ascribed to individual fields for visualisation purposes only and do not represent real field density states). **c,** For each region, the proportion of fields at each density state was used to estimate the area of winter wheat at each density state. The mean costs (£ ha^{-1}) and yield losses (t ha^{-1}) at each density state were scaled up by the area (ha) of winter wheat crops at the corresponding density state. The costs (or yield losses) at each density state were then summed to give total regional cost (£ or t). Yellow shading indicates winter wheat-growing regions. Regions shown are UK government office regions where we collected data: YH Yorkshire and the Humber; EM East Midlands; WM West Midlands; EE East of England; SE South East. (For crops other than winter wheat the variation in density state within fields, and the proportionate area of each density state within regions, were not considered as we have no data on the yield penalties due to black-grass in crops other than wheat. Average field density states, and total crop areas, were used instead).



Supplementary Figure 4 | Comparison of measured and estimated yields, using **a,** the full dataset and **b,** with failed crops removed.



Supplementary Figure 5 | The cost of herbicide applied to control black-grass infestations in winter wheat was not related to the average black-grass density state of a field in the summer after herbicide application (likelihood ratio test using maximum-likelihood simplification of minimal adequate REML model, χ^2_1=0.0982, p=0.754). Each point represents one field.

Supplementary Tables

Supplementary Table 1 | Field-level model estimates of wheat yield (from model 'mixed eff.poly', see red symbols in Supplementary Figure 1) at each black-grass density state in each year. Data used are the 17 fields for which high-resolution wheat yield and black-grass density data were available (Supplementary Figure 1).

		Estimated mean wheat yield[◊] ($t\ ha^{-1}$) at each black-grass density state[†]			
Field	Year	Low density	Medium density	High density	Very high density
1	2014	11.50 (11.24, 11.69)	11.80 (11.42, 12.16)	11.50 (11.03, 11.96)	10.80 (9.63, 11.51)
1	2017	9.82 (9.56, 10.01)	10.10 (9.71, 10.52)	NA	NA
2	2014	9.75 (9.55, 10.14)	10.90 (10.54, 11.13)	11.00 (10.64, 11.22)	10.00 (9.58, 10.66)
2	2017	8.12 (7.95, 8.39)	9.32 (8.82, 9.51)	NA	NA
3	2015	9.70 (9.25, 10.18)	9.85 (9.57, 10.21)	9.42 (9.09, 9.77)	8.38 (7.57, 9.10)
4	2016	NA	5.93 (5.48, 6.51)	5.54 (5.25, 5.95)	4.66 (4.27, 5.00)
5	2014	9.77 (9.53, 10.04)	9.93 (9.42, 10.51)	9.32 (8.29, 10.55)	NA
5	2016	5.66 (5.40, 5.93)	NA	NA	NA
6	2014	11.50 (11.21, 11.78)	11.10 (10.90, 11.48)	9.70 (9.45, 10.01)	7.12 (6.73, 7.50)
6	2015	11.50 (11.28, 11.73)	11.20 (10.89, 11.53)	NA	NA
6	2017	9.82 (9.59, 10.05)	9.51 (9.24, 9.79)	8.07 (7.75, 8.37)	NA
7	2014	10.10 (9.48, 10.74)	10.20 (9.91, 10.61)	9.65 (9.41, 9.90)	8.33 (7.93, 8.72)
8	2014	12.00 (11.73, 12.23)	11.40 (10.89, 11.67)	8.61 (8.16, 8.99)	3.73 (3.27, 4.45)
9	2015	12.00 (11.82, 12.23)	12.00 (11.33, 12.47)	NA	NA
10	2014	11.30 (11.07, 11.66)	11.80 (11.41, 12.09)	11.20 (10.37, 11.89)	NA
11	2014	11.00 (10.77, 11.29)	11.20 (11.00, 11.47)	10.60 (10.38, 10.81)	9.12 (8.79, 9.43)
11	2017	9.37 (9.15, 9.57)	9.58 (9.33, 9.79)	8.95 (8.66, 9.17)	7.49 (7.06, 7.81)
12	2015	9.03 (8.79, 9.28)	8.64 (8.23, 9.44)	7.36 (6.74, 9.04)	NA
13	2014	NA	10.10 (9.52, 11.03)	9.35 (8.91, 9.98)	7.80 (7.50, 8.09)
13	2016	NA	NA	5.24 (4.76, 5.90)	3.68 (3.39, 3.95)
14	2016	6.30 (5.38, 6.99)	6.54 (5.93, 7.24)	6.46 (6.05, 7.01)	6.06 (5.49, 6.55)
15	2015	11.10 (10.90, 11.30)	11.00 (10.75, 11.43)	10.30 (9.51, 10.86)	NA
15	2017	9.41 (9.22, 9.60)	9.32 (9.03, 9.77)	NA	NA
16	2014	10.70 (10.40, 10.93)	10.90 (10.37, 11.18)	NA	NA
17	2014	11.20 (10.93, 11.43)	NA	NA	NA

