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Long-term trends in migrating *Brassicogethes aeneus* in the UK

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Abstract

BACKGROUND: The pollen beetle (*Brassicogethes aeneus*) causes significant yield loss in oilseed rape (*Brassica napus*). Predicting population changes remains a scientific challenge, especially since its phenology and abundance varies dramatically over space and time. We used generalized additive models to investigate the long-term trends in pollen beetle annual, seasonal and monthly counts from Rothamsted 12.2 m suction-traps. We hypothesised that the beetle's abundance is positively related to the area of oilseed rape at a national and regional level. We used random forest models to investigate the inter-generational relationship within years.

RESULTS: Although *Brassicogethes aeneus* annual counts and area of oilseed rape grown in the UK both increased by 162% and 113%, respectively, over the time period studied, they were not significantly related. The size of the immigrating pollen beetle population (up to 1 June) can be explained both by the size of the population in the previous summer and prevailing winter temperatures, indicating a positive feedback mechanism.

CONCLUSION: Currently, pollen beetle numbers continue to increase in the UK, meaning that control issues may persist. However the relationship between counts in spring, during the susceptible phase of the crop, and counts in the previous summer indicates that it may be possible to forecast the counts of the spring migration of *Brassicogethes aeneus* a few months in advance using suction-trap samples, which could aid decisions on control options.
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Supporting information may be found in the online version of this article.

Keywords: pollen beetle; *Meligethes aeneus*; monitoring; decision support; suction-trap

1 INTRODUCTION

Long-term monitoring of agricultural pests allows us to forecast future outbreaks over space and time.[1,2] Currently, most insecticide application decisions are made either prophylactically or based on breaches of economic thresholds of pest prevalence following crop inspection.[3–5] However, thresholds are not economically viable in all cropping systems,[6,7] are often inaccurate and not widely used by growers.[7] Predictions of pest risk generated from forecasts can be a major benefit if this knowledge is disseminated to growers, allowing them to take preventative rather than prophylactic measures to control the target pest,[3,8,9] provided that these forecasts are issued within a generous potential treatment window.

There are very few datasets that allow long-term quantitative trends in insect populations to be derived.[10,11] Perhaps the best known is the Rothamsted Insect Survey[12] database and archives. The database contains more than 50 million records, primarily of moth and aphid count data over more than 50 years across the UK from a network of light traps and 12.2 m suction-traps[13,14]; furthermore, the archive contains ~200 000 samples of bycatch from 39 suction-traps.[15] This long-term dataset has enabled forecasting tools to be developed for some species of aphid that show a strong relationship between winter temperature and their

phenology and abundance.[12,16] The dataset has also shown the potential for forecasting in other taxa found in the bycatch, for example biting midges.[17] The bycatch has recently been demonstrated to have the potential to inform studies of a range of aerial taxa,[18–21] however, previous to the work reported here, pollen beetles (*Brassicogethes (Meligethes) aeneus* (Fab.)) had not been studied in detail using the 12.2 m suction-trap network.

Much of the recent research on long-term insect trends has focussed on declines in abundance, with habitat loss often cited as an important driver of these declines[11,22–27] conversely, in the UK and northern and eastern Europe, the pollen beetle has seen its area of habitat increase in recent years.[28,29] The development

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of reduced glucosinolate and eruic acid varieties of oilseed rape (OSR) in Canada in the 1970s[30,31] led to a rapid rise in the area under oilseed cultivation in Europe.[32] In the UK, the crop briefly became the second most widely grown crop in the country, reaching a peak in 2012 at 756 000 ha with more than 600 000 ha grown in most years – representing around 9–12% of the total cropped area.[33,34] This increase in hectarage was reflected across most of northern and eastern Europe.[29,32] It has already been demonstrated that *B. aeneus* is able to rapidly shift to OSR from native brassica hosts when these crops are introduced to an area.[28] This ability to shift to OSR has allowed the beetle to exploit the crop's increase that occurred in Europe in the second half of the 20th century and become an abundant pest throughout the region.[28] The crop area has plateaued since 2012, declining in all years except 2018, along with yield in most years.[34] The crop is now at its lowest acreage in a decade.[34] Whether or not these changes in cropping practise relates to population changes of pollen beetles is unknown.

Pollen beetles are a pernicious pest of OSR,[35,36] causing feeding damage in buds which can lead to bud abscission.[36–38] They are univoltine,[36,39,40] with the new adult generation emerging in mid- to late-summer and hibernating over winter before emerging in spring to feed and reproduce.[36] As most winter OSR is past the susceptible stage by the time the beetles emerge from hibernation the damage to these crops is usually minimal,[36] although early beetle emergence or late flowering can lead to economic loss.[41] In late spring, however, feeding damage to spring-sown OSR, and horticultural brassica crops, can be extensive[2,42–44] because both the beetles that overwintered and their progeny are active. Measuring seasonal phenology and abundance of *B. aeneus* throughout the season and across years could give insight into how the populations fluctuate through time with changes in climate and land-use and allow the development of forecasting and DSS (Decision Support System) tools.

The main aims of this study were to understand the long-term pollen beetle population trends in the UK and to elucidate the meteorological and landscape level drivers of these trends in order to assess the potential for forecasting beetle counts using suction-traps. Our hypotheses are that (i) pollen beetle counts follow the national trend for OSR area sown, (ii) that counts of pollen beetles in the spring can be predicted by counts in the preceding summer and (iii) that annual fluctuations can be explained by key meteorological drivers.

2 MATERIALS AND METHODS

2.1 Pollen beetle counts from suction-traps
Rothamsted Insect Survey (RIS) suction-traps[12,45] have been used to monitor and forecast aphids in the UK since 1964.[16] The traps sample aerial insect populations at 12.2 m above ground level by drawing air at a rate of 45 m³ min⁻¹;[45] samples are collected daily with the aphids removed, identified and counted and the bycatch stored in a mixture of ethanol and glycerol.[18] The presence of glycerol means that, though samples do become dehydrated over time, they remain undamaged on rehydration.

For the duration of this study the 12 suction-traps sites were used to investigate annual pollen beetle population fluctuations over time, but only a subset of these traps was used to report annual population change over decades, prioritising sites that had an unbroken time series (Supporting Information, Table S1, Fig. S1). Two sampling regimes were used:

(i) To investigate differences between counts of *B. aeneus* in the spring and summer we identified and counted *B. aeneus* from the bycatch from all 12 suction-trap sites for the period between January through to September, the known flight period of *B. aeneus* in the RIS samples, for the years 2015–2018. At Preston, due to low beetle counts in high volume samples, only 2015 samples were processed.

