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ANALYSIS

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The costs of human-induced evolution in an agricultural system

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Pesticides have underpinned significant improvements in global food security, albeit with associated environmental costs. Currently, the yield benefits of pesticides are threatened as overuse has led to wide-scale evolution of resistance. Despite this threat, there are no large-scale estimates of crop yield losses or economic costs due to resistance. Here, we combine national-scale density and resistance data for the weed *Alopecurus myosuroides* (black-grass) with crop yield maps and an economic model to estimate that the annual cost of resistance in England is £0.4 billion in lost gross profit (2014 prices) and annual wheat yield loss due to resistance is 0.8 million tonnes. A total loss of herbicide control against black-grass would cost £1 billion and 3.4 million tonnes of lost wheat yield annually. Worldwide, there are 253 herbicide-resistant weeds, so the global impact of resistance could be enormous. Our research supports urgent national-scale planning to combat resistance and an incentive for increasing yields through food-production systems rather than herbicides.

Resistance to xenobiotics (for example, antibiotics, antimycotics and pesticides), caused by high frequency of application[1–4], is a severe and growing economic[5], food security[1,6] and public health crisis[3,6,7]. In the past, pesticides enabled increases in food production but they are increasingly less efficient[1,8]. This is a threat to global food security. However, there are no large-scale estimates of the effects of pesticide resistance on crop yields.

Future food security will rely on sustainable intensification[9,10], which aims to boost yields from the same area of land but with reduced environmental impact. Pesticide resistance threatens both these goals: yields are threatened by higher pest densities[1,8] and the environment is threatened because the usual response to resistance has been increased pesticide use[11,12]—despite the knowledge that pesticides harm water and soil quality and biodiversity[12–15]. Increasing population and extreme competition for land are strong motivations to investigate food security. As pesticide resistance is implicated in three elements of the United Nation's water–food–energy–ecosystems nexus, there is an incentive to assess its effects.

National- and global-scale economic costs of xenobiotic resistance are poorly quantified but, where this has been attempted in human healthcare settings for antimicrobial resistance, costs run into billions[16] or trillions[17] of US dollars and even these enormous numbers are thought to be underestimates[5]. In agriculture, large-scale cost estimates are lacking but anecdotal evidence[18] combined with crop areas suggests that, in the United States, increased chemical costs due to glyphosate resistance may exceed US$10 billion annually. Costs due to yield loss would further increase this figure.

The likely sizes of the social, economic and environmental costs mean that a coordinated global policy response, driving governance integration across sectors is needed[19]. In healthcare, the World Health Organization endorsed a Global Action Plan for antimicrobial resistance in 2015; however, there is no equivalent in animal and crop production. This is despite the fact that agriculture accounts for 37% of land use globally (World Bank Open Data, 2018), an estimated 4 million tonnes of pesticides are applied worldwide each year (FAOStat, 2019), resistance to pesticides is well-documented[20–23] and there is a long-term upward trend in pesticide use[24]. United Nations resistance advice (Guidelines on Prevention and Management of Pesticide Resistance, FAO 2012) and a handful of informal, largely agrochemical industry-led, groups exist (for example, CropLife International, IRAC, AHDB resistance action groups) but the lack of government involvement means that problems of resistance continue. Even in healthcare where a global plan exists, creation of national action plans is hampered by a lack of evidence, particularly on the true costs of resistance and the cost-effectiveness of policies[25]. Determining the national costs associated with xenobiotic resistance is a critical first step in creating a national action plan.

We address this issue for herbicide resistance in the United Kingdom. Mirroring the global state of affairs, the United Kingdom has a national Antimicrobial Resistance Strategy but no national resistance policy in place for other classes of xenobiotic such as pesticides. This is despite (1) a continuing upward trend in the area to which pesticide is applied (FERA PUS stats, 2019), (2) evidence that resistance is affecting output[1] and (3) UK government awareness of the issue (POSTnote 501, 2015). Here, we combine a national-scale dataset of the density and resistance status of the most economically significant weed in western Europe[26], black-grass (BG, *Alopecurus myosuroides*), with 10 years' worth of past management history, corresponding yield data (Fig. 1) and an economic model (Supplementary Methods) to estimate the economic and food-production effects of herbicide-resistant BG in England. Using this approach, we provide a national-scale estimate of yield losses and the full economic costs due to herbicide resistance. We distinguish between losses due to weed infestation, 'I' (both resistant and susceptible plants) and losses due to resistant plants, 'R'. Our results suggest a pressing need for governmental action to address resistance issues and for other countries to undertake their own national-scale assessments.

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Costing resistance at the field scale

Estimated yield loss due to BG infestation in winter wheat was, on average, 0.4 t ha^{-1} (Table 1), or 5% of the average estimated potential wheat yield (8.3 t ha^{-1}) in the absence of BG. We estimated this by applying yield penalties due to BG infestation (Fig. 1) to the crop yield estimation component in our economic model (details in Methods and Supplementary Information). Resistance frequencies were then used (Methods) to calculate that most of this lost yield (0.38 t ha^{-1}) was due to resistant plants. At low densities of BG the yield loss was negligible, whereas at the highest weed densities mean yield loss was 1.8 t ha^{-1}, 100% of which was due to resistant plants (Table 1 and Fig. 3).

The mean economic cost of resistance (C_R, defined as the production losses and additional costs due to resistant BG) in winter wheat was £75 ha^{-1} at low BG density and £450 ha^{-1} at very high density (Table 1 and Fig. 2c). Estimates of C_R will vary, potentially greatly, according to the input and output prices used. The costs calculated here using 2014 prices represent 7% and 37%, respectively, of potential gross profit from winter wheat in these fields in the absence of resistant BG and compare to average total agricultural costs (English cereal farms, 2014) of £1,076 ha^{-1} (Farm Business Survey Region Reports, 2019). Across all density states, the mean C_R in winter wheat was £155 ha^{-1} (Table 1) or 14% of potential gross profit. C_R within density states varied widely, ranging from £0–493 ha^{-1} in winter wheat fields with low BG density to £355–773 ha^{-1} in fields with very high densities (raw data not shown). At very high density states, 100% of the total costs of BG infestation came from resistant plants (Table 1 and Fig. 3).