[◊] Grey figures in brackets are 95% confidence intervals generated by parametric bootstrapping, as described above.
[†] NA = the density state was not observed.

Supplementary Table 2 | Model-estimated yield, and derived yield loss, at each density state in an hypothetical 'average' field. This yield loss is the yield penalty applied in BGRI-ECOMOD. Data used are the 17 fields (Supplementary Figure 1) for which high-resolution wheat yield and black-grass density data were available.

Black-grass density state	Model-estimated mean wheat yield, t ha^{-1} (95% confidence interval)		Mean yield loss, % reduction (95% confidence interval)	
absent-low	9.22	(9.07, 9.35)	0	(0, 0)
medium	9.32	(9.18, 9.47)	0*	(-3.12, 0.72)
high	8.53	(8.35, 8.72)	7.45	(4.9, 9.79)
v.high	6.85	(6.49, 7.19)	25.60	(22, 29.5)

* Model-estimated yield loss at medium density is -1.1. See Supplementary Methods for explanation of the zero in the table.

Supplementary Table 3 | Our estimates of yield loss compared to data from controlled plot experiments in which wheat yields were measured in relation to black-grass density treatments.

Source	Experiment details	Yield loss estimates (% reduction) at each black-grass density state◊ (range given in brackets) †			
		low density 1-160 plants per 20x20m grid cell	medium density 161-450 plants per 20x20m grid cell	high density 451-1450 plants per 20x20m grid cell	very high density >1450 plants per 20x20m grid cell
Our estimates	Observational dataset	0 (0 – 0)	0 (0 – 5)	7 (0 – 28)	26 (13 – 69)
Naylor, 1972[2]	randomised block design, 4 reps, England	-	0	13	29 – 32
Wilson, 1979[3]	randomised block design, 4 reps, England	-	-	-	9 – 19
Wilson, 1980[4]	randomised block design, 3 reps, England	-	-	-	13 – 35
Vizantinopolous et al, 1998[5]	randomised block design, 4 reps, Greece	-	-	-	10 – 30
Mannan, 2003[6]	randomised block design, 1 rep, Turkey	-4 – 4‡	4.87 (1 – 16)‡	4 – 21‡	7 – 26‡
Storkey et al, 2003[7]	collated data from a series of competition trials (winter wheat & BG)	-	-	-	Max of 60 – 70
Tatnell, 2004, given in Benjamin, 2010[8]	randomised block design, 4 reps, England	-	-	-	31 – 47
Domaradzki, 2006[9]	randomised block design, 3 reps, Poland	-	-	-	53 – 61

◊ Black-grass densities from published studies have been grouped according to the density states used in this study.
† A dash indicates these density states were not investigated.
‡ Exact values not presented in paper, apart from the value 4.87. Approximate ranges obtained from Figure 2c of the paper.

Supplementary Table 4 | Model testing against regional gross margins, cereal farms, from Farm Business Survey data. Figures in brackets are 95% confidence intervals.