(ii) Two sites were selected for investigation of the long-term trends of *B. aeneus* counts based on trap longevity, consistency of operation and known high counts: Rothamsted Tower 1987–2014 and Brooms Barn 1989–2014; *B. aeneus* from these site years were counted in the same way as the 2015–2018 samples.

In all samples, *B. aeneus* were counted, but were not distinguished from the closely related *Brassicogethes viridescens* (Fab.) which is comparatively rare[46,47] and random subsamples failed to identify any *B. viridescens* in suction-trap samples. To assess the interaction between generations within the year and the effect of overwintering on beetle numbers, the annual total of beetles caught at the trap was subdivided for each year at 1 June. Those caught between the start of the year and 31 May were assumed to be those emerging from hibernation and migrating to breeding sites, with those caught from 1 June onwards assumed to be those of the new generation.

2.2 Oilseed rape (OSR)
Regional-level OSR cultivation around the suction-trap sites were accessed from the UK Department of the Environment, Food and Rural Affairs (Defra) statistics portal using their regional definitions for England.[33,48] Total area of OSR sown (in hectares), yield (in t ha⁻¹) and production (in tonnes) from 1983–2019 for the UK as a whole and 2001–2015 for English regions were derived (Table S2).

2.3 Statistical models
The following analyses were carried out:

(i) an assessment of the long-term trends in annual *B. aeneus* counts at Rothamsted and Brooms Barn.

(ii) an assessment of the relationship between annual *B. aeneus* counts and the area sown of OSR both at a national scale and at a scale local to the suction-traps.

(iii) an exploration of how *B. aeneus* counts change between years and generations, using daily or weekly beetle counts.

All analyses were carried out in R versions 3.5.0 and 3.6.1[49] using RStudio Version 1.1.453.[50] *A priori* the statistical distribution of all observations (daily count of *B. aeneus* and annual values for area of OSR) was assessed using the fitdistrplus library along with the *post hoc* model diagnostics in the routine gam.check; the negative binomial or the quasipoisson distributions proved to be the best fits to these data.[51,52] Winter OSR forms more than 95% of the total OSR area grown in the UK[33,48] and from the OSR dataset it was not possible to distinguish area of spring and winter-sown OSR for all years so the total annual value was used (Table S2).

Long-term trends were modelled using generalized additive models (GAMs) and generalized additive mixed models (GAMMs) using the mgcv library[52] and poptrend, an extension of the mgcv library that tests for the presence of both short-term trends within the spline and long-term trend over the entire time series.[53] See Supporting Information, Appendix S1 for more details on GAMs. For models produced by mgcv, the significance of the smooth

terms are constrained such that they each sum to a zero mean over the covariate values. The shape of the spline can be deduced but this does not extend to any systematic difference between temporal means. Instead, a Wald zero-effect test is provided to indicate if the smoother is equal to zero. Significant P-values indicate that smooths have significantly departed from zero. Parametric coefficients would only test between factor levels, with the reference value being the start of the time series and is not in itself informative and is not reported. The Akaike information criterion (AIC) method was used for model selection.[54,55] AIC was estimated using the AIC() function in base R.

2.3.1 Long-term trends in pollen beetle counts

Annual *B. aeneus* population trends for the east of England, using Rothamsted and Brooms Barn data, alongside some seasonal subsets of the data as defined in Table 1, were estimated using pop-trend. A smoothing spline for year was fitted with a negative binomial distribution for overdispersed data and automatic selection of optimal degrees of freedom. The dispersion parameter theta (Θ) was estimated at 3.707 after estimation using the nb function of mgcv. Year was a fixed effect and site were set as random effects.

2.3.2 Relationship between the number of pollen beetles and area of OSR at different temporal and spatial scales

After testing for temporal autocorrelation, the relationship between *B. aeneus* counts and the area of OSR sown in the UK, at local and national scales, was assessed using a GAM within the mgcv package.[52] A cubic spline was used for the area and year fixed effects, with the individual suction-traps (Rothamsted Tower and Brooms Barn sites) set as a factor for area and year terms which allows individual model trends for area and year by site. Data were overdispersed and hence a negative binomial was used. The model used restricted maximum likelihood (REML), which penalises overfitting.[52]

For the shorter time period (2001–2015) where regional data were available for OSR area, Pearson correlation analyses were performed using the cor function in base R and plotted using the ggscatter function from the ggpubr library.[56] Data from all sites from 2015 were compared with winter OSR area sown for the region (Table S1). Correlation analyses were preferred over more complex models, such as GAMs, due to the reduced power from the restricted (1 year) dataset.

2.3.3 Relationship between the number of pollen beetles in spring and summer

Each calendar year contains two generations of *B. aeneus* – an overwintered generation and their offspring, which fly in late summer. To investigate the relationship between the counts of these generations, daily data from all 12 suction-traps were used (Table S1, Fig. S1). Count data for each year was divided into the two generations, with an ecologically relevant estimated cut-off date marking the generational division set at 1 June and summed to give a value for each generation in each trap year. Two correlation analyses were carried out (i) comparing the counts of pollen beetles in the spring with the counts of pollen beetles in the following summer and (ii) comparing the counts of pollen beetles in the summer with the counts of pollen beetles in the following year's spring, that is, testing whether (i) the counts of the parent generation are related to the counts of their offspring and (ii) whether counts of pollen beetles in the summer are reflected in the size of the population post-hibernation. Pearson correlation analyses were performed using the cor function in base R and plotted using the ggscatter function from the ggpubr library.

2.3.4 Drivers of overwintered beetle counts

To further determine what drivers determined the size of the counts of pollen beetles in the spring two models were used: a GAM and a random forest machine learning approach, please see Appendix S1 for more information on these techniques.

In addition to the count of beetles in summer of the preceding year, the following meteorological parameters were selected as random effects: Winter Rainfall, designated as the mean rainfall during the months December, January and February; Winter Grass Temperature, designated as the accumulated day degrees of the Grass Minimum Temperature below 0 °C during the months December, January and February; Autumn Rainfall, designated as the mean rainfall during the months September, October and November; and Spring Temperature, designated as the accumulated day degrees of air temperature over 6 °C during the months March, April and May. The rainfall parameters were selected to explore the effects of precipitation during overwintering (Winter Rainfall); and waterlogging of the soil prior to, or during, the beetles selecting their overwintering sites (Autumn Rainfall). The temperature parameters were selected to explore the effects of low temperatures at ground level where beetles are overwintering (Winter Temperature) and the direct effects of warm, or cold springs on pollen beetles emerging from hibernation (Spring Temperature).