Across a rotation, the mean C_R in low density fields was £58 ha^{-1}, and £280 ha^{-1} in very high density fields (Table 1). Again, 100% of the costs were due to resistant plants in fields with very high BG density, whereas in low density fields just under 70% of costs came from resistant plants. The per hectare C_R in winter wheat was higher than the per hectare C_R across a rotation (Table 1 and Fig. 2c,d) due to the negative impact of the weed on wheat yield (no yield penalties were applied to other crops in the rotation). Overall, as average BG density increases, so does the proportion of the cost or yield loss that is due to resistant plants (Table 1), in line with previous findings[1] that resistance drives weed abundance. Field-scale resistance impacts are thus greater in regions with higher BG densities, especially in winter wheat crops (Fig. 2), and resistance impacts in the United Kingdom reduce along a gradient from south to north (see Fig. 4). See Methods for a discussion of the assumptions that underpin these estimations.

The use of herbicides targeting BG in winter wheat did not differ across different final (preharvest) densities of weed infestation ($\chi^2_1 = 0.0982$, $P = 0.754$; Fig. 3b and Supplementary Fig. 5). Thus, in fields with low final BG density, herbicide costs constituted 82% of total costs (this applies to both the cost of infestation C_I and to C_R), whereas in fields with high and very high final BG densities, the biggest source of lost income was yield loss (60% and 77% respectively, Fig. 3). In some of the low density fields, relatively intense herbicide use will be justified where high levels of susceptibility remain in the weed population and, therefore, where these herbicides are still effective in reducing yield loss potential. However, in low density fields with high levels of herbicide resistance (in our data, 75% of fields with low and medium BG density had high resistance (>60% survival) to Atlantis), intense herbicide application may be counterproductive as (1) herbicide costs will outweigh benefits of BG control, (2) it will impose an unnecessary environmental burden[12,27–29] and (3) it will have the unwanted effect of selecting for even higher frequencies of resistance within populations[1,30]. In these situations, a reduction in herbicide use may bring economic benefits but would need to be accompanied by cultural and physical control methods to maintain low weed population sizes as part of an integrated weed management programme. We expand on this in the discussion.

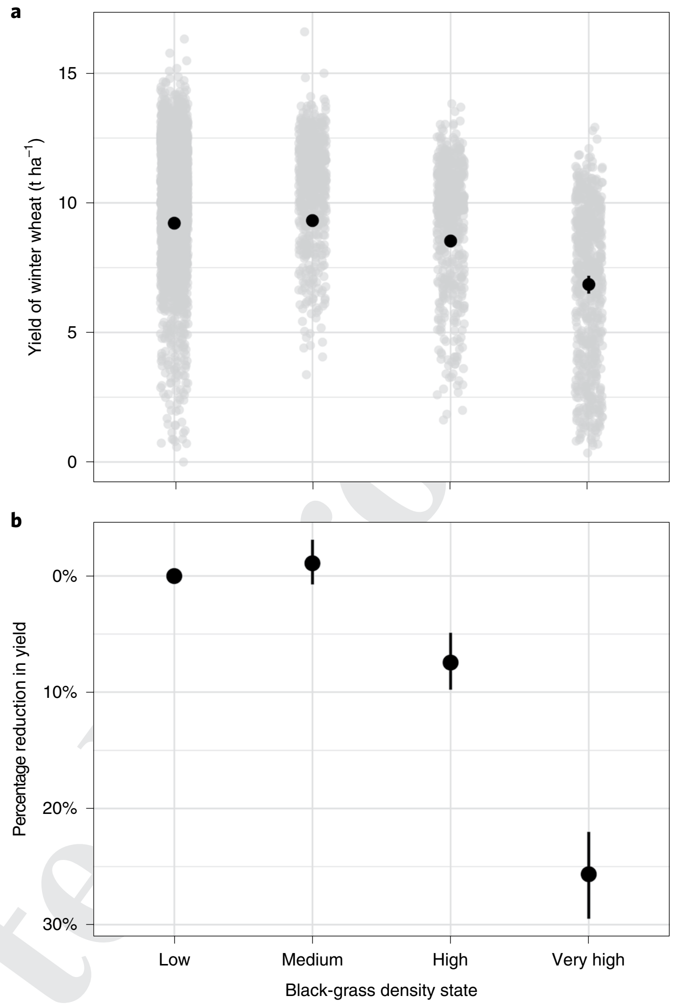

Fig. 1 | Estimating yield penalties using black-grass density and winter wheat yield data. a, The average effect of black-grass density on the yield of winter wheat. Black points are model-estimated average yields, bars show 95% CIs generated from 10,000 parametric bootstrap resamples (some CIs are narrow enough to be obscured by the point; all values and CIs given in Supplementary Table 2). Grey points show observed yield for each 20 × 20 m^2 plot from 17 fields over 4 yr. See Supplementary Information for individual field estimates across years. **b**, Average yield loss of winter wheat relative to the reference state, calculated on the basis of yield estimates and bootstrap resamples. Reference state, low density (note the estimate for low density is fixed at 0). Percentage reduction for subsequent density states as follows: medium 0%; high 7.45%; very high 25.60% (Supplementary Table 2). The *y* axis of **b** is reversed so that the direction of the effect of black-grass density is the same between **a** and **b**. Further details in Supplementary Information.

The impact of resistance at a national scale

Total annual wheat yield loss for England was 0.86 million tonnes (mt; Supplementary Table 5), almost all of which (0.82 mt) was due to resistant plants (Fig. 4a and Supplementary Table 6). Sensitivity analyses suggest that annual wheat yield losses due to resistant BG (YL_R) in England may be as low as 0.3 mt or as high as 3 mt (Supplementary Table 11) given uncertainties in our yield penalty estimates (further details in Supplementary Information). Whichever figure we accept, our estimates run counter to global goals of increased yields[31–33] and are particularly concerning in view of the current wheat yield stagnation in northwestern Europe[34,35]. United Kingdom annual domestic wheat consumption hovers

Fig. 2 | Field-scale costs and yield loss due to resistant black-grass. These estimates were generated by running empirical field management and black-grass density data (number of fields = 66) through BGRI-ECOMOD. **a**,**b**, Yield loss due to resistant black-grass (YL_R, t ha^{-1}): average field-scale yield losses in winter wheat (**a**); maximum field-scale yield loss in winter wheat in the event of total loss of herbicide control (**b**). **c**–**e**, Cost of resistance (C_R, £ per ha): average field-scale C_R for years in winter wheat crops (**c**) and all years' data across a rotation (**d**); maximum field-scale C_R in the event of total loss of herbicide control (**e**). Fields are overlaid on a map of modelled density (square root) of *A. myosuroides* averaged over 2015–2017. This density map was generated by fitting a generalized additive model to the data reported in Hicks et al.[1], with spatial covariates representing latitude and longitude.

around 15 mt (DEFRA); the highest yield loss values from our sensitivity analyses represent nearly a fifth of this.