Region	Number of BGRI fields per region†	ECOMOD mean gross margin £ ha^{-1}	FBS mean gross margin‡ £ ha^{-1}
YH	9	938.2 (911.3, 965.1)	853.0 (722.4, 983.7)
EM	19	935.9 (905.6, 966.2)	859.3 (753.8, 964.9)
WM	6	883.9 (867.3, 900.5)	754.5 (588.1, 920.9)
EE	24	888.3 (854.0, 922.6)	820.9 (749.7, 892.0)
SE	8	763.8 (712.9, 814.7)	679.8 (595.6, 764.0)

† Of the subset of 66 fields used for this analysis, this indicates how many fall within each region.

‡ Mean gross margin on cereal farms was calculated from cereal enterprise gross margin plus basic payment (Single Payment Scheme, SPS) gross margin on cereal farms in the Farm Business Survey 2013/14.

Supplementary Table 5 | Costs and yield loss due to black-grass infestation (C_I and YL_I), scaled to regional level and to England.

Region [1]	YL_I, winter wheat (tonnes) (+/- 95% CI) [2]	C_I in winter wheat crops (£) (+/- 95% CI) [2]	C_I across a rotation (all crops) [3] (£) (+/- 95% CI) [2]
YH	35,601 (12,549 – 52,970)	22,821,658 (21,153,172 - 24,473,884)	61,429,837 (53,355,202 - 69,469,504)
EM	97,979 (79,010 – 140,468)	44,217,462 (40,751,067 - 47,685,366)	86,493,720 (75,124,567 - 97,813,638)
WM	61,273 (42,322 – 75,699)	43,321,730 (40,318,637 - 46,330,101)	38,577,060 (33,506,305 - 43,625,856)
EE	222,772 (158,749 – 270,002)	84,262,675 (75,977,109 - 92,524,303)	121,788,150 (105,779,727 - 137,727,248)
SE ◊	217,521 (192,487 – 250,090)	76,972,949 (72,900,799 - 81,056,998)	56,987,691 (49,496,954 – 64,445,990)
Total, BGRI regions	635,146 (485,117 – 789,228)	271,596,474 (251,100,784 - 292,070,653)	365,276,457 (317,262,755 – 413,082,235)
ENGLAND	856,464 (643,585 – 1,002,931)	345,611,894 (318,456,070 - 372,826,438)	444,227,420 (385,836,022 - 502,365,953)

[1] These are UK Government Office Regions: EE East of England; YH Yorkshire and the Humber; EM East Midlands; WM West Midlands; SE South East; Total, regions = all previous regions summed; England = this includes all UK Government Office Regions in England, so we are extrapolating beyond the regions where the project had field sites.

[2] 95% CIs were calculated using bootstrapping.

[3] For rotation costs, scaling up was to the total area of the following crops: wheat, barley, OSR, field beans & dried peas, and, for regions EM, EE and for England, also sugar beet.

◊ Although data was collected from fields in the South East (SE) of England, data was collected from only a small number of fields in the northernmost part of the region, so we are not confident that this figure is representative of the whole region. We have included the data as it's the best estimate available so far.

Supplementary Table 6 | Costs and yield loss due to resistant black-grass (C_R and YL_R), scaled to regional level and to England.

Region [1]	YL_R, winter wheat (tonnes) (+/- 95% CI) [2]	C_R in winter wheat crops (£) (+/- 95% CI) [2]	C_R across a rotation (all crops) [3] (£) (+/- 95% CI) [2]
YH	26,139 (5,836 - 46,257)	11,121,498 (8,886,158 - 13,348,365)	52,490,350 (43,330,608 - 61,693,416)
EM	93,745 (54,758 - 116,216)	39,063,092 (35,451,675 - 42,674,090)	73,906,848 (61,009,855 - 86,864,842)
WM	59,718 (41,154 - 74,531)	38,867,735 (35,518,239 - 42,211,178)	32,963,190 (27,211,003 - 38,742,584)
EE	213,083 (158,749 - 270,002)	74,106,798 (65,184,928 - 83,031,774)	104,065,108 (85,905,398 - 122,310,712)
SE ◊	216,013 (186,873 - 244,476)	75,639,552 (71,585,284 - 79,702,003)	48,694,641 (40,197,263 - 57,232,211)
Total, BGRI regions	608,698 (447,370 - 751,482)	238,798,675 (216,626,284 - 260,967,409)	312,120,135 (257,654,125 - 366,843,765)
ENGLAND	823,271 (613,441 - 972,787)	305,651,700 (275,342,646 - 335,954,908)	379,581,875 (313,343,565 - 446,133,487)

Legend as for Supplementary Table 5.