For the GAM the long-term data from Brooms Barn and Rothamsted were used. The GAM function in the mgcv R package was used to create four models using a reverse selection process where the least significant variable was removed in an iterative process from the full model with all terms and a final model with three terms. AIC was then used to select the best model from these. Each model contained penalised thin-plate splines for each explanatory variable with REML cross-validation[57,58] and the number of knots not fixed (i.e., the model was allowed to suggest the best value for this number).[52,59] Due to only two sites being used it was not possible to include any random effects of, for example, year or site. Year was included as a fixed effect. See Appendix S1 for more information.

TABLE 1. Subsets of *Brassicogethes aeneus* count data from Rothamsted suction-traps (1987–2018) analysed alongside the full dataset with calculated theta (Θ) values

Season/month	Duration	Dispersion parameter theta (Θ)
Spring	1 March–31 May	3.961196
Summer	1 June–30 September	4.163855
March/April	1 March–30 April	3.305895
May	1–31 May	4.361432
June	1–30 June	3.521173
July	1–31 July	2.858764
August/ September	1 August–30 September	0.695337

Note: March/April and August/September were combined due to generally low counts in those months.

For the random forest analysis RandomForest,[60] rpart[61] and partykit[62] libraries were used. RandomForest was used to fit classification trees to the full dataset [i.e., all sites (Table S1), all years (1987–2018)], combining the predictions from these trees to produce a decision tree with predictions based on variables ranked by predictive value.[63] Each model run generated 5000 trees with each run having an 'mtry' parameter (the number of variables available for splitting at each tree node) of four (the square root of the number of variables). There is some discussion as to the suitability of RandomForest for analysis that includes variables that vary in their scale of measurement as they do with the *B. aeneus* dataset,[64] however the tree partitioning algorithm should be independent of scaling for most circumstances, since they are merely attempting to establish thresholds within the data. Each model was run ten times (creating 50 000 trees) to obtain an estimate of variation in variable importance.

3 RESULTS

3.1 Long-term trends in pollen beetle counts
In total 37 143 pollen beetles were recorded. Both Rothamsted and Brooms Barn showed similar values for *B. aeneus* counts in each year (Fig. 1), and they were closely correlated ($t = 6.549$, df = 28, $P < 0.001$, $r = 0.78$). An apparent 5–6 year cycle in the data is not supported by further analysis (see Fig. 2 and later). Trend analysis using the poptrends package suggests that beetle populations at the two sites have increased by 162% (standard error (s.e.) 5.5%, 607%); there was no significant trend in numbers until around 2006, when a significant upturning began a positive trend that continued to increase significantly until the dataset ends in 2018 (Fig. 2). At the seasonal level there was a non-significant trend in counts in all years except 2010–2012 where the upward trend was significant in the spring (Fig. S2(a)) whilst the trend in the summer matched the annual trend, although there was no significant change in the curvature (Fig. S2(b)). At the monthly level, populations in March/April showed no significant trend (Fig. S3(a)), whilst May, June and August/September showed a similar pattern to the annual data (Fig. S3(b)–(e)) although the magnitude of the trend differs across months. March/April and May showed no significant curvature changes aside from the end points (Fig. S3(a),(b)) with the upward trend in May starting later than the full dataset, around 2007 (Fig. S3 (b)). June and August/September showed upward curve changes and 2006–2007 and 2009–2010, respectively (Fig. S3(c),(e)), also comparable to the full dataset though the significant positive trend started earlier, around 2004. July showed a more complex result, with upward curvature noted around 1995–1997, 2001 and 2005–2006 but only the trace of a significantly increasing trend around 2011 and a significant decline in 2003–2004 (Fig. S3(d)). Of those that show a significant upward trend, the magnitude is similar across all datasets with the exception of August/September which has much steeper trend.