In terms of economics, the total annual cost of BG infestation in England was £0.44 billion across all crops (termed rotation cost from now on; Supplementary Table 5), £0.38 billion per year of which was due to resistant plants (Fig. 4b and Supplementary Table 6). In winter wheat crops, C_I was £0.35 billion per year, of which C_R was £0.31 billion (Fig. 4c and Supplementary Table 6). At a regional scale, some rotation costs are higher than those in winter wheat. This is because, although field-scale rotation costs are lower than those in winter wheat, the total cereal crop area is much larger than the winter wheat area and so the scaled-up rotation costs are relatively higher. In the West Midlands (WM) and South East (SE) of England, the average C_R per ha in winter wheat crops was particularly high compared to other regions (WM £387 ha^{-1}, SE £270 ha^{-1}, EM £159 ha^{-1}, EE £206 ha^{-1}, YH £88 ha^{-1}, abbreviations as in Fig. 4); as a result, the scaled-up costs in these two regions remained higher in winter wheat than across rotations. Values for the SE region should be treated with caution as we used just eight fields from this region in our analysis and all of them were concentrated in one area (where there are high densities of resistant BG[1]; see Supplementary Fig. 3). The estimates for this region are therefore unlikely to be representative of the entire region.

Sensitivity analyses showed that annual rotation C_R might be as low as £0.3 billion per year or as high as £0.8 billion per year (Supplementary Table 11). Nevertheless, even at the lower end, the costs are large. To put these figures into perspective, total income from all types of farming in England was £3.9 billion in 2014. Herbicide resistance is therefore having a severe impact on English arable farming and these results underscore the need to manage resistance through coordinated action at a national level.

Potential costs and crop losses

Because resistance is increasing over time and driving BG density[1], we also estimated yield losses and costs in winter wheat under a total loss of herbicide control (Fig. 2b,e) by assuming that all

Table 1 | Field-scale yield loss and economic costs due to black-grass infestation (I) and resistant plants (R) at different densities of black-grass in England

Average black-grass density state of field	Average yield loss in winter wheat[a] (t ha⁻¹)			Average cost[a] (£ per ha)					
				in winter wheat			across rotations		
	R	I[c]	R/I[b]	R	I	R/I	R	I	R/I
Absent/low	0.0 (−0.1, 0.1)	0.0 (−0.1, 0.1)	ND	75 (56, 93)	106 (90, 123)	0.71	58 (44, 72)	85 (73, 98)	0.68
Medium	0.3 (0.2, 0.4)	0.4 (0.2, 0.4)	0.75	135 (120, 149)	158 (148, 168)	0.85	103 (91, 115)	123 (114, 132)	0.84
High	0.8 (0.7, 0.9)	0.9 (0.8, 1.0)	0.89	264 (249, 280)	276 (261, 291)	0.96	185 (173, 197)	193 (182, 204)	0.96
Very high	1.8 (1.7, 1.9)	1.8 (1.7, 1.9)	1.00	450 (434, 466)	450 (434, 466)	1.00	280 (263, 297)	280 (263, 297)	1.00
Mean across all densities	0.38 (0.2, 0.6)	0.41 (0.2, 0.6)	0.93	155 (135, 174)	178 (152, 204)	0.87	112 (92, 132)	131 (114, 148)	0.85

[a]Values are means, estimated by running empirical field management and black-grass density data (number of fields = 66) through BGRI-ECOMOD, see Methods. 95% CIs (generated by bootstrapping) in brackets. [b]R/I gives the proportion of the cost of infestation that is due to resistance. [c]Infestation = resistant + susceptible plants. ND, not determined.

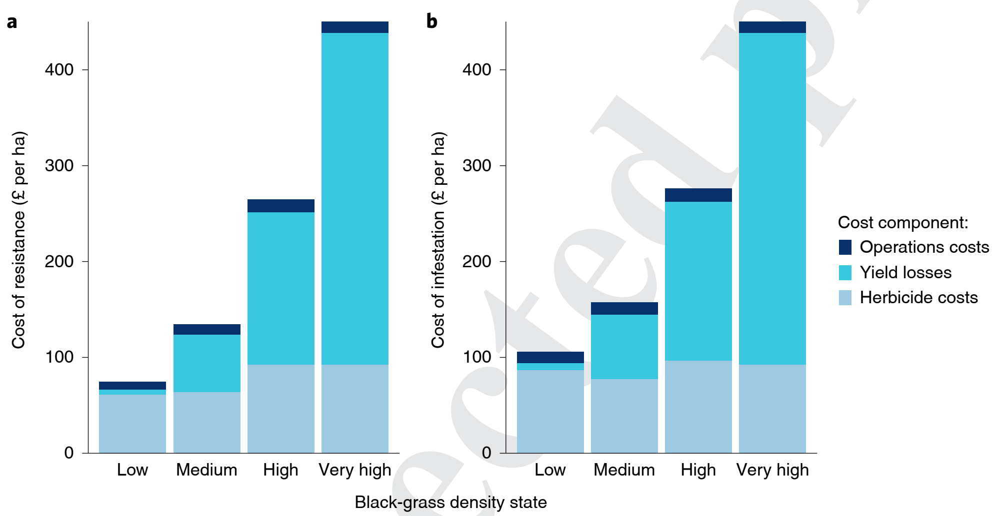

Fig. 3 | The relative contribution of herbicide costs, lost yield and operations costs to total costs in winter wheat crops. Values are average per hectare costs estimated by running empirical field management and black-grass density data through BGRI-ECOMOD (number of fields = 66). **a**,**b**, Costs due to resistant black-grass plants (**a**) and costs due to infestation (**b**). Herbicide costs consider only those herbicide applications targeting black-grass. (Error bars intentionally omitted as the purpose is to illustrate the contribution of component parts and, when data are presented in this way, error bars of individual components influence each other and are misleading).

quadrats in every field were in a very high density state and that 100% of costs and yield losses were due to resistant plants (Methods). Under this scenario of ubiquitous very high BG density, wheat YL_R ranged from 1.4 to 2.3 t ha⁻¹ and on average was 2 t ha⁻¹, representing over a quarter (28%) of average potential estimated wheat yield (8.3 t ha⁻¹) in the absence of BG. The C_R in winter wheat under this scenario ranged from £294 ha⁻¹ to £904 ha⁻¹, and on average was £467 ha⁻¹. This means that, if the problem continues unchecked, the costs of infestation in winter wheat could approach half of the average agricultural costs on English cereal farms (£1,076 ha⁻¹). We do not suggest that such a scenario will occur; however, it is worth estimating these impacts (1) to illustrate the potential consequences of inaction and loss of glyphosate and/or pre-emergence BG herbicides and (2) to present a frame of reference, allowing the extent of the current situation to be assessed in relation to the worst possible case.