Supplementary Table 7 | Maximum costs and yield losses due to resistant plants (C_R and YL_R), estimated assuming ubiquitous very high black-grass density, scaled to regional level and to England.

Region [1]	Maximum YL_R in winter wheat (t) (+/- 95% CI) [2]	Maximum C_R in winter wheat crops (£) (+/- 95% CI) [2]	Maximum C_R across a rotation (all crops) [3] (£) (+/- 95% CI) [2]
YH	445,718 (411,114 - 464,155)	101,413,164 (98,603,734 - 104,221,021)	135,064,547 (125,775,872 - 144,326,056)
EM	609,033 (583,851 - 645,309)	142,227,672 (138,192,491 - 146,254,491)	190,172,003 (177,093,471 - 203,212,285)
WM	336,453 (309,819 - 355,527)	96,072,612 (91,982,815 - 100,172,718)	84,818,606 (78,985,451 - 90,634,701)
EE	935,383 (864,693 – 975,946)	220,884,525 (210,950,775 - 230,841,631)	267,773,157 (249,357,830 - 286,134,627)
SE ◊	460,108 (418,520 - 491,240)	123,528,057 (117,066,099 - 129,985,836)	125,297,690 (116,680,703 - 133,889,477)
Total, BGRI regions	2,786,695 (2,587,997 - 2,932,176)	684,126,030 (656,795,914 - 711,475,697)	803,126,004 (747,893,325 - 858,197,145)
ENGLAND	3,445,987 (3,259,606 - 3,618,952)	842,131,692 (809,560,532 - 874,679,176)	976,713,899 (909,543,213 - 1,043,688,134)

Legend as for Supplementary Table 5.

Supplementary Table 8 | Maximum costs and yield losses due to resistant plants (C_R and YL_R), estimated using the top quintile and top decile of weed density data. 95% CIs in brackets.

	Top quintile of density data	Top decile of density data
YL_R in winter wheat		
Mean YL_R (t/ha)	1.2 (0.9 - 1.5)	1.4 (1.1 - 1.7)
Annual YL_R, England (t)[1]	2,066,857 (1,617,057 - 2,695,095)	2,586,730 (1,976,403 - 3,054,441)
Economic C_R		
Winter wheat		
Mean C_R (£/ha)	331 (284 - 379)	381 (313 - 451)
Annual C_R, England (£)[1]	594,871,899 (510,630,666-679,163,940)	686,026,583 (561,478,125 - 810,504,903)
Rotation		
Mean C_R (£/ha)	223 (188 - 257)	245 (194 - 295)
Annual C_R, England (£)[1]	753,901,153 (638,543,373 - 869,570,737)	828,940,966 (658,190,861 - 999,650,660)

[1] Scaling up followed the methods detailed in Supplementary Methods.

Supplementary Table 9 | National-scale metrics calculated using data from two time periods: the entire span (2004 – 2014), and more recent years (2010 – 2014). 95% confidence intervals given in brackets. Values are yield losses (in winter wheat) and costs (in winter wheat and across a rotation) due to black-grass infestation.

	Time period			
Metric	2004 - 2014		2010 - 2014	
YL_I, ww (t)	856,464	(643,585 - 1,002,931)	861,127	(674,618 - 1,033,964)
C_I, ww (£)	345,611,894	(318,456,070 - 372,826,438)	363,164,572	(329,616,610 – 396,765,983)
C_I, rot (£)	444,227,420	(385,836,022 - 502,365,953)	499,623,934	(464,425,976 – 534,885,934)

Supplementary Table 10 | Yield penalties due to black-grass infestation used in the sensitivity analysis.