3.2 Relationship between the number of pollen beetles and area of OSR at different temporal and spatial scales
Trend analysis suggested that area of OSR cultivation in the UK increased by 113% (s.e. 84%, 145%) between 2001 and 2015; area increased significantly from the start of the dataset until 2011 and remained relatively stable from then until the dataset ends in 2015 (Fig. S4). The GAM of annual *B. aeneus* counts from
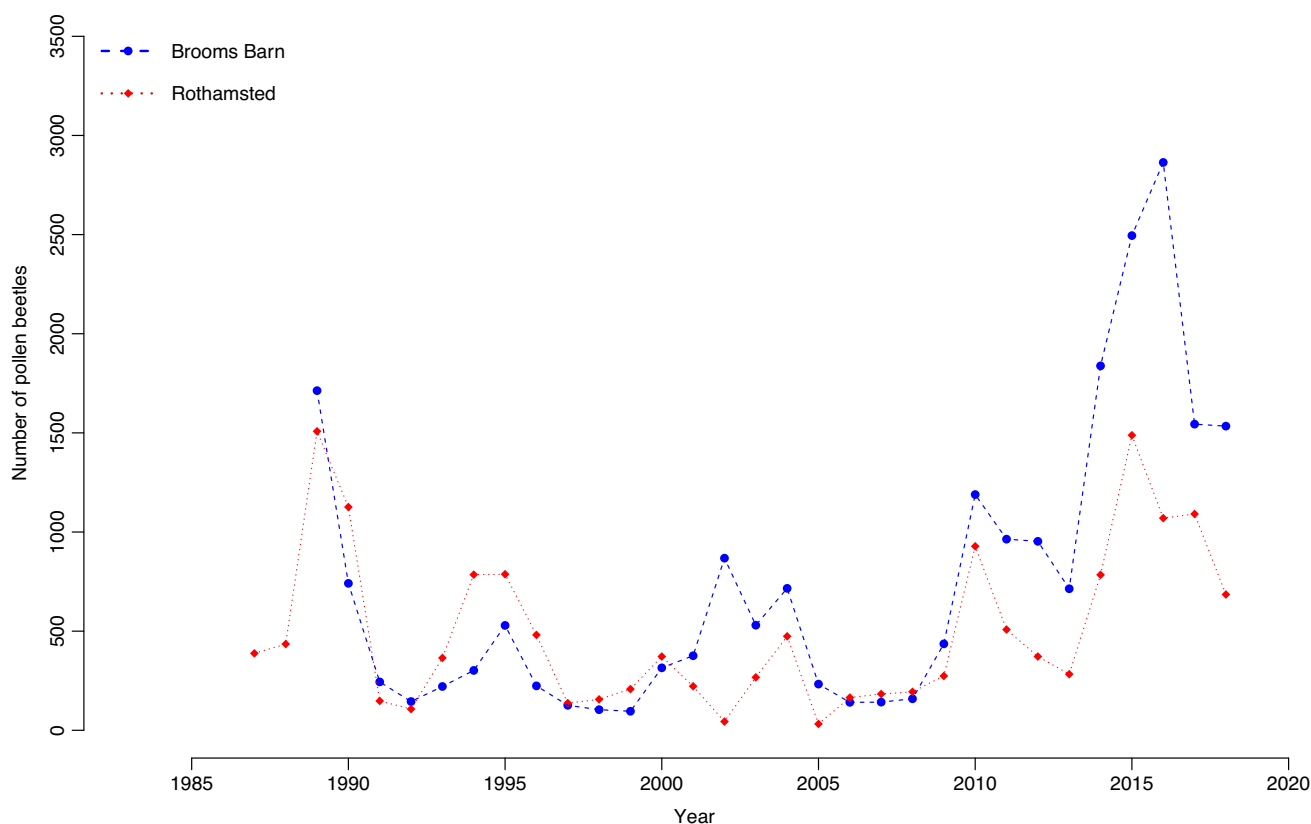
Figure 1. Annual count of *Brassicogethes aeneus* caught by Rothamsted and Brooms Barn suction-traps UK, 1987–2018.
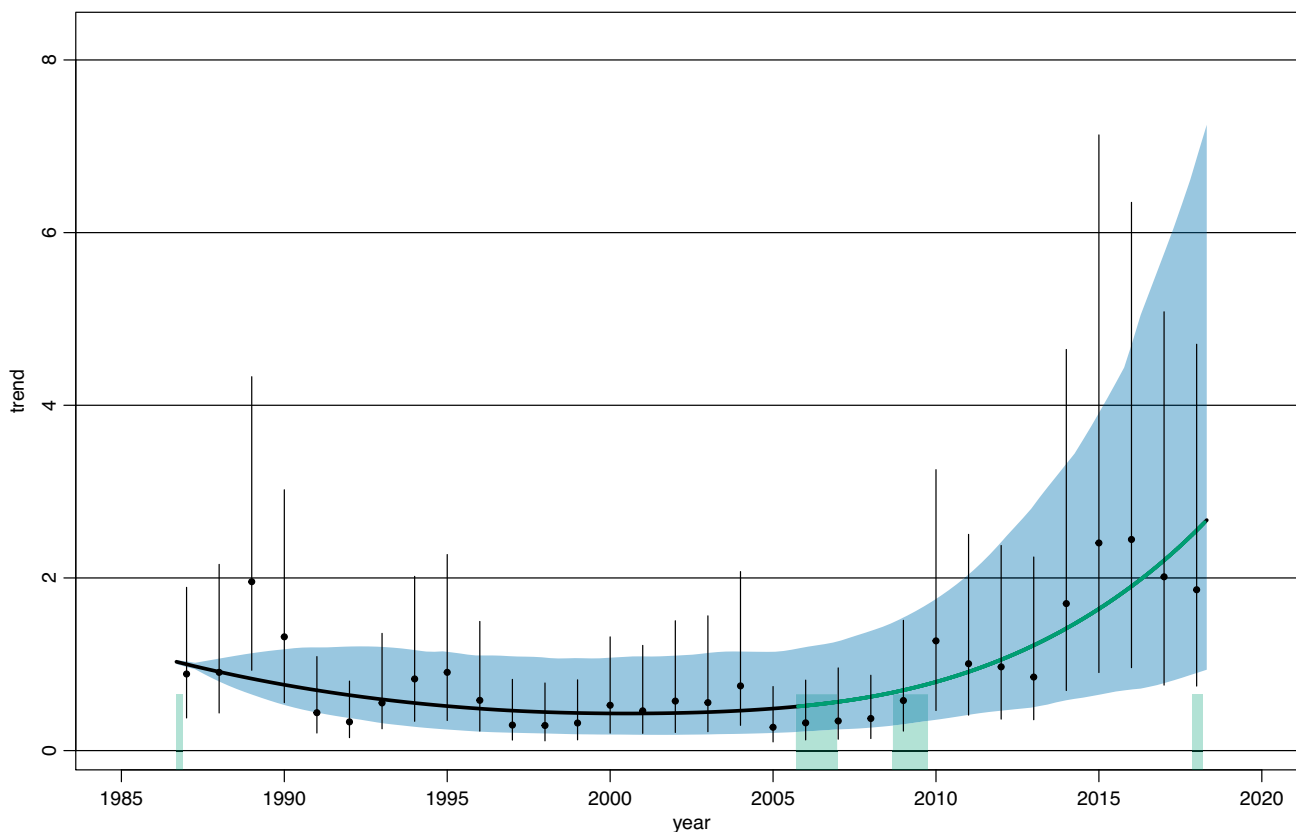
Figure 2. Standardised regional trend for the annual count of *Brassicogethes aeneus* caught in suction-traps at Rothamsted and Brooms Barn. All trends are relative measures that are standardised against the total predicted area in the first year (the reference year). If significant, short-term increasing trends are depicted along the spline in green, shown on top of the long-term trend coloured black. The green rectangles on the *x* axis indicate periods with significantly positive curvature. Beetle populations have increased by 162% (s.e. 5.5%, 607%) over the time period.

TABLE 2. Summary statistics for the generalized additive model of the relationship between *Brassicogethes aeneus* counts in suction-traps at Rothamsted and Brooms Barn 1987–2018 and year and area of oilseed rape

A. Parametric coefficients	Estimate	Standard error	*t*-Value	*P*-Value
(Intercept)	5.7463	0.4176	13.7599	<0.0001*
Area	0.0014	0.0008	1.7057	0.0881

| B. Smooth terms	edf	Ref.df	*F*-Value	*P*-Value
s(fST)	0.0174	1.0000	0.0182	0.3228
s(fST, Year)	0.5457	2.0000	1.2381	0.1405

Note: Standard error is the standard error of the estimates, edf is the estimated degrees of freedom – a larger edf implies a more complex, wiggly, spline. Ref.df is the reference number of degrees of freedom used for computing the test statistic and *P*-values.

suction-traps at Rothamsted and Brooms Barn showed a non-significant relationship with year (Table 2, Fig. 3): Despite pollen beetle numbers and area of OSR[34] both increasing over time, there was no significant relationship between the number of pollen beetles and area of OSR sown. The annual number of beetles in 2015 was only weakly correlated with the area of winter OSR crop in the respective region (Fig. S5) ($t = 2.392$, df = 10, $P < 0.05$, $r = 0.6$).

3.3 Relationship between the number of pollen beetles in spring and summer

Correlation analysis using data from all suction-trap sites suggested that the relationship between the counts of pollen beetles

entering hibernation and the counts of pollen beetles emerging in the following spring was significantly positive ($t = 5.283$, df = 96, $P < 0.001$, $r = 0.47$; Fig. 4(a)), despite some instances when counts of pollen beetles in the summer measured in the low 200s led to high counts of pollen beetles in the following spring at Hereford, Wellesbourne and Brooms Barn. There was also a significantly positive correlation between counts of pollen beetles in spring and their progeny, that is, the counts of beetles the following summer ($t = 11.108$, df = 85, $P < 0.001$, $r = 0.77$; Fig. 4(b)). Of note is that counts in the summer were generally lower than those in the spring but these correlations show that fluctuations in numbers tend to follow through into the subsequent generation.
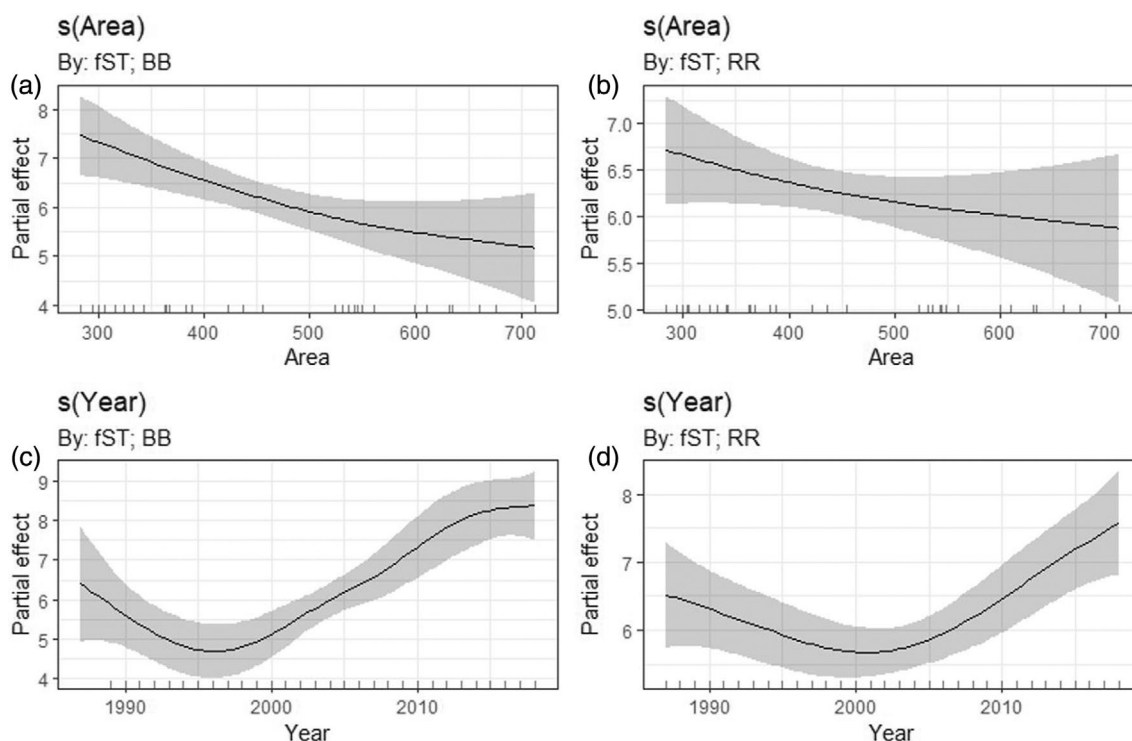
Figure 3. Generalized Additive Model of the relationship between the area (a, b) of oilseed rape sown in the UK and year (c, d) with annual *Brassicogethes aeneus* numbers caught in suction-traps at Brooms Barn (BB: a, c) and Rothamsted (RR: b, d) 1987–2018. The estimated smoothed terms are a transformed function of area or year. The solid line shows the calculated relationship with 95% confidence intervals represented by grey shading. Rug marks on the *x* axis represent sampling points. Partial effects (*y* axis) are the isolated effects of the particular interaction on the numbers caught.

3.4 Drivers of overwintered beetle counts

Closer examination of the potential drivers of the counts of pollen beetles in the spring resulted in a model including all the weather covariates selected. Despite several terms being non-significant in the model (Table 3), model selection using AIC suggested that this 'all covariates' model was the best option compared to models that excluded some covariates. GAM plots (Fig. 5) showed that, although not significant, year and winter temperature had linear effects on counts of the counts of pollen beetles in the spring, with later years and lower temperatures having positive effects on beetle population numbers. The relationship with other parameters was more complex: winter rainfall had little effect though extremely wet winters appear to result in higher beetle counts in spring (although it should be noted that this is based on very few data points – only 3 years with a mean daily rainfall of > 3 mm); increased autumn rainfall appears to have a generally negative effect on beetle counts at the extremes, although between ~1.5 and 3 mm d^{-1} the effect of greater rainfall is positive; spring temperature has a significant, but humped relationship with beetle counts, with extreme high and low temperatures having negative influence on numbers. The size of the counts of pollen beetles had a significant positive effect on counts of pollen beetles in the spring in the following year, though not linear, and it must be noted that the data where counts > 750 beetles are sparse, which may explain the levelling of the relationship between counts of 500 and 1000 pollen beetles in the summer.

The random forest analysis (Fig. 6) indicates that the counts of beetles caught in summer of the previous year explains the counts of beetles in the following spring. If counts from 1 June onwards fall below 92 (eight instances) then spring counts the

following year are below 200. If summer counts are between 92 and 244 (14 instances) then spring counts are generally low – a 30% chance of 0–200, 60% of 200–600 and 10% of 600–1000. Summer counts of 245 or more increase the chance of higher counts in the following spring. If accumulated winter temperatures are below −30.7 °C (ten instances), spring counts of 600–1000 are expected 50% of the time, with a 20% chance of 200–600 or 1000–1400 and a 10% of 0–200 beetles. Warmer winters with accumulated temperatures greater than 30.7 °C (11 instances) lead to spring counts being generally higher with 40% of counts greater than 1400, 30% 1000–1400, 20% 600–1000 and 10% 200–600.

In short, counts of *B. aeneus* in the summer can forecast counts of beetles flying after emerging from hibernation. When these counts are medium to low, assessment of no other factor is needed to forecast low or very low counts, respectively. When summer total counts are above 245 then winter accumulated temperature needs to be considered, with increased temperatures in winter leading to higher numbers of beetles migrating in spring.

4 DISCUSSION

4.1 Increase of pollen beetles and OSR

Our hypothesis that pollen beetle counts would follow the national trend for OSR area sown as expected from previous research[28] was not proven. It is clear that *B. aeneus* populations are increasing in the UK (Fig. 2), along with an increase in the area of its cropped host plant[34] over the time periods studied, however, there is no correlation in the increase between these variables in the long-term at a national scale (Table 2, Fig. 3) and
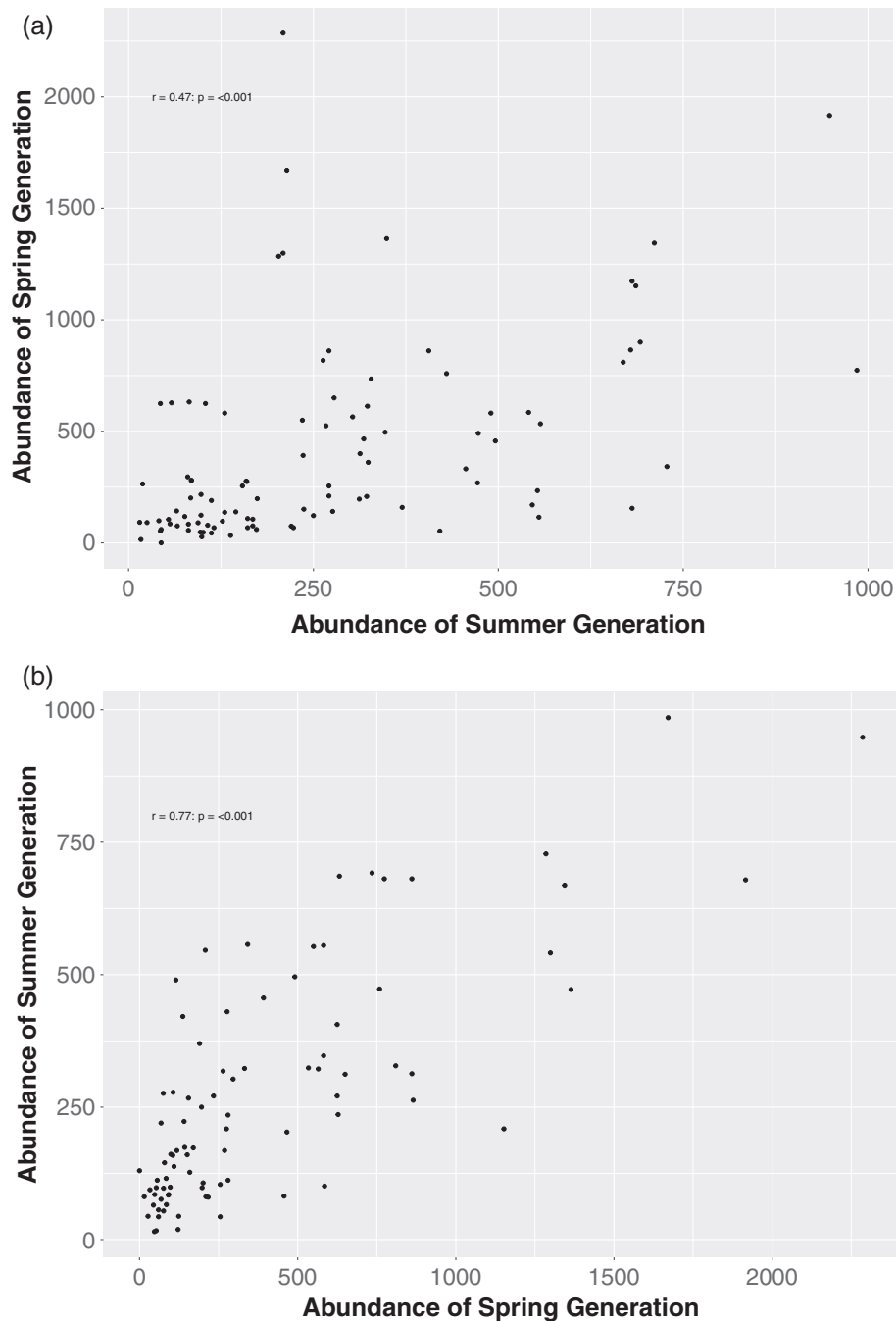
Figure 4. (a) Correlation plot showing the relationship between the counts of *Brassicogethes aeneus* caught before 1 June (Spring Generation) and the counts caught after 1 June the previous year (Summer Generation). (b) Correlation plot showing the relationship between the number of *B. aeneus* caught after 1 June (Summer Generation) and the beetles caught before 1 June in spring (Spring Generation). Beetles caught in suction-traps at ten sites (2015–2018) and two sites (1987–2018) in the UK.

regionally, there is only a weak positive correlation between 2000 and 2015 (Fig. S5). The continual increase in the *B. aeneus* population as opposed to the trend in OSR area sown reaching an asymptote in 2011 (Fig. S4), and the fact that *B. aeneus* populations continue to increase beyond 2011 helps to explain the lack of a strong relationship between the two variables in most cases. This may indicate that *B. aeneus* populations may not yet have reached saturation with habitat area in the UK (i.e., the carrying capacity, or maximum population size that can be supported sustainably within the ecosystem, for *B. aeneus* in new OSR habitat

has not been filled[65]). Alternatively it may be the relatively recent development of pyrethroid insecticide resistance in *B. aeneus*[66] that has led to increased populations. Either way, this apparent continued increase in *B. aeneus* may have severe consequences for growers as this could mean (a) increased yield loss as larger populations overwhelm permitted control measures,[28,41] (b) a larger pool of individuals allowing greater adaptation within the population[67,68] and thus (c) increased likelihood of insecticide resistance developing. The strong negative relationship found between counts and cropped area in the UK (Fig. 3(a),(b))

TABLE 3. Summary statistics for generalized additive models of relationship between the numbers of *Brassicogethes aeneus* caught in suction-traps in the spring and meteorological and population parameters selected to explain the counts

A. Parametric coefficients	Estimate	Standard error	*t*-Value	*P*-Value
(Intercept)	241.3517	13.5578	17.8016	<0.0001

B. Smooth terms	edf	Ref.df	*F*-Value	*P*-Value
s(Year)	1	1	2.1051	0.1545
s(Winter.Rain)	2.6575	3.3068	0.917	0.4626
s(Winter.Grass.Acc)	1	1	1.6062	0.2123
s(Autumn.Rain)	6.0412	7.0431	1.9913	0.0771
s(Spring.Temp.Acc)	3.3432	4.1091	2.8991	0.0337
s(Summer)	4.9882	5.8891	17.2944	<0.0001

Note: Standard error is the standard error of the estimates, edf is the estimated degrees of freedom – a larger edf implies a more complex, wiggly, spline. Ref.df is the reference number of degrees of freedom used for computing the test statistic and *P*-values.
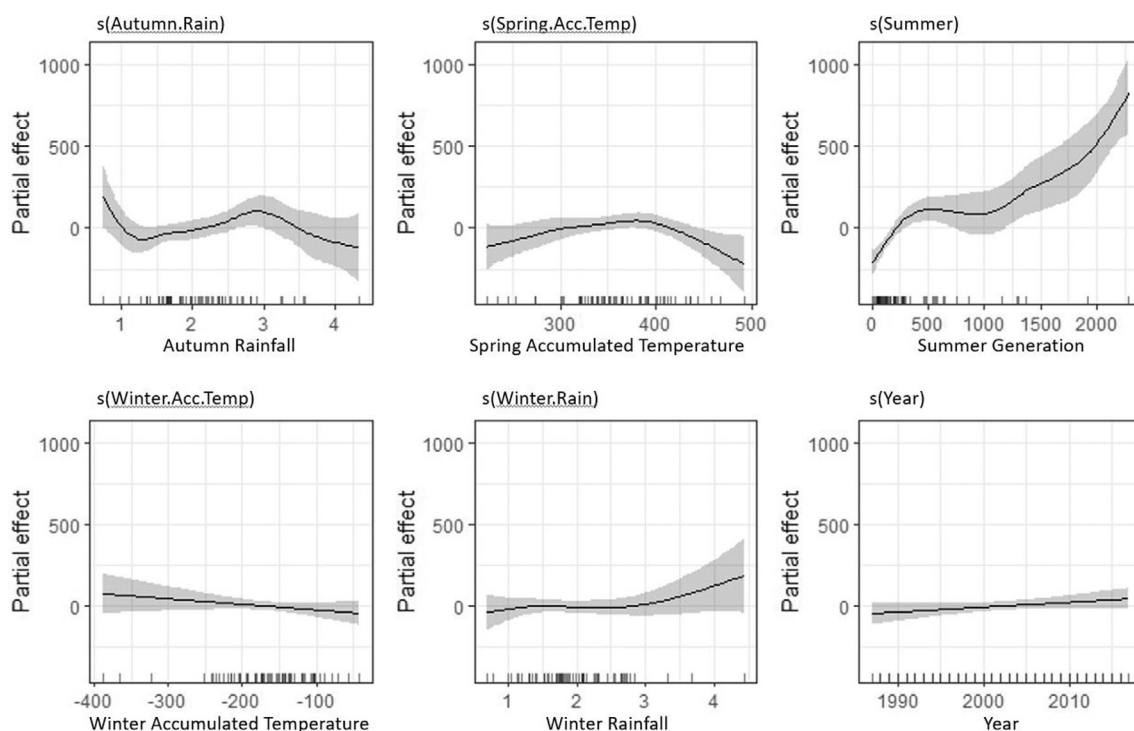

Figure 5. Generalized Additive Model (GAM) of the relationship between the numbers of *Brassicogethes aeneus* caught in suction-traps at Rothamsted and Brooms Barn (1987–2018) in the spring, and meteorological and population parameters selected to explain the counts. The estimated smoothed terms are a transformed function which on the *y* axis is centred on zero and scaled by the effective degrees of freedom. Partial effects (*y* axis) are the isolated effects of the particular covariate on the numbers caught. This GAM is estimated by penalised restricted maximum likelihood to minimise overfitting, hence linear terms with estimated degrees of freedom for year and winter temperature equal to 1. Conversely, the remaining drivers were non-linear, the most complex of which was autumn rainfall. Only accumulated spring temperature and summer beetle numbers were significant. See Supporting Information, Appendix S1 for further information.

indicates a much weaker relationship between pollen beetles and their host than previously thought. It could reflect the fact that, in later years the area of OSR in the east and southeast regions (where Rothamsted Tower and Brooms Barn suction-traps are located) has stayed stable or has decreased, despite increases in cropping area in other regions, all the while *B. aeneus* counts have been on an increasing trajectory. However, in the absence of regional cropping data for the post-2015 period, the role, or not, of OSR can only be speculation and may have ignored lagged effects between increased resource and increased pest

populations or management changes in the region. With cropped area of OSR set to drop significantly in the short term[48] it will be insightful to see whether *B. aeneus* populations continue to increase or whether they follow the well-established population cycle dynamics seen in other ecological systems, reaching a point where numbers crash before returning to a density-dependent multi-year cycle, albeit at higher counts than previously.[69–71]

The increasing overall trend in *B. aeneus* counts is in alignment with the cabbage stem flea beetle (*Psylliodes chrysocephala* L.), which has shown large increases in larval counts in recent years.[72]
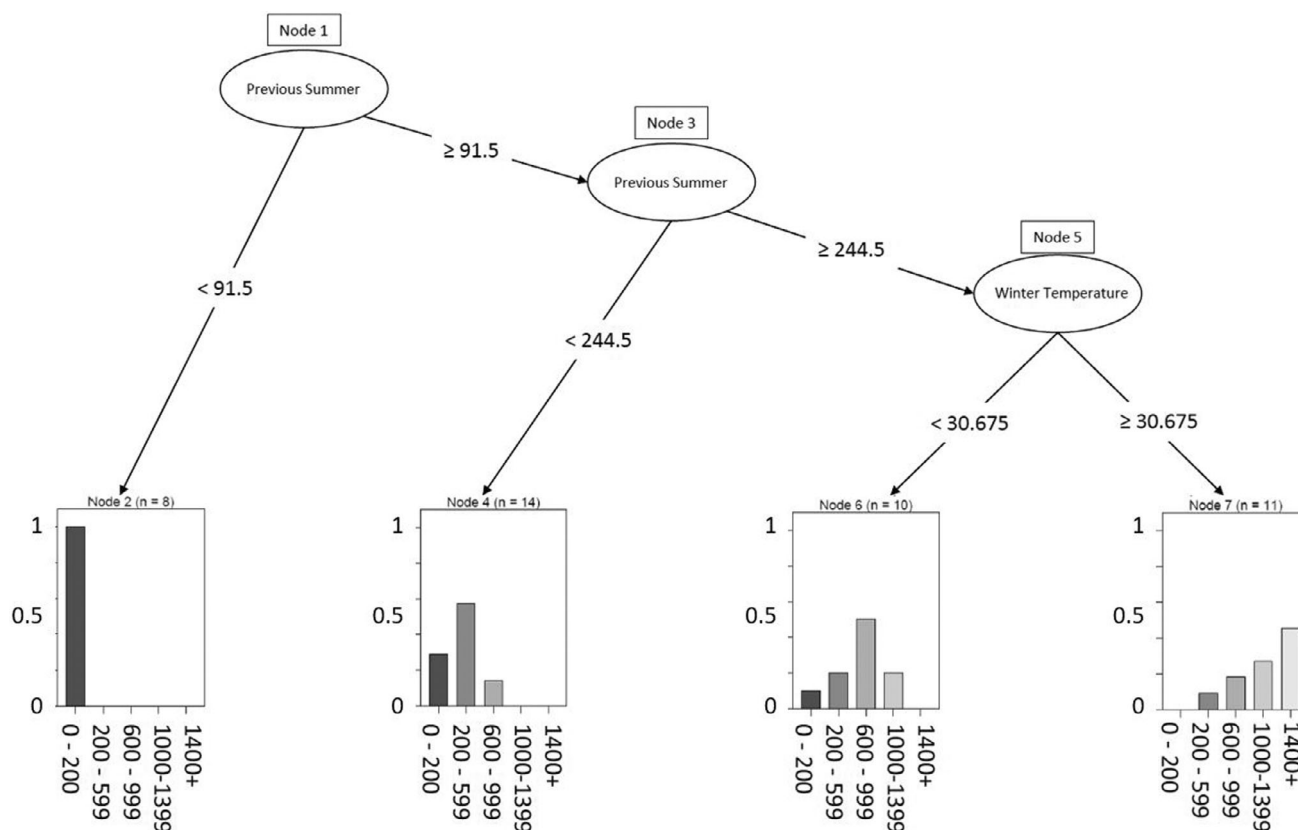
Figure 6. Random forest decision tree showing predicted counts of *Brassicogethes aeneus* in spring, given the counts caught in suction-traps in the previous summer and accumulated winter temperature. Each decision node (Nodes 1, 3 and 5) is split by the determinant factor in that node. Each terminal node (Nodes 2, 4, 6 and 7) gives a probability distribution of summer counts in suction-traps (1 = 100% probability). Low to moderate counts in the previous summer (Nodes 1 and 3) result in low to moderate counts in spring (Nodes 2 and 4); higher counts in the summer (Node 3) lead to high counts (Node 7) if accumulated winter temperatures are high (Node 5) or moderate counts (Node 6) if winter temperature remains below 30.68 day degrees.

Conversely, these beetle trends are contrary to the trend in brassica-feeding butterflies in England, with the small white butterfly (*Pieris rapae* (L.)) and large white butterfly (*Pieris brassicae* (L.)) both showing non-significant declines between 1990 and 2018.[73] These different responses demonstrate that the complex interactions within an ecosystem mean that there is large variability between species, both in magnitude and/or direction of any individual driver of change.[74]

4.2 Pattern of increase within year

We found that the pattern of the increasing annual trend in *B. aeneus* counts is generally consistent with trends measured within year [though it appears that August/September counts are increasing at a greater rate (Fig. S3(e))], but inconsistent with early season (March/April, Fig. S3(a)) and July (Fig. S3(d)) trends, suggesting that the increase in seasonal counts is not driven consistently by the same drivers within a season when partitioned by month(s). The different pattern in July is hard to explain, it could perhaps be a function of delayed or advanced emergence of the new generation or related to the timing of OSR development in different years.

4.3 Relationship between the number of pollen beetles and area of OSR at different temporal and spatial scales

The relationship between the counts of pollen beetles in spring and summer in suction-traps both within and between years is a promising finding, indicating that there may be potential to forecast numbers migrating in the spring – the period when crops are most at risk – based on counts taken in the summer of the previous year. Given that there is a large amount of variation in this relationship, any conclusions drawn must be viewed as tentative. Reports on *B. aeneus* counts released in late summer could allow growers to adjust their crop rotations accordingly to choose an alternative to OSR, or to distance fields within farms to minimise risk[75] in years of high forecast counts, and alternatively to increase OSR planting when forecast counts are low. This could also allow growers more flexibility when ordering insecticide in advance or save money by not purchasing product. It potentially would also allow growers to be ready and prepared to deal with *B. aeneus* problems in a timely manner. In the UK the only pest forecast model able to predict pest pressure on an as yet unsown crop forecasts virus in sugar beet,[76] with research ongoing with some success in other crops, for example in wheat bulb fly (*Delia coarctata* Fállen).[77] Elsewhere an autumn forecast model is available for sugarbeet weevil (*Bothynoderus punctiventris* Germ.) in the Ukraine, although details are scant.[78,79]

4.4 Drivers of overwintered beetle counts

The GAMs and random forest analysis indicate that the counts of pollen beetles in the summer of the previous year are an important predictor of the counts of pollen beetles in the following spring – reinforcing the findings of the basic correlation analysis. The two analyses – GAM and Random forest – suggest that the meteorological parameters included within those models could

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be modifying drivers. The GAM (Table 3) showed that, although the counts of pollen beetles in the summer and spring temperature were the only significant drivers, model selection could not exclude any of the meteorological terms in developing the best model. Conversely the random forest analysis showed that, at high counts of pollen beetles in the preceding summer, winter temperature will modify the counts of pollen beetles the following spring. Both analyses do indicate that the most powerful predictor of counts of pollen beetles in the spring is the counts of pollen beetles recorded in the previous summer. This means that counts taken from suction-trap samples in July and August could be used to make an initial assessment of the size of the *B. aeneus* migration the following spring, providing early warning to growers as to the level of risk expected in spring. This would facilitate decision-making, helping growers to plan and adjust their management strategies in advance. In the UK, winter OSR drilling dates would come too early for such warnings to inform crop selection decisions, though they may influence the selection of spring-sown crops. Early warnings may allow growers to make better plans for crop management (chemical or otherwise) during the pollen beetle migration period in the spring.

Importantly, the data and analyses presented here are from suction-trap samples taken at 12.2 m and populations at this height may not translate into pest outbreaks in the field. The relationship between counts of suction-trapped aphids and field counts has been demonstrated,[80–83] however for pollen beetles this proved intractable[84] and has not been investigated for other taxa. Further work is required to demonstrate that field outbreaks can be predicted by suction-trap counts of pollen beetles before early warnings could be made with confidence.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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