Scaling up these 'worst-case' estimates we find that potential YL_R in English winter wheat under a scenario of total loss of herbicide control is 3.4 mt yr⁻¹ (95% CI 3.3–3.6 mt; Supplementary Table 7), representing just under a quarter of UK domestic wheat consumption. Potential annual rotation C_R is £1 billion (95% CI £0.9 billion–£1.0 billion; Supplementary Table 7). To present a more conservative worst-case estimate, we also estimated YL_R and C_R using just those fields in the top quintile and top decile of the BG density range: these gave potential annual yield losses in winter wheat of 2.1 mt and 2.6 mt respectively, and rotation C_R of £0.8 billion (Supplementary Table 8).

A comparison of current and potential yield loss (Supplementary Tables 6 versus 7) shows that yield loss in the worst-case scenario could be four to six times greater than it is now, except towards the northern edge of the BG range where it is seventeen times higher, reflecting the fact that herbicide-resistant BG is not yet such a pressing problem in this area. The only region in which current resistance impacts are closer to potential impacts is in SE England, where a large proportion of fields have very high average BG

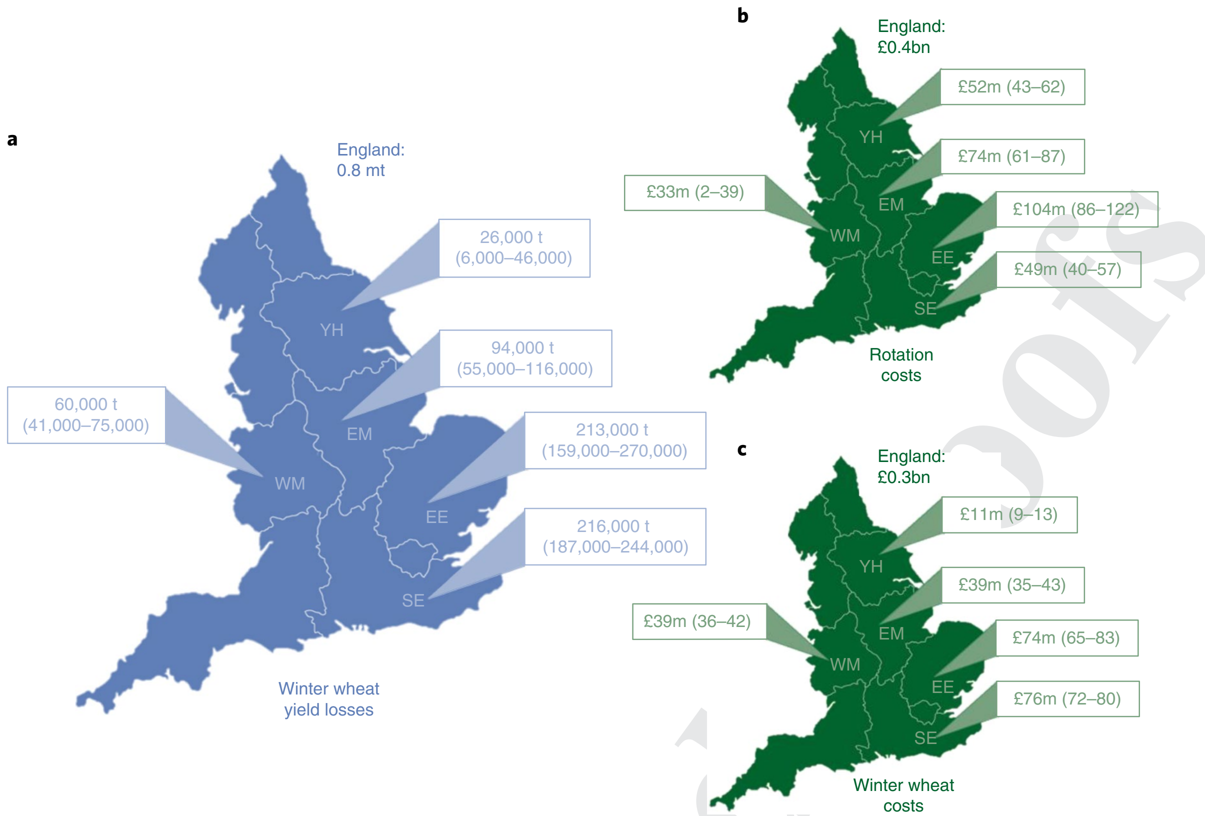

Fig. 4 | Annual impacts of herbicide-resistant black-grass at regional and national scales. a, Annual winter wheat yield losses due to resistance (YL_R). National YL_R given in million tonnes (mt); regional figures in thousand tonnes. **b**,**c**, Annual economic cost of resistance (C_R) across all crops (**b**) and in winter wheat crops (**c**). National C_R in billion (bn) £s, regional C_R in million (m) £s. Figures in brackets are 95% CIs. Regions are UK Government Office regions: EE, East of England; SE, South East; YH, Yorkshire and the Humber; EM, East Midlands; WM, West Midlands. For each region, the mean per hectare C_R and YL_R at each black-grass density state were multiplied by the crop area estimated to have that density state. For full details of scaling-up process see Methods and Supplementary Information.

density (Supplementary Fig. 3); however, as previously mentioned, estimates for the SE are unlikely to be representative of the region and should be viewed with caution.

Under the worst-case scenario, C_R is around two-and-a-half to three times the current C_R, except in winter wheat in northern regions: here, potential C_R in winter wheat is around nine times current C_R, again reflecting the fact that resistance is not yet so widespread in northern areas of England. To contextualize these costs in terms of the agrochemicals market, in 2014 herbicides contributed £0.2 billion to the United Kingdom National Agrochemical Market, the total value of which was £0.6 billion (ECPA Industry Statistics, 2018). Some of our estimates of the costs of resistance in England are greater than the entire value of herbicides to the UK agrochemicals market.

Our estimates indicate that low BG densities currently account for just over half of England's wheat-producing area (Supplementary Fig. 3) so there is a strong incentive to prevent densities increasing. In Europe, resistant BG has been recorded in 14 countries, including Europe's top wheat producers (Germany and France; Eurostat, 2018). European wheat consumption is forecast to increase slightly over the next 10 yr, so we urge wheat-producing countries to undertake their own national-scale resistance impact assessments.