Black-grass density state	Black-grass density (plants per 20m x 20m grid cell)	Limits suggested by our model (% reduction)		Yield penalties (% reduction) used in sensitivity analysis	
		lowest value	highest value	lowest value	highest value
low	1-160	0.00	0.00	0.00	0.00
medium	161-450	0.00	5.14	0.00	5.14
high	451-1450	0.00	28.10	0.00	45.00
very high	>1450	13.02	68.90	13.00	70.00

Supplementary Table 11 | Sensitivity analysis results: the effect of varying the yield penalty on yield loss and costs due to resistant plants (YL_R and C_R).

	WINTER WHEAT YIELD LOSS Total YL_R (tonnes) (95% CI)[2]		WINTER WHEAT COSTS Total C_R (£) (95% CI)[2]		ROTATION COSTS[3] Total C_R (£) (95% CI)[2]	
Region [1]	Calculated using the lowest yield penalty	Calculated using the highest yield penalty	Calculated using the lowest yield penalty	Calculated using the highest yield penalty	Calculated using the lowest yield penalty	Calculated using the highest yield penalty
YH [4]	7,037 (-13,900 - 26,521)	101,003 (80,891 - 128,427)	7,461,787 (5,836,740 - 9,089,709)	25,497,166 (20,817,390 - 30,173,362)	38,377,872 (31,760,164 - 44,970,144)	107,059,738 (85,068,522 - 129,008,101)
EM [4]	24,460 (-4,392 - 57,066)	362,475 (307,478 - 408,655)	25,775,854 (22,314,009 - 29,241,043)	90,658,370 (83,582,094 - 97,747,013)	54,036,362 (44,718,575 - 63,318,336)	150,740,999 (119,777,186 - 181,644,476)
WM	20,992 (7,982 - 30,913)	200,837 (176,529 - 225,024)	31,441,580 (28,603,752 - 34,270,286)	65,966,889 (60,752,245 - 71,177,074)	24,100,755 (19,944,929 - 28,240,608)	67,231,986 (53,421,817 - 81,015,244)
EE	62,029 (15,282 - 104,198)	783,426 (708,236 - 876,453)	45,115,398 (37,565,053 - 52,639,657)	183,663,402 (168,626,464 - 198,716,518)	76,086,317 (62,966,335 - 89,155,872)	212,252,028 (168,653,191 - 255,765,908)
SE	71,591 (59,021 - 81,019)	744,677 (693,685 - 798,121)	47,899,281 (45,530,936 - 50,272,765)	177,264,008 (167,074,560 - 187,452,191)	35,602,672 (29,463,507 - 41,718,240)	99,317,979 (78,917,004 - 119,679,201)
Total, BGRI regions	186,109 (63,993 - 299,717)	2,192,418 (1,966,819 - 2,436,679)	157,693,900 (139,850,490 - 175,513,459)	543,049,835 (500,852,753 - 585,266,156)	228,203,977 (188,853,510 - 267,403,200)	636,602,730 (505,837,720 - 767,112,930)
ENGLAND	258,227 (90,094 - 449,440)	2,919,418 (2,710,625 - 3,192,326)	197,216,672 (168,582,179 - 225,920,814)	708,315,833 (662,659,144 - 753,904,953)	277,528,054 (229,672,364 - 325,199,808)	774,198,235 (615,169,637 - 932,916,949)

[1] These are UK Government Office Regions. Only those where the BGRI had fields are used. EE East of England; SE South East; YH Yorkshire and the Humber; EM East Midlands; WM West Midlands; Total, regions = all previous regions summed; England = this includes all UK Government Office Regions in England, not just the regions where the BGRI had field sites.

[2] Confidence intervals were calculated using bootstrapping.

[3] For rotation costs, scaling up was to the total area of the following crops: wheat, barley, OSR, field beans & dried peas, and, for regions EM, EE and for England, also sugar beet.

[4] Costs for very high density states could not be calculated in these regions as none of the fields used in the cost analysis had any quadrats in very high density state. These costs will therefore be under-estimated.

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