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Emerging health threat and cost of *Fusarium* mycotoxins in European wheat

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Mycotoxins harm human and livestock health, while damaging economies. Here we reveal the changing threat of *Fusarium* head blight (FHB) mycotoxins in European wheat, using data from the European Food Safety Agency and agribusiness (BIOMIN, World Mycotoxin Survey) for ten years (2010–2019). We show persistent, high, single- and multi-mycotoxin contamination alongside changing temporal-geographical distributions, indicative of altering FHB disease pressure and pathogen populations, highlighting the potential synergistic negative health consequences and economic cost.

Mycotoxins are fungal secondary metabolites that are toxic to humans and livestock. They occur when fungal pathogens infect crops and contaminate their products. Mycotoxins contaminate 60–80% of crops, with 20% of global crops exceeding European Union (EU) legal food safety limits[1].

Fusarium head blight (FHB) is a mycotoxigenic preharvest fungal disease of cereals, including wheat, which is a pivotal crop for human nutritional security[2], livestock feed and international trade. Different *Fusarium* species within the FHB complex produce various mycotoxins that threaten human and livestock health, causing a wide range of toxic effects[3]. Therefore, the EU commission sets legal limits on FHB mycotoxin levels in food, but only guidelines for feed[4]. Grain exceeding the legal mycotoxin limit is downgraded from food to animal feed at an economic cost. Multi-mycotoxin synergisms are also an emerging concern for human and animal health[5].

Effective FHB management requires an understanding of the current and changing scale of the disease. FHB symptoms on United Kingdom wheat have increased substantially since 2000 (Extended Data Fig. 1), but equivalent data on the incidence of FHB symptoms are lacking for Europe. However, FHB mycotoxins in the food and feed supply chains are monitored by the European Food Safety Agency (EFSA) and agribusiness (BIOMIN, World Mycotoxin Survey). These datasets have been used to assess global mycotoxin occurrence[1,6], whereas FHB mycotoxin reports from individual European countries have been reviewed[7]. However, we require a clearer picture of the scale of the FHB mycotoxin problem in European food and feed wheat. Therefore, this work aimed to use these comprehensive mycotoxin datasets to quantify the changing threat from, and estimate the economic cost of, FHB in Europe. This spatiotemporal analysis of FHB mycotoxins in food and feed will provide quantitative insights into disease pressure, pathogen population composition and economic effect, thus facilitating future mycotoxin research and modelling, risk mitigation strategies and improved legislation.

EFSA and BIOMIN data for the FHB mycotoxins deoxynivalenol (DON), fumonisin (FUM), zearalenone (ZEN) and T-2 were analysed for a ten-year period (2010–2019). DON occurrence (the percentage of wheat samples testing positive for DON) and levels (concentration of DON in a sample) were evaluated. In line with previous reports[1,6] and the dominance of DON-producing *Fusarium graminearum* and *F. culmorum* on European wheat[8], DON was the most common FHB mycotoxin in European food and feed wheat (Fig. 1a). European countries showed a positive correlation between food and feed, both in DON occurrence and levels (Extended Data Fig. 2a,b). This finding was as expected because wheat is divided into the food or feed streams postharvest based on quality (for example, protein content). If a geographic region experiences high disease pressure, this will increase DON in wheat throughout that region, regardless of whether the grain will later be designated as food or feed. DON occurrence and levels were lower in food wheat than in feed wheat. This suggests that supply chain management, such as postharvest downgrading of grain exceeding the DON limit for human consumption to animal feed, works effectively to reduce DON entering the food stream. DON in feed wheat may therefore be a more realistic indicator of FHB pressure in the field.

DON was detected in food wheat from all European countries studied (average occurrence 47%, Fig. 1a), being most common at higher latitudes, with 93–69% wheat contamination in Sweden, the United Kingdom and Denmark. The occurrence of DON in United Kingdom wheat was consistent with recorded incidence of FHB disease