Discussion

Here we report a national-scale estimate of the impacts of human-induced evolution of herbicide resistance. The scale of our findings illustrates that pesticide resistance has implications for national food security and economics. Annual potential losses of the order of 3 mt and £1 billion are large enough that national-scale policy measures are needed to reduce the impact and spread of resistance.

Resistance management is currently the responsibility of individual practitioners, whose collective actions constitute a national response. However, when pesticides are effective, there is an economic incentive for individual practitioners to use them and to crop mostly high-value crops such as winter wheat. This behaviour is unsustainable as it drives resistance[1,30], which we show has a negative impact on crop yields and income nationally. Our results suggest that leaving resistance management to individual practitioners is inadequate and that a national, targeted response is required. There is precedent for regulating pesticide use through environmental and health policies: there is now an urgent need for national-scale policy to regulate pesticide use in relation to resistance impacts on yield and economics.

When designing resistance management policy, governments should explicitly link economic, agricultural, environmental and health aspects. Joined-up legislation could encourage this: in Europe, for example, resistance management could be incorporated into existing legislation such as the EU Directive on the Sustainable Use of Pesticides (Directive 2009/128/EC), which already legislates to reduce pesticide risk to human health and the environment. Integration of these different policy arenas could ensure that legislation for reduced pesticide use based on environmental or health concerns also delivers resistance management benefits, and vice versa. From environmental and sustainability policy perspectives, the impacts estimated here could be used to further justify, in food security and economic terms, reduced pesticide use through practices like integrated pest management (IPM).

Resistance management policy via a national action plan should aim to (1) reduce the spread of resistance into unaffected areas and (2) find and communicate, non-chemical ways of reducing high weed populations in regions that have high resistance. A key aspect will be to reduce use of, and reliance on, pesticides because use is driving resistance. Reduced use has been recommended for other classes of xenobiotics, such as in the management of insect vectors of human disease[36] and has been implemented for prostate cancer[37]. Pesticide use could be reduced by improving crop rotation and using other IPM practices such as seedbed sanitation, careful choice of sowing dates and densities, direct sowing, physical control methods, field hygiene measures and regular monitoring[38–40].

Because resistance management could be a contentious issue, a national action plan should be formulated after public consultation, consensus-building and collaboration[41]. Providing the public with high-quality evidence and information is crucial to the success of these consultations: an assessment of the economic outcomes of reducing herbicide use and of the cost-effectiveness of a range of potential policies or mitigation strategies, would be a useful next step, both for the consultation process and subsequent policy design.

Statutory limits on pesticide use will probably be necessary and incentives and enforcement will be required to change behaviour. Agricultural policy could be used to incentivize and support farmers to change their management practices, for example, by stipulating improved crop rotation to qualify for income support or by providing support payments during the initial phase of reducing pesticide use and increasing IPM. This would be especially important where resistance is not currently a problem and it would be useful to estimate the short-term opportunity cost to individual practitioners of reducing pesticide use in areas with low resistance. Alternatively, governments could incorporate resistance management into Payments for Ecosystem Services schemes (or set up schemes where none exist) whereby farmers are rewarded for outcomes such as improved water quality or biodiversity, or maintenance of pesticide susceptibility in pest populations. Governments could also leverage commercial interest, for example, by introducing tax incentives for water companies to set up farmer advisory or support schemes to reduce pesticide use. Enforcement could take the form of caps on pesticide use and fines for breaking those limits or for spreading resistant weed seeds. Additionally, governments could legislate for disincentives to the herbicide manufacturing industry—for example, by higher taxation rates on sales over a threshold volume—and could reduce the influence of the agrochemicals industry by allocating public money to fund farm advisory services as well as research and development.

Finally, any pesticide resistance policy must also target glyphosate resistance. Glyphosate-resistant weeds are found on most continents[20] but are not yet in the United Kingdom. However, English farmers are increasingly reliant on glyphosate to control herbicide-resistant BG and there has been a dramatic increase in its use[42], ramping up the evolutionary pressure on BG to develop resistance to glyphosate, too[30]. In the United States, glyphosate resistance is widespread and the problem dwarfs that being faced with BG in England. A US-wide assessment of resistance-related costs and yield losses would inform national food-security planning. Worldwide there are many pesticide-resistant species[23,43,44]. Our findings should be a catalyst to other countries to develop national-scale estimates of the impacts of resistance as a first step in assessing the need for their own pesticide resistance strategies.

Methods

Field data. Field management data was obtained for years 2004–2014. Black-grass density and resistance, and winter wheat yield, were sampled from 2014–2017. For details see ref. [1]. Black-grass density states are given in Supplementary Table 10. To estimate costs of resistance, we used a subset of 66 fields from the full dataset (138 fields) and field management histories up to 2014. This subset comprised fields with ≥3-yr management history and with complete historical data on tillage operations and herbicide applications. Where soil type was not specified by the farmer, we extracted soil type from the National Soil Resources Institute NATMAP1000 database (Soils Data, Cranfield University (NSRI) and for the Controller of HMSO, 2016). We used BG density data from all 138 fields in the scaling-up process.

The cost of BG infestation (C_I) comes mainly from two factors: (1) the direct impact of BG on wheat yield through competition; (2) the cost of herbicides targeting BG (which may also be applied in crops other than wheat) and their application. There are also some additional, lesser costs, for example those incurred for an inversion plough. With respect to herbicides, we were interested only in calculating costs related directly to BG infestation: in the field management dataset, we therefore identified all herbicide applications specifically targeting BG. For all other herbicide costs (adjuvants, desiccants and applications not specifically targeting BG) we calculated an average value per crop from our dataset and incorporated this into the sundry costs in BGRI-ECOMOD. For the 13 observations where farmers had grown crops not included in BGRI-ECOMOD, we used proxy crops. Spring oilseed rape was the proxy for borage, millet and mustard (one observation of each); ware potatoes were the proxy for onions (one observation); and barley was the proxy for oats (seven observations) and triticale (two observations).

Economic model. We custom-built an economic model, BGRI-ECOMOD, capable of incorporating a wide range of farm management options and including a user-specified yield penalty for varying levels of weed infestation. The model code supplied incorporates the mean yield penalties from our data (see Fig. 1 and Supplementary Information); however, we enable users to specify yield penalties so that BGRI-ECOMOD can be used for different weed species, or be updated in light of new BG yield penalty data, or for running sensitivity analyses on the yield loss–weed density function. The model performs gross margin analysis (see equations (3–16) Supplementary Methods) and incorporates the effect of variables such as soil type, sowing date, tillage practices and yield penalties associated with crop sequences. This allows us to estimate the costs associated with a range of management practices aimed at reducing BG populations. It is built in R (ref. [45]) and uses a simple data-entry system. For further details see Supplementary Information and Code availability.

The baseline for this analysis was harvest 2014 because this was the first year in which we undertook field surveys of BG density and crop yield. All costings were therefore made using 2014 prices[46,47] (for example, we assumed a wheat price of £164 t^{-1}, which was the average for feed wheat (£155 t^{-1}) and milling wheat (£173 t^{-1}) in 2014). Prices given on GitHub, see Data availability. For herbicide prices we calculated mean values from our dataset: selective herbicides targeting BG = £19.50 l^{-1}, glyphosate = £2.43 l^{-1}. Estimates of the cost of resistance will vary, potentially greatly, as input prices (especially herbicide) and output prices (especially winter wheat) change each year.

The model can be run for multiple fields and years. This makes it useful for estimating economic impacts of current and historical weed infestations, for working with very large datasets—thereby enabling more reliable up-scaling to policy-relevant scales—and for aiding within-year decision-making at the field scale or multiyear planning at a farm or landscape scale.

Estimating yield loss due to black-grass. High-resolution yield data, available for 17 fields from years 2014–2017 (Supplementary Fig. 1), were used to estimate the BG density–wheat yield relationship (Fig. 1 and Supplementary Table 1) using a mixed effects model fitted using the lmer() function in the lme4 library[48] in R (ref. [45]; model details in Supplementary Methods and Supplementary Fig. 2). From this model we predicted mean yield at each density state in an 'average' field (Fig. 1a and Supplementary Table 2). Parametric bootstrap 95% confidence intervals (CIs) around these means were estimated from 10,000 resamples[49] from the model posterior with the 'bootMer()' function from lme4. We calculated the percentage reduction in yield (Fig. 1b) from the reference state ('low') for the other three density states using 1 – (predicted yield for state D/ reference state yield). These estimates of yield loss are in line with published yield losses due to BG in controlled plot experiments (Supplementary Table 3). We generated 95% CIs on the percentage reduction (used to inform limits in sensitivity analyses) by calculating the percentage reduction for each density state for each of the 10,000 bootstrap samples, then taking the 95% quantiles of those distributions of estimated percentage reductions. The resultant yield penalties applied in BGRI-ECOMOD are given in Supplementary Table 2. Further methodological details in Supplementary Information.

Estimating field-scale C_R and YL_R. Our aim was to estimate the average cost and yield loss per hectare for different densities of resistant BG at a baseline point in time (2014, see above). Costs were calculated using 2014 prices (and so will differ if using prices from other years).

Stage 1 was to estimate costs and yield losses due to BG infestation (I). First, we derived a yield penalty for each weed density state as described above and applied them as parameters in BGRI-ECOMOD. We then ran the historical field management data and BG density data from the 66 fields through BGRI-ECOMOD to estimate (1) yield loss due to BG infestation (YL_I), and (2) costs due to yield loss and herbicide application (chemical + operations costs) resulting from BG infestation (C_I), for every field in every year (maximum date range 2004–2014). We did this by running the model both with and without BG infestation, then subtracting the estimated gross profit or yield obtained in the presence of BG from that estimated in the absence of BG (the potential profit or yield).

For wheat, running the model with BG infestation involved four model runs because different BG density states resulted in different wheat yield penalties, so we had to run our field management history through the model once for each density state: in subsequent model runs, BG density for all fields was set at absent/low, then medium, then high and then very high states, each time using the observed herbicide and spraying data. For each field we then calculated mean gross profit and yield weighted by the proportion of each density state in the field (see Supplementary Fig. 3). Finally, the model was run without BG infestation, so the density state of all fields was set to absent/low and herbicide applications and spraying operations targeting BG were set to zero. The weighted mean gross profit (or yield) was then subtracted from the potential profit (or yield) to give a cost and yield loss due to BG infestation in winter wheat crops for each field. For other crops the process was simpler as BG density and yield were not surveyed. Therefore, to estimate C_I across all crops (which, for any given field, is effectively C_I across a rotation), the model was run only twice, with and without BG infestation, and then the calculated costs were averaged over the number of year's management history for each field, giving a mean rotation C_I for each field.

Stage 2 was the estimation of costs and yield losses due to resistant (R) plants. For each field, the frequency of resistance to mesosulfuron was then used to calculate the proportion of the costs or yield losses that were due to R plants, giving a cost of resistance (C_R) and yield loss due to resistance (YL_R). We chose the frequency of resistance to mesosulfuron because, of three actives tested, mesosulfuron (an ALS inhibitor) was the strongest driver of BG abundance in our fields in 2014 (D.C. et al., manuscript in preparation). Furthermore, ALS target-site resistance was identified as a particular concern back in 2007[26].

Using these field-scale estimates, for both winter wheat crops and rotations, we derived an average C_R and YL_R per hectare for each of the four weed density states. This was our baseline C_R and YL_R. Further methodological details given in Supplementary Fig. 3.

To estimate the worst-case scenario in winter wheat crops (cost and yield loss under a total loss of herbicide control), we used the methodology described in (2) above but assumed in the second model run that all quadrats in every field were in a very high density state. Because at very high density 100% of costs and yield losses were due to resistant plants, we assumed 100% of costs and yield loss were due to resistance. Herbicide applications remained unchanged—we used the herbicide application data from the management history—although, in reality, where BG was initially absent herbicide applications would have been likely to increase. The resulting per hectare costs differ very slightly to those calculated previously for very high density states because the management history data of all fields was used in this worst-case estimate, rather than the data from just those fields with very high average density states. We also made two more-conservative estimates of a worst-case scenario by scaling up the average costs and yield losses from fields in the top decile and top quintile of observed BG density states.

The relative contribution of herbicide application, yield loss and operations costs to overall cost in winter wheat crops (Fig. 3) was assessed by extracting individual components from ECOMOD output (output generated by running empirical field management data from 66 fields through ECOMOD, as described above). The effect of weed density on herbicide use in winter wheat crops was assessed using a generalized linear mixed effects model and performing a likelihood ratio test using maximum-likelihood simplification of the minimal adequate REML model. The model was fit with the lmer function in package lme4 (ref. [48]) and included farm as a random effect to account for multiple fields on the same farm. Model fit was assessed by visual inspection of residual plots, which indicated no signs of heteroscedasticity or non-normality.