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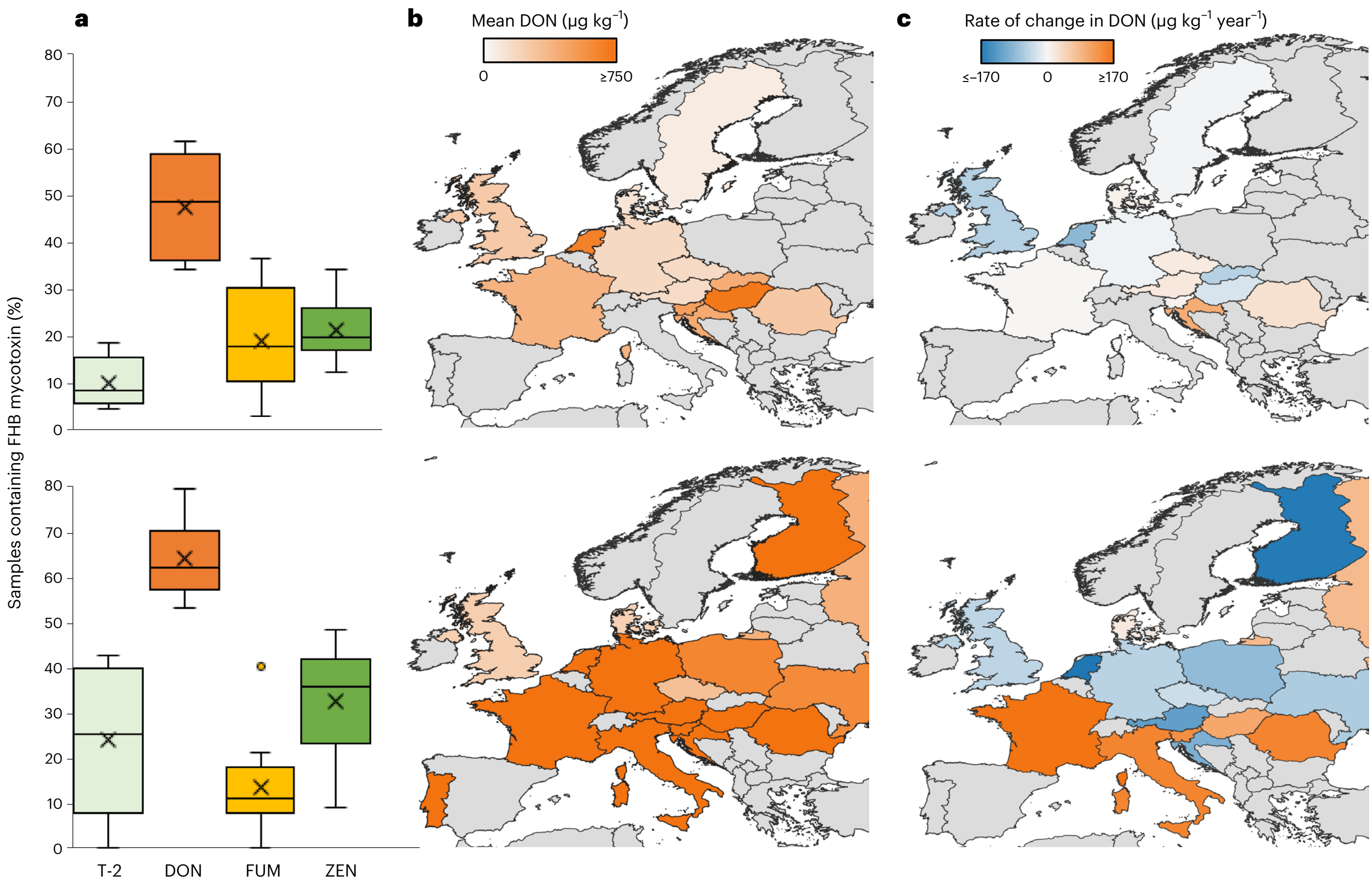

Fig. 1 | FHB mycotoxins in European food (top) and feed (bottom) wheat, 2010–2019. a, Percentage samples containing the FHB mycotoxins T-2, DON, FUM and ZEN. Box plots: centre lines indicate the median; box limits indicate the 25th and 75th percentiles; whiskers indicate the range; outliers are represented by dots. *N* food = 3,467, 6,519, 588, 4,953 samples. *N* feed = 2,673, 6,547, 2,090, 5,388 samples. **b**, Mean DON concentration (μg kg^{-1}). **c**, Rate of change in DON level (μg kg^{-1} yr^{-1}). White indicates no change. Grey indicates insufficient data.

symptoms in the field over the same period[9] (Extended Data Fig. 1). DON occurrence remained relatively stable in most countries over the decade. Concerningly, DON levels were moderately high in contaminated food wheat (mean 358 μg kg^{-1}), 5% of samples exceeded the 750 μg kg^{-1} legal limit for cereals for direct human consumption and the highest DON concentration recorded was 14,505 μg kg^{-1}. The highest ten-year mean DON concentrations were in Hungary (722 μg kg^{-1}) and the Netherlands (670 μg kg^{-1}) (Fig. 1b). These were attributable to 'peak' years of elevated DON levels in 2010, 2011, 2015 and 2019 in Hungary and 2012 in the Netherlands. Contrary to expectation, a modest negative correlation between DON occurrence and mean level was seen in individual European countries (Extended Data Fig. 2c). Countries where DON was more common tended to record lower DON concentrations. For example, Sweden, Denmark and the United Kingdom showed a high occurrence of DON but at low concentrations, perhaps reflecting effective food supply chain mitigation to keep levels within legal limits. Nonetheless, the omnipresence of DON in food and at higher concentrations during peak years necessitates continuous and responsive FHB management. This raises concerns of chronic dietary DON exposure affecting human health. Indeed, the EFSA estimates that European chronic dietary exposure to DON exceeds the tolerable daily intake for children and is high in adolescents and adults[10].

The situation in feed wheat was more concerning. DON was again the most common FHB mycotoxin (Fig. 1a), detected annually in every country, but at a higher prevalence (64%) than in food. In contrast to food, there was a positive correlation between DON prevalence and concentration in feed (Extended Data Fig. 2d). The ten-year average concentration of DON in contaminated feed wheat was 858 μg kg^{-1}, exceeding the limit for human consumption. Of this, 1.5% exceeded EU maximum guidance values for animal feed (8000 μg kg^{-1}), with DON concentrations of up to 49,000 μg kg^{-1} detected. Lower-latitude countries showed the highest prevalence (93–85% in France, Italy and Slovenia) and mean DON levels (1,393–1,279 μg kg^{-1} in France, Hungary and Romania) (Fig. 1b). The lowest, but still relatively high, DON levels (312–216 μg kg^{-1}) were Denmark, the United Kingdom and Czechia. European livestock are therefore continuously exposed to high DON levels in feed wheat, potentially with negative animal health consequences.

A geographical pattern of changing threat from DON in feed wheat has emerged over the last decade. DON levels increased in countries below ~47° N latitude (Portugal, France and Romania; at a rate of +362 to 148 μg kg^{-1} yr), but decreased in countries above this latitude (the Netherlands, Finland and Austria; −258 to 118 μg kg^{-1} yr^{-1}) (Fig. 1c). This trend was attributable to higher DON levels in peak years in the early 2010s and lower-level peaks in the late 2010s in higher-latitude countries, compared to lower-latitude countries, which had lower levels in the early 2010s and high-level peaks in 2018 and 2019. Peaks years of DON concentrations correspond to reported European FHB epidemics (Romania 2019 (ref. [11]), Italy 2016 (ref. [12]), United Kingdom 2012 (ref. [9]); Extended Data Fig. 1). Increasing DON levels in peak years in lower latitudes was suggestive of increasingly severe FHB epidemics. This could be attributable to changing agronomic practices and climate. The adoption of minimum tillage farming practices and maize cultivation is known to increase FHB disease by providing a substrate for

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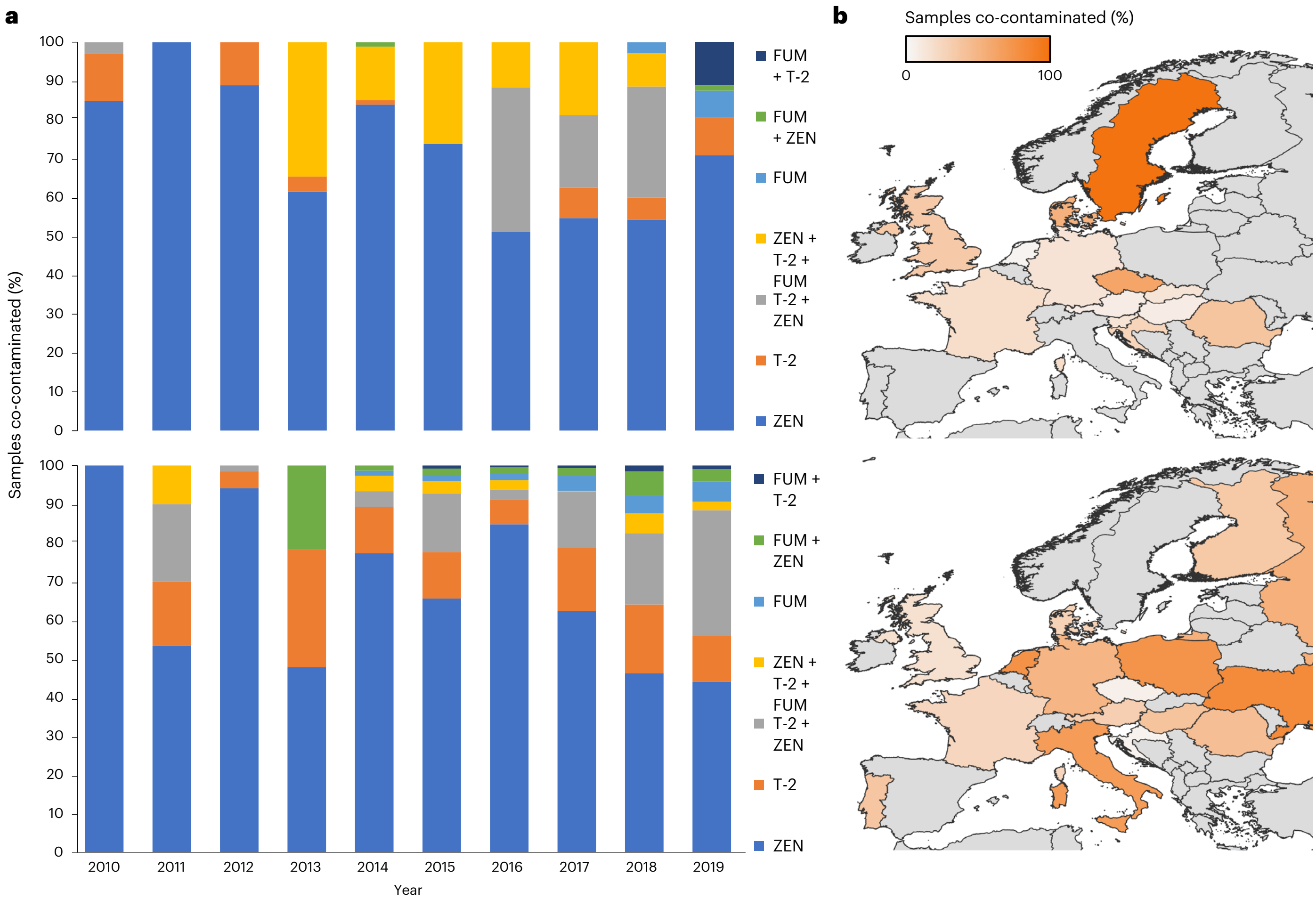

Fig. 2 | Multi-mycotoxin contamination in European wheat intended for food (top) and feed (bottom), 2010–2019. a, Frequency of DON co-contamination with other FHB mycotoxins (%). **b**, Percentage of wheat co-contaminated in European countries. White indicates no co-contamination. Grey indicates insufficient data[17,34].

Fusarium to overwinter and produce inoculum in the spring[13,14]. Wheat infection occurs during anthesis and is promoted by high humidity and temperatures[15]. Climate change is projected to cause earlier anthesis, coinciding with wetter, warmer weather, thus increasing the severity of FHB epidemics[16]. Indeed, countries with similar trends in DON levels also tended to have similar climates[17] (Extended Data Fig. 3). There were exceptions to this pattern; whereas most temperate oceanic (Cfb) countries showed DON levels were decreasing, DON levels in France (also classified as temperate oceanic (Cfb)) were increasing, akin to countries with Mediterranean (Csa) climates. This highlights the need for access to finer geographic resolution mycotoxin records to account for countries with distinct internal climatic zones, but also the need to understand differences in non-climatic factors, such as agronomic practice or pathogen population structure, to help explain this variation. Interestingly, lower-latitude regions of Europe have also been predicted to be increasingly at risk from other cereal mycotoxins, due to host-crop range expansion and climate change[18]. *Fusarium* populations vary in fungicide sensitivity[19], and therefore emergence of fungicide resistance could also be a contributing factor. Collectively, this highlights the need to monitor FHB mycotoxin outbreaks and fungicide resistance for improved forecasting and threat mitigation.

Although DON dominates, concern is growing about synergisms between co-occurring mycotoxins. We evaluated the risk of co-contamination with other FHB mycotoxins. It should be noted that wheat tested for DON was not necessarily also tested for all other mycotoxins, and thus non-detection of a co-contaminant could be due to absence or a lack of testing. Approximately 25% of food and 45% of feed wheat containing DON tested positive for other FHB mycotoxins. The percentage of samples co-contaminated was stable over the decade, but the mycotoxin profile changed and multiple co-contaminants became more frequent (Fig. 2a), with ZEN and T-2 being the most common co-contaminants in food and feed. The high co-occurrence of ZEN with DON was expected, as they are both produced by *F. graminearum* and *F. culmorum*[20]. FUM co-contamination suggested the additional presence of *F. proliferatum* or *F. verticillioides*[21]. *F. verticillioides* is common at lower latitudes in Europe and emerging at higher latitudes due to the warming climate and increased cultivation of maize at higher latitudes[18,22–24]. Since 2010, the relative proportion of other mycotoxins, including T-2, has increased. This suggests that the FHB pathogen population in Europe has changed, with the T-2-producing *F. langsethiae* or *F. sporotrichioides* increasingly coinfecting wheat crops alongside DON-producing species. *F. langsethiae* was reported in 2004 on oats, barley and wheat from higher latitudes in Europe (Austria, Czechia, Denmark, the United Kingdom, the Netherlands and Germany)[25], but has since been found in wheat in Poland[26], Sweden[27] and as far south as Italy[28]. Co-contamination incidence varies between European countries (Fig. 2b). Surprisingly, the prevalence of co-contamination in a country was inconsistent between food and feed, perhaps reflecting inadequate testing for non-DON mycotoxins. Although sample size of non-DON mycotoxins increases year on year in the feed dataset, it does not in food data. The limited testing for other FHB mycotoxins compared to DON means that co-contaminants may go undetected, and so the levels of co-contamination we report may be an underestimate. Therefore, it is imperative that multi-mycotoxin

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screening is undertaken if we are to fully understand the changing threat from pathogens and mycotoxins.

Across Europe in 2010–2019 we estimated that 75 million tonnes of wheat[29] (5% of food wheat) exceeded the 750 μg kg^{-1} DON limit. Downgrading to feed equates to a loss of approximately €3 billion (Extended Data Table 1). The percentage of food wheat exceeding the DON limit was highest in 2012 (10.7%), a known FHB epidemic year[9,30,31], but the cost of DON downgrading was highest in 2015, when the difference in value between food and feed wheat was greatest (86.74€ per tonne)[32]. Our estimates do not include losses from reduced yields, other FHB mycotoxins, or the cost of fungicide applications and mycotoxin testing, meaning this economic cost is a fraction of the total impact of FHB.

We have shown that FHB mycotoxins are ubiquitous across Europe, with DON persistently detected in wheat, raising concerns about the health effects of chronic dietary exposure. DON concentrations were worryingly high in feed wheat and mycotoxin outbreaks were becoming more severe in lower-latitude regions of Europe, possibly attributable to agronomic and climatic changes. Although lower contamination in food suggests the EU legal limits have a positive effect, rigorous monitoring and outbreak-responsive management of FHB mycotoxins must continue to protect human and livestock health. Changing mycotoxin profiles, such as increasing co-contamination with DON and T-2, indicate shifting dynamics in FHB pathogen populations and could have synergistic negative health implications. Our conservative economic estimates demonstrate the significant cost of DON contamination in European wheat. Our study quantifies the threat and cost of FHB mycotoxins, which should inform projections of food security scenarios in future climates, supporting the legislation and implementation of appropriate mycotoxin mitigation strategies.

Methods

To quantify the threat of FHB toxins in European food and feed wheat, we analysed data on mycotoxins in grain commodities to identify mycotoxin (1) occurrence, (2) levels and (3) how these varied across Europe, over time (2009–2019). Data on food were sourced from the EFSA, in accordance with Regulation (EC) 1049/2001 regarding public access to documents. The methods used for sampling and analysis are described in Commission Regulation (EC) 401/2006. Data on feed were supplied by BIOMIN Holding, Austria. Data were analysed using Microsoft Excel for Microsoft 365 MSO (v.2202). Data were filtered to retain samples with (1) an origin country in geographical Europe (as defined by the United Nations[33]), (2) being identifiable as wheat and (3) sampled between 2010 and 2019. EFSA data were filtered to retain samples identifiable as suitable for food; BIOMIN data were already solely for feed. After filtering, the EFSA dataset consisted of 6,519 samples, of which 3,035 contained DON, and the BIOMIN feed dataset consisted of 6,547 samples, of which 4,213 contained DON. Data from all countries were included in the European summary statistics. As a criterion for selecting data from individual countries to be presented, we set a minimum requirement of three samples from each of three different years (minimum of nine samples in total from a country). DON throughout refers to DON excluding its derivatives, because data on these were not available in the BIOMIN dataset. Mean DON level was calculated for the samples that tested positive for DON. To analyse co-occurrence over the decade, the percentage of samples from all countries containing DON that also contained any combination of FUM, ZEN and T-2 was calculated. The prevalence of co-occurrence in each European country was calculated as the percentage of samples containing DON that also contained FUM, ZEN or T-2. Nivalenol was excluded from the co-occurrence analyses because data on nivalenol were present in the EFSA dataset, but not the BIOMIN dataset. Maps were generated in QGIS v.2.22.11 using base-map data from GADM v.4.1.

For economic cost analysis, the percentage of samples exceeding the 750 μg kg^{-1} DON legal limit for direct human consumption[4] was calculated from the EFSA data, for each year. The total food wheat production (total soft plus durum wheat) of the EU-28 was sourced from Eurostat[29]. The tonnes exceeding the DON limit each year was estimated by multiplying the percentage of samples exceeding limit by the total food wheat production. The difference in value per tonne between food and feed wheat was calculated by subtracting the average feed wheat price in the EU-28 (€ per tonne) from the average bread and durum wheat price in the EU-28 (€ per tonne), with prices sourced from the European Commission[32]. Value lost by downgrading the tonnes exceeding the legal DON limit was calculated by multiplying the tonnes lost by the value per tonne. This was done for each year and summed to give the total value lost over the ten years (Extended Data Table 1).

$$C = (P \times W) \times (V_{\text{food}} - V_{\text{feed}})$$

where C denotes the cost of downgrading (€), P the percentage of samples above the 750 μg kg^{-1} legal limit for DON in food for direct human consumption (%) (EFSA) and W the total food wheat production of the EU-28 (tonnes)[29]. V_{food} denotes the value of food wheat per tonne and V_{feed} the value of feed wheat per tonne (€ per tonne)[32].

Reporting summary

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

Data availability

Extended data are available for this paper. Correspondence and requests for materials should be addressed to N. Brown. All data are included in this article and its Supplementary Information files. Food raw data are publicly available on request from the EFSA in accordance with Regulation (EC) 1049/2001 regarding public access to documents. Feed raw data provided by BIOMIN are not publicly available due to them containing information that may be of commercial interest and therefore are subject to a confidentiality and non-disclosure agreement. DEFRA winter wheat survey data were provided by J. Turner, Fera Science Limited, and are available on request as data supporting their paper https://doi.org/10.1111/ppa.13433. Summary data derived from these raw data are available in the Source data.

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Author contributions

L.J. contributed to the project design, performed the analyses and wrote the manuscript. D.B. and S.G. advised on the project and contributed to the preparation of the manuscript. N.B. contributed to the project's conceptual design, funding and analyses, in addition to manuscript preparation.

Competing interests

The authors declare no competing interests.

Additional information

Extended data The extended data are available for this paper at https://doi.org/10.1038/s43016-022-00655-z.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s43016-022-00655-z.

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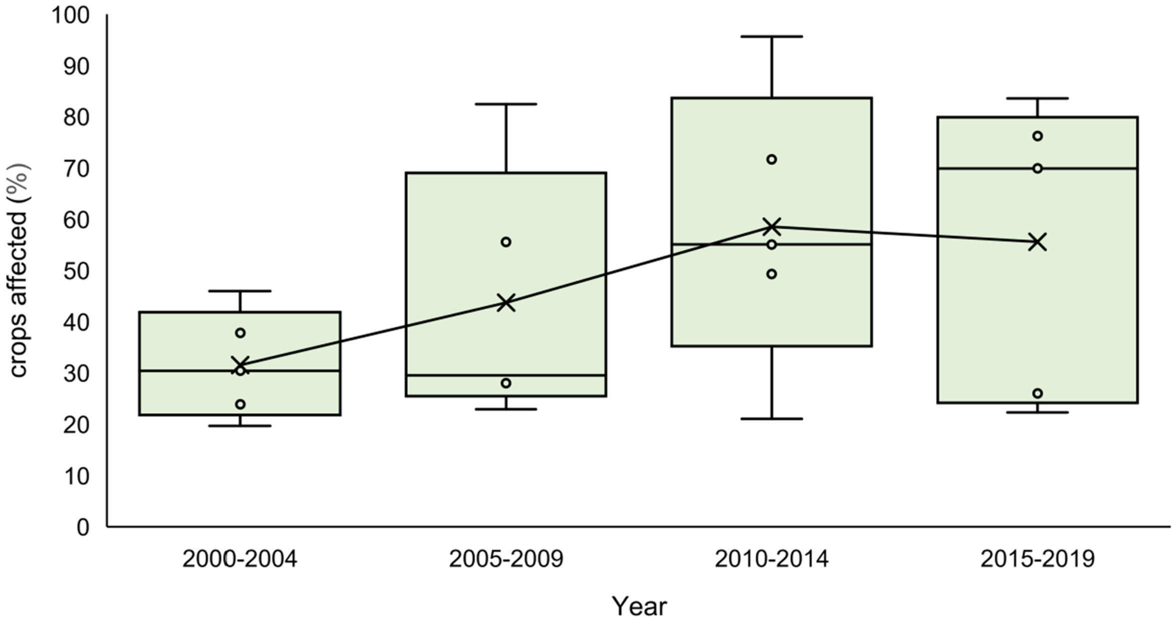
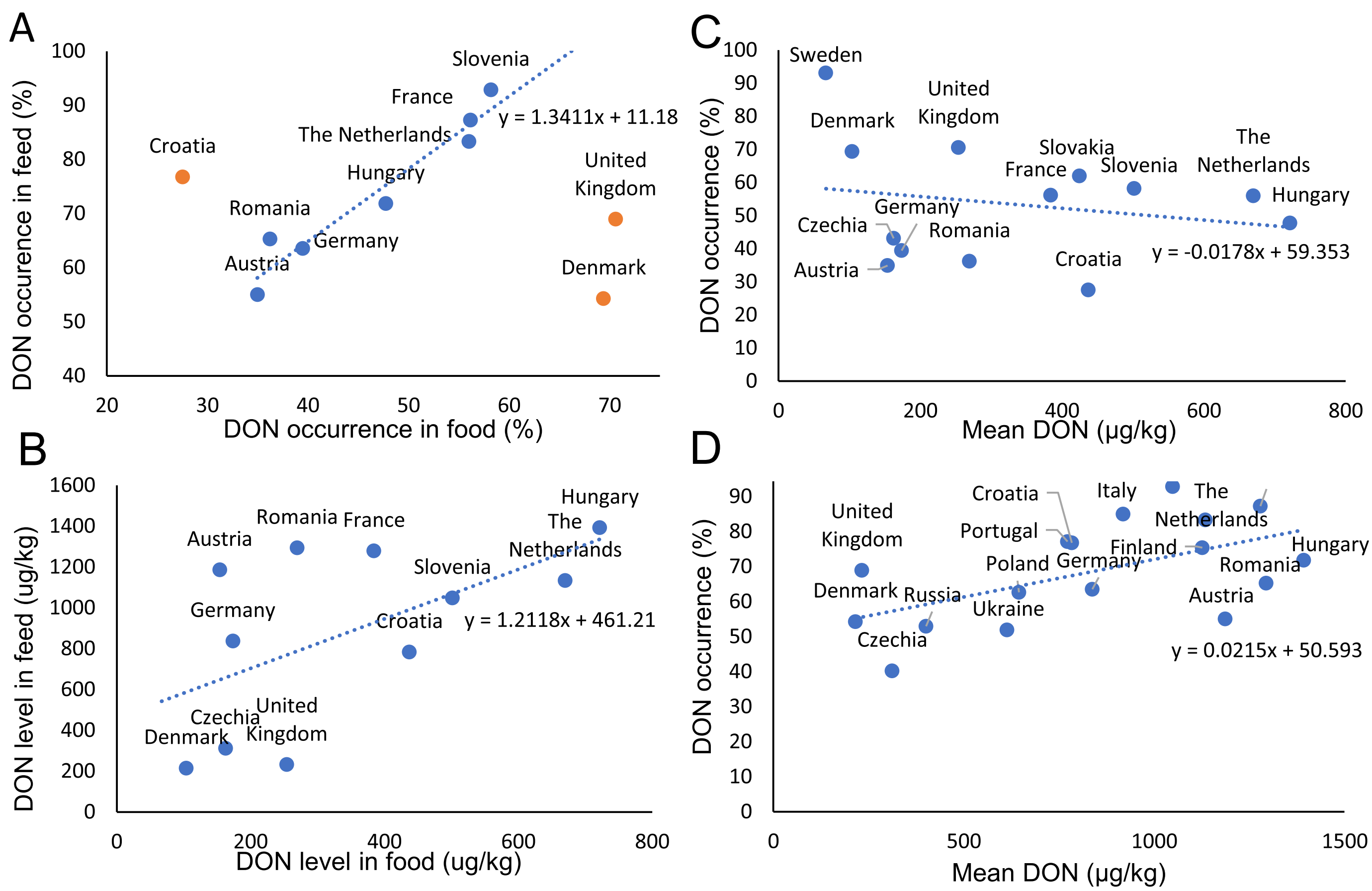


Extended Data Fig. 1 | Prevalence of FHB symptoms in UK wheat between 2000–2019, showing an increase in FHB incidence. Source: DEFRA winter wheat survey.



Extended Data Fig. 2 | Correlations between DON level and DON occurrence in food and feed wheat from individual European countries. (**A**) DON occurrence in food and feed are strongly positively correlated, with the exclusions of Croatia, UK and Denmark (in orange). (**B**) DON levels in food and feed are slightly positively correlated. DON occurrence and mean DON levels are slightly negatively correlated in food (**C**) and positively correlated in feed (**D**).

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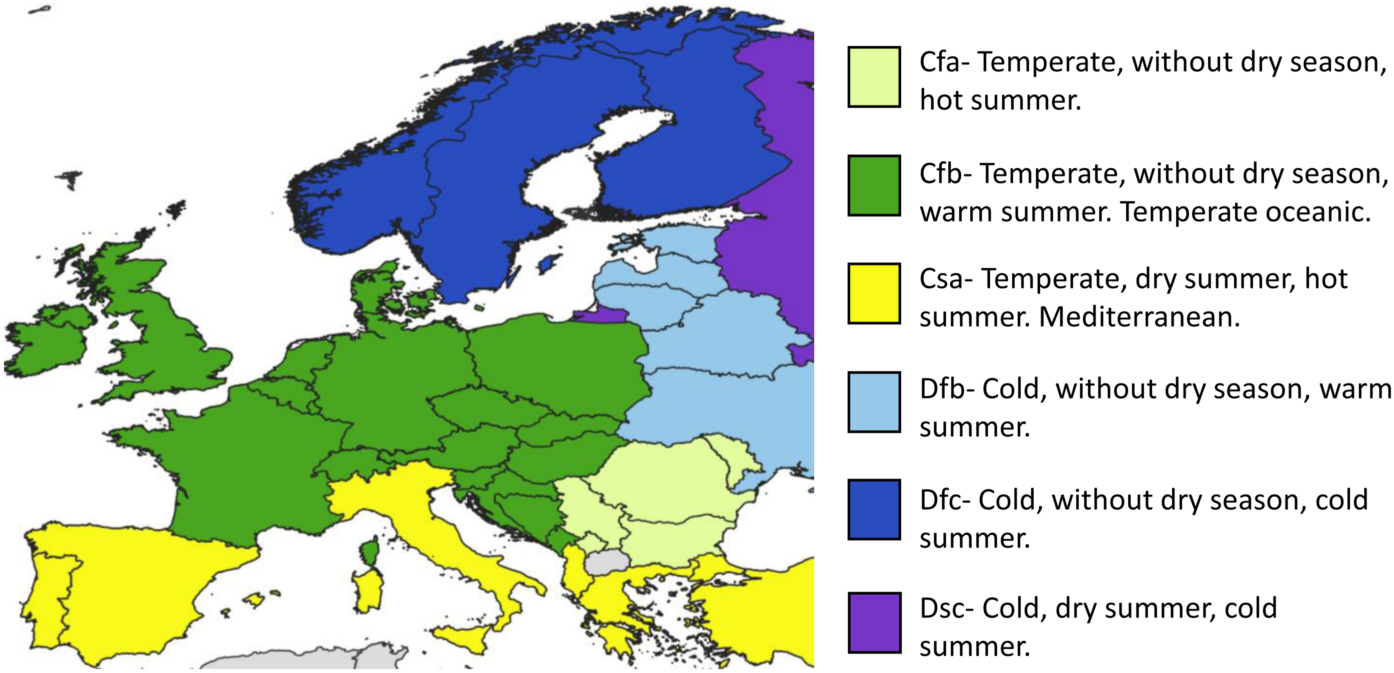

Extended Data Fig. 3 | Köppen–Geiger climate classification of European countries 1986–2010. For simplicity, countries were classified based on the climate that constituted the greatest percentage of its land mass[17,34].

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Extended Data Table 1 | Estimated value lost due to downgrading EU+UK wheat intended for food to feed due to FHB DON contamination above the EU legal limit

Year	N wheat samples tested for DON [a]	Calculated % samples with DON above legal limit for food (750ppm)	Food wheat production (total Soft + Durum wheat EU 28, tonnes)[29]	Calculated tonnes lost (tonnes*(% over limit)	Average Bread & Durum wheat Wheat price EU+UK €/t [32]	Average Feed wheat price EU+UK €/t [32]	Calculated Difference food-feed per ton	Calculated value of tonnes downgraded (tonnes*(value lost per ton)) Millions
2010	376.0	10.6	137290590	14605381.91	170.90	142.98	27.91	€ 407.7
2011	530.0	4.9	139725100	6854438.868	251.72	201.93	49.79	€ 341.3
2012	1025.0	10.7	134326980	14415578.34	252.14	218.62	33.52	€ 483.2
2013	632.0	5.1	144275000	7305063.291	236.85	206.22	30.63	€ 223.7
2014	855.0	1.5	157346000	2392395.322	235.41	169.14	66.27	€ 158.5
2015	708.0	3.8	160938960	6137502.712	245.79	159.06	86.74	€ 532.4
2016	694.0	2.9	144699150	4170004.323	192.45	143.14	49.32	€ 205.7
2017	660.0	0.8	151953270	1151161.136	189.09	155.85	33.23	€ 38.3
2018	505.0	2.2	138072530	3007520.455	191.48	171.86	19.62	€ 59.0
2019	538.0	9.9	155841480	15352413.46	204.95	171.76	33.19	€ 509.6
Total				75391459.82				€ 2,959.2

nature research

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Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
☒	☐	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used.
Data analysis	Data were analysed using Microsoft® Excel® for Microsoft 365 MSO (Version 2202 Build 16.0.14931.20704) 64-bit.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Food raw data are publicly available upon request from the European Food Safety Authority (EFSA) in accordance with Regulation (EC) No 1049/2001 regarding public access to documents.
Feed raw data provided by BIOMIN are not publicly available due to containing information that may be of a commercial interest and therefore were provided subject to a confidentiality and non-disclosure agreement for the current study.
DEFRA winter wheat survey data were provided by Dr Judith Turner, Fera Science Ltd, and are available upon request as data supporting their paper DOI: 10.1111/ppa.13433.
Summary data derived from these raw data are available within the paper and its supplementary information files.

Field-specific reporting

Please select the one below that is 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/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

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

Study description	To quantify the threat of FHB toxins in European food and feed wheat, we analysed existing data on mycotoxins in grain commodities to identify mycotoxin a) occurrence, b) levels and c) how these varied across Europe over time (2009-2019).
Research sample	Samples were of wheat from geographical Europe (as defined by the United Nations) sampled between 2010-2019. EFSA data were filtered to retain samples identifiable as suitable for human food; BIOMIN data were already solely for animal feed (see supplementary data for our classifications of wheat, food and feed). The food dataset was provided by the EFSA and consisted of 6519 samples, of which 3035 contained the mycotoxin deoxynivalenol (DON). The feed dataset was provided by the company BIOMIN and consisted of 6547 samples, of which 4213 contained DON.
Sampling strategy	Sample sizes were as large as possible, given the size of the existing datasets used and the criteria applied (see above).
Data collection	The feed data were collected by the EFSA as part of their chemical contamination monitoring programme, and sources included: official national programmes, surveys, industry/private programmes and official EU programmes. The EFSA data sampling strategies included: objective, selective, convenient, suspect (0.6% of all unfiltered samples) and census sampling. Sample analysis methods included LC-MS/MS, ELISA, and HPLC. The feed samples were collected and analysed by BIOMIN as part of their BIOMIN World Mycotoxin Survey, as previously described by Kovalsky et al., 2016 (doi:10.3390/toxins8120363).
Timing and spatial scale	Data were collected between 2010 and 2019.
Data exclusions	Data were initially filtered to include only samples meeting our criteria of: wheat from geographical Europe (as defined by the United Nations) sampled between 2010-2019 and intended for food or feed. For samples that had been tested multiple times and returned the same toxin concentration, the duplicated results were excluded. When presenting data from individual countries (e.g., figures 1B, 1C and 2B), we set a minimum requirement of a country having 9 samples, with 3 samples from each of 3 different years for that country to be included.
Reproducibility	Reproducibility of experimental findings was not relevant to our study because our study was observational rather than experimental.
Randomization	Randomisation was not relevant to our study because our study was observational rather than experimental.
Blinding	Blinding was not possible in our study because we were using previously gathered datasets.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☒	☐	Animals and other organisms
☒	☐	Human research participants
☒	☐	Clinical data
☒	☐	Dual use research of concern

Methods

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