Scaling up the cost of resistance. Fields were chosen to be representative of UK arable farming. Farms were predominantly arable, the geographic range (Oxfordshire to Yorkshire) encompassed the main winter wheat-growing areas of the United Kingdom, and a range of farm sizes was included. Within farms, field selection was based on those that were in winter wheat in the first survey year. Farmers were asked to select their 'best' and 'worst' fields in terms of BG infestation. We therefore assumed fields to be representative of both arable farming and BG resistance and density distributions within our wider study area and in England as a whole (evidence for which can be seen in that ECOMOD provides similar gross profit estimates to those in the Farm Business Survey[50], Supplementary Table 4). We scaled up the costs of resistance accordingly.

In winter wheat, C_R and YL_R were scaled up to regional winter wheat areas (DEFRA, 2014). For each region, we estimated the area of wheat at each BG density state by taking the proportion of that region's surveyed fields at each density state, then multiplying the regional wheat area by these proportions (Supplementary Fig. 3; all 138 fields in the dataset were used in this process). Next, for each density state and region, these wheat cropping areas were used to scale up the per hectare C_R and YL_R (Supplementary Methods, equation (1)). For each region, costs for each density state were summed to give a regional total (Supplementary Methods, equation (2)). This methodology ensures that the up-scaling of costs and yield losses in winter wheat better reflects regional differences in BG density[1]. The costs across rotations were scaled up directly to regional cereal cropping areas (DEFRA, 2014) as we have no data on BG density in crops other than wheat. Further details in Supplementary Methods.

Assumptions. We assume that the herbicide-resistant BG phenotype is present in every field, based on previous work[1] which found that only 1% of fields in our dataset had no resistance to any of the three herbicides tested. Furthermore, of the 126 fields from our dataset with the best-quality phenotyping data (these include northern fields, where resistance is less of a problem), only one field had <10% survival when fenoxaprop was applied at field rate. We are confident that that there is some level of herbicide survival in almost every field. In terms of the effect of herbicide, we assume that resistant (R) plants survive a field-relevant dose of herbicide. At the individual scale this means that R is binary (0|1) after herbicide. At the population scale it is more continuous (0–1): herbicide reduces BG abundance by the proportion of susceptible (S) individuals.

We assume that herbicide does not drive the BG seedbank to zero before the field evolves resistance. Weed eradication using herbicide alone is almost always impossible due to spatial and temporal refuges from herbicide treatments (for example, field margins, seedbank, asynchronous germination and transfer of weed seed between fields on machinery), so there are almost inevitably herbicide 'escapes' capable of maintaining a population. More broadly, feasibility studies of general weed eradication programmes have highlighted the concerted and prolonged effort required for eradication to be successful[51]. Despite relatively small field sizes, this degree of effort is unlikely to be met for most farms, particularly using herbicide alone.

We assume that the resistant BG phenotype has the same impact on yield as the susceptible wildtype. There is good evidence illustrating how limited the effects of both non-target-site resistance (NTSR) and some predominant target-site resistance (TSR) mutations are on relative performance of R and S BG biotypes[52–54] and thus any influence on competition with the crop is likely to be negligible. Comparisons of NTSR and susceptible BG found no consistent fitness costs, either when grown alone or in competition with winter wheat[52,54]. In a study of three ACCase TSR mutations in BG[53], one mutant allele (Gly-2078) did result in a small reduction in biomass and seed production; however, this mutation is rare, with a frequency of only 0.34% based on previous genotyping of 8,256 haplotypes from UK BG[55]. Additionally, there is some evidence that the small fitness costs associated with this mutation are rapidly lost in BG populations due to compensatory evolution[56]. Two mutations (Leu-1781 and Asn-2041), which are considerably more common in UK BG[55], had no effect on vegetative biomass, height or seed production compared to S wildtype plants. We are thus confident in our assumption that R phenotypes of BG have the same impact on yield as the S wildtype.

To calculate C_R across the time span of our dataset (2004–2014) we assumed that the density state of a field as recorded in 2014 also applied to all the preceding years for which we had management history data (we had no density data pre-2014). Hicks et al.[1] found slight evidence for a within-field increase in density between 2014 and 2016, and showed that resistance is driving BG density. However, this increase in density is not at a magnitude to change the categorical density state of a field unless over a fairly long timescale and could well simply represent normal inter-annual fluctuations. To test the validity of using the entire time span, we re-ran the analysis on just the later part of the time series (2010–2014 inclusive). Although this gave slightly higher costs (Supplementary Table 9), the costs estimated using 2010–2014 data fell within the 95% CIs estimated using 2004–2014 data, indicating that the assumption holds here.

To estimate the worst-case scenario in winter wheat crops, we assumed all quadrats in every field were at very high density state and that resistant plants were responsible for 100% of costs and yield losses. This scenario would arise only if no action were taken to address current problems of herbicide resistance and assumes that farmers keep applying herbicide even once its efficacy is limited. Although there is evidence for these types of behaviours[1,57,58], this scenario is not anticipated and we present it only to highlight the worst possible effects of inaction.

Model testing and evaluation. Model tests were carried out on yield and gross margin. For evaluation of yield estimates, we first removed from the dataset any observations ($n = 13$) where a farmer grew a crop not modelled by BGRI-ECOMOD. The model accurately estimated yield both with ($R^2 = 0.91$, slope = 1.05; Supplementary Fig. 4) and without ($R^2 = 0.97$, slope = 1.05, Supplementary Fig. 4) failed crops in the dataset (BGRI-ECOMOD is unable to predict crop failure). We also evaluated yield estimates without the heavy crops (potatoes, sugar beet) to remove their influence on the relationship: the model still estimated yield well ($R^2 = 0.74$, slope = 1.01). Estimated regional gross margin fell within the 95% CIs for the regional values obtained from Farm Business Survey data (Supplementary Table 4). Furthermore, the model was robust to sensitivity testing on tractor work rates during different tillage operations, which was the management variable for which published data were lacking. We varied the proportions used to calculate tillage work rates in relation to ploughing work rate: the range tested was +30% to −30% (±5%, ±10%, ±20% and ±30%) of initial values. There was no effect on the per hectare C_R (results not shown).

The model was, however, sensitive to the yield penalty applied for BG infestation. We observed considerable variability in the yield loss–weed density relationship (Supplementary Fig. 1), especially at the highest density, and so ran a sensitivity analysis based on the extremes from our data and the literature (Supplementary Table 10). The consequences of using different yield penalties are given in the results and in Supplementary Table 11. Full details of model tests and sensitivity analyses are given in Supplementary Methods.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Model data and input template are available at https://github.com/alexavarah/BGRI-ECOMOD. Data used to generate the yield penalty can be accessed at https://github.com/alexavarah/BGcosts. The field management dataset has been deposited in the University of Sheffield Online Research data archive (ORDA) and can be accessed at https://figshare.com/s/eb21f4d1862741d50ceb.

Code availability

Model code is available at https://github.com/alexavarah/BGRI-ECOMOD.

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Author contributions

Data were collected by H.H., D.C., L.C. and R.H. BGRI-ECOMOD was designed by A.V. and K.A. and built by K.A. A.V. did all analysis. S.C. and D.C. generated the yield penalty estimates and associated figures, and S.C. contributed to sensitivity analysis work. R.F. contributed the density map in Fig. 2. A.V. drafted the initial manuscript and H.H, D.C., S.C, P.N., D.Z.C., R.F. and K.N. contributed to refining it. Funding was acquired by R.F., D.Z.C., P.N. and K.N.

Competing interests

P.N. supervises a PhD student cofunded by Bayer (not part of this project). All other authors have no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41893-019-0450-8.

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Data used to generate the yield penalty can be accessed at https://github.com/alexavarah/BGcosts.
The field management data set has been deposited in the University of Sheffield Online Research data archive (ORDA) and can be accessed at https://figshare.com/s/eb21f4d1862741d50ceb.

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We used large-scale farm management data and black-grass (Alopecurus myosuroides) density survey data, plus a small yield loss survey dataset which was partly from a previously published study (Hicks, H. L. et al. Nat. Ecol. Evol. 2, 529–536 (2018)), and a dataset of resistance frequencies in the black-grass populations used in the study. From the yield loss survey data we estimated a yield penalty due to black-grass and used this, together with the farm management and weed density data, to estimate the costs and yield losses due to black-grass infestation using a custom-built economic model. We then applied resistance frequencies to model output to calculate the proportion of losses due to herbicide-resistant black-grass in England.
Research sample	As in Hicks et al. (2018, Nature Eco & Evo): The sample sizes for the survey work were based on previous surveys of similar size and scope. The sample size for the experiments were based on previous experiments in other species that yielded reliable results. FARM MANAGEMENT DATA: we used a subset of 66 fields on 35 farms from a previously published study (Hicks et al. 2018, Nature Eco & Evo). WEED DENSITY SURVEYS: 138 fields. See Hicks et al. (2018, Nature Eco & Evo) for details. YIELD LOSS DUE TO BLACK-GRASS: 17 fields over 4 years (2014-2017) for which high resolution yield data was available - for each of these fields the entire field was surveyed. RESISTANCE FREQUENCY DATA: frequency of resistance to mesosulfuron was assessed for the black-grass population in each of the 66 fields used.
Sampling strategy	FARM MANAGEMENT DATA: from Hicks et al (Nature Eco & Evo, 2018): "Study sites were selected to cover a large geographic range, and to include a variety of farm sizes, crop rotations and management strategies within each region. Two fields were selected on each farm, one known to have large black-grass populations and one with a smaller weed population. For accurate comparison, all fields selected were cropped with winter wheat for harvest in 2014.... " WEED DENSITY SURVEYS: from Hicks et al (Nature Eco & Evo, 2018): "One hundred and thirty-eight fields with black-grass present were censused in a six-week period from 1 July 2014.....Fields were divided into contiguous 20 × 20 m grid squares and weed density was estimated in each grid square. The surveys followed a density-structured approach, recording the density state of black-grass rather than numerical abundance." YIELD LOSS DUE TO BLACK-GRASS: Entire field sampled by obtaining yield maps from combine harvester data, plus black-grass density surveys as described above. See Hicks et al. (2018, Nature Eco & Evo). RESISTANCE TESTING: from Hicks et al (Nature Eco & Evo, 2018): "Black-grass seeds were collected from ten different locations within each field surveyed in 2014, using a semi-random seed collection strategy..."
Data collection	FARM MANAGEMENT DATA: from Hicks et al (Nature Eco & Evo, 2018): "Historical field management data were requested for each of the 138 fields that we surveyed for weed density. Data were available for 96 fields and up to 10 years of data were collated for each field. For each year, we recorded the following: crop, first cultivation type and herbicide applications (product name and date of application)." We extracted soil type for each field from the National Soil Resources Institute NATMAP1000 database. WEED DENSITY SURVEYS: From Hicks et al (Nature Eco & Evo, 2018): "Fields were divided into contiguous 20×20 m grid squares and weed density was estimated in each grid square. The surveys followed a density-structured approach, recording the density state of black-grass rather than numerical abundance. Each grid square was assigned to 1 of 5 density states that correspond to the number of plants per 20m×20m square: 0 (absent), 1 (1–160 plants), 2 (160–450 plants), 3 (450–1,450 plants) and 4 (1,450+plants). These density states have been shown to accurately capture the variation within field populations and the 20×20 m grid size sufficient to be representative of 1 m2 subplots where black-grass plants were physically counted. Areas within fields that were sprayed off or cut early were classified as state 4, to reflect management for very high levels of black-grass infestation." YIELD LOSS DUE TO BLACK-GRASS: combine harvester data. See Hicks et al. (2018, Nature Eco & Evo). RESISTANCE ASSAYS: from Hicks et al (2018, Nature Eco & Evo): "A. myosuroides seedlings were germinated and allowed to grow for 18–21 days until reaching the 3-leaf stage before spraying with herbicide. We tested for resistance to 3 herbicides at the following rates: Atlantis (mesosulfuron + iodosulfuron at 300 g ha−1), Cheetah (fenoxaprop at 1.25 l ha−1) and Laser (cycloxydim at 0.75 l ha −1)....Plants remained in the glasshouse for three weeks following herbicide treatment, at which point plant mortality was recorded before harvesting above-ground biomass from each pot. Plant material was dried at 80 °C for 48 h before weighing..."
Timing and spatial scale	138 fields from across England were surveyed during a six-week period from 1 July 2014. Field management history ranged from 3 years to 10 years. Yield penalty was estimated from data from 17 fields, from 2014-2017, across counties from Oxfordshire to Yorkshire in the north and Norfolk in the east.
Data exclusions	Of the fields for which we obtained management history, those with fewer than 3 years' management history and those lacking yield, tillage or herbicide application data were excluded from the modelling. Density data from all 138 fields were used in the scaling-up process.
Reproducibility	Not relevant.

Randomization	Observational study: we did not assign to groups.
Blinding	As above: this is an observational study.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Wheat fields, summers of 2014-2017
Location	138 wheat fields across England, exact locations not available for privacy reasons.
Access and import/export	not applicable
Disturbance	none

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Unique biological materials
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology
☒	☐	Animals and other organisms
☒	☐	Human research participants

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging