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Unraveling the prevalence of soil-borne fungal pathogens in the North China Plain: a global analysis approach

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Abstract Soil-borne fungal plant pathogens lead to worldwide economic yield losses. However, despite the agricultural importance of the North China Plain (NCP), little is known about the occurrence and severity of soil-borne fungal pathogens that could potentially affect the yields of three main crops in this area: wheat, maize and soybean. By combining searches in public databases, we identified a set of main soil-borne fungal pathogen species potentially affecting crop production in the NCP. We investigated their distribution patterns at three scales: globally, in China and in the NCP, and evaluated how these patterns were determined by a range of variables related to climate, spatial drivers and crop area density of the three crop species. We found 25 main soil-borne fungal pathogens that could potentially affect the yields of wheat, maize and soybean in the NCP. Twenty of these fungal pathogens were prevalent across the globe, and 13 were very frequent in the NCP. Significant positive relationships between pathogen prevalence and crop area density were only found for two specialist pathogens. Our work provides an overview of the main soil-borne fungal pathogens in one of China's most intensively cultivated regions, shedding light on potential, previously overlooked, fungal threats for agricultural production in the area. This baseline information may contribute to the development of sustainable management strategies aimed at mitigating disease outbreaks caused by soil-borne pathogens in the future.

Keywords Wheat · Maize · Soybean · Plant pathogen distribution · Host availability · Environmental drivers

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Introduction

Many plant pathogens cause serious impacts on crops globally, leading to major yield losses (Savary et al., 2019; Ristaino et al., 2021). This includes soil-borne fungal pathogens, many of which have global distributions (Scherm et al., 2013; Termorshuizen, 2014; De Coninck et al., 2015; Delgado-Baquerizo et al., 2020; Al-Sadi, 2021; Marquez et al., 2021) and can lead to economically important losses in agriculture worldwide (De Coninck et al., 2015). Examples of globally important soil-borne pathogens are the fungus *Fusarium graminearum*, the causal agent of Fusarium head blight of cereals (Summerell et al., 2010; Chen et al., 2019a; Karlsson et al., 2021), reducing yields of crops such as wheat and maize (Savary et al., 2019); and *Rhizoctonia solani*, which causes root rot in many crops including wheat, maize, soybean and rice (Ghosh et al., 2017; Ajayi-Oyetunde & Bradley, 2018; Lin et al., 2021).

The North China Plain (NCP) is an important and intensively managed agricultural production area in China (National Bureau of Statistics of China, 2021). The main crops cultivated in the NCP are wheat, maize and soybean, altogether accounting for 63% of the total planted area (National Bureau of Statistics of China, 2021). The highly intense agricultural production in the region is achieved through the profuse use of irrigation, fertilizers and pesticides (Miao et al., 2011; Sun et al., 2011; Brauns et al., 2018; Wang et al., 2019; Liu et al., 2020; Mu et al., 2022), all of which are likely to favour the incidence of soil-borne diseases. For instance, the enrichment of nitrogen in soils caused by overuse of fertilizers has been shown to favour the accumulation of soil-borne pathogens in agro-systems (Walters & Bingham, 2007; Paungfoo-Lonhienne et al., 2015; Wei et al., 2018), and the widespread use of fungicides may induce the plant pathogens' tolerance to them (Mikaberidze et al., 2017; Corkley et al., 2022). *Fusarium* species have been isolated from diseased wheat stems in randomly selected wheat fields of the NCP (Xu et al., 2018; Zhang et al., 2015, 2020), and also isolated in maize (Meng, 2019) and soybean (Yang, 2012) fields in this region. Moreover, these soil-borne diseases have been reported to reduce yields of these main crops in the NCP (Fu, 2017; Zhang et al., 2020). However, apart from these well-known pathogens, other soil-borne fungal pathogens in the region remain understudied. Numerous studies conducted in the NCP have primarily focused on documenting the symptoms associated with soil-borne pathogens (Xue, 2006; Zhu, 2012; Zhang et al., 2012; Zhao et al., 2015; Ji & Han, 2016; Li, 2018; Xin & Yu, 2021; Zhou et al., 2021), and many are published in Chinese journals with limited scope (CNKI, https://www.cnki.net). However, there is a dearth of information regarding the specific causal agents responsible for these symptoms. Furthermore, although a few studies have employed cultivation techniques to identify certain pathogens in the NCP (Wang, 2019; Liu et al., 2021), these investigations have been limited to specific locations. To manage the soil-borne diseases effectively and promote sustainable agricultural development in the NCP, it is crucial to unravel the prevalence of pathogen species that pose a potential threat to crop production.

Characteristic agricultural areas such as the NCP may have specific assemblages of fungal pathogens owing to the peculiarities of the dominant production systems—including the main crop species and management practices—in addition to the general environmental factors that govern the distribution of all fungi. In particular, the density of host crop species can be a crucial factor in recruiting and multiplying crop-specific pathogens (Zhu et al., 2000; Hiddink et al., 2010), with monocultures tending to accumulate specific pathogens in soils, as compared to more diverse plant communities where the presence of such pathogens becomes diluted (Zhu et al., 2000; Hiddink et al., 2010; Boudreau, 2013; Ampt et al., 2018; Mommer et al., 2018). For instance, monocultures of wheat, maize and soybean have been shown to accumulate high abundances of soil-borne fungal pathogens specialized in attacking each crop, such as *Gaeumannomyces graminis* in wheat (Ramanauskienė et al., 2018; Gargouri et al., 2020), *Stenocarpella maydis* in maize (Flett & Wehner, 1991; Pinto et al., 2022), and *Macrophomina phaseolina* in soybean (Pérez-Brandán et al., 2014). On the other hand, the intensive use of fungicides (Price et al., 2015; Ons et al., 2020; Mu et al., 2022), as well as other management practices associated with the main crops in the area (Li et al., 2018; Wang et al., 2019; Chen et al., 2019b; Liu et al., 2019; Sun et al., 2020), could have effects on the regional soil-borne fungal communities that are difficult to predict and remain understudied.

Irrespective of the effects regional agricultural production systems may have on pathogen distribution, fungal occurrence will also be affected by major environmental factors that may confound the effects of cropping systems. Different regions of the globe have characteristic assemblages of fungi, including soil-borne pathogens (Vujanovic et al., 2006; Tedersoo et al., 2014, 2022), due to variation in major environmental drivers that operate at different spatial scales, including factors such as climatic conditions (Tedersoo et al., 2014; Větrovský et al., 2019; Delgado-Baquerizo et al., 2020) or large-scale changes in soil properties (Tedersoo et al., 2014, 2022). In addition to these well-defined variables, other spatial drivers of fungal distribution comprise variables that are difficult to quantify, such as the differential dispersal abilities of fungal species (e.g. whether they produce propagules enabling long-range or very restricted dispersal, or are likely affected by geographic barriers; Peay et al., 2010; Wardle & Lindahl, 2014; Bever et al., 2015; Chaudhary et al., 2022), and historical factors such as human-driven transportation of crop seeds across landscapes or changes in land use (Desprez-Loustau et al., 2010). These spatial drivers that lead to differences in the pathogens' distribution due to different dispersal ability should be accounted for. Examples of environmental patterns in soil-borne pathogen distribution include those of *Fusarium* spp. in asparagus fields in eastern Canada, determined by temperature and soil properties (Vujanovic et al., 2006); the restricted distribution of *Colletotrichum kahawae* attributed to geographic barriers (Silva et al., 2012); or the relatively well-documented spread of *Verticillium dahliae* due to anthropogenic movement (Short et al., 2015).

Here, to understand the potential threats of pathogens occurrence in the NCP, we assessed the distribution of soil-borne fungal pathogens on crops that are dominant in the NCP—maize, wheat, soybean—at three levels: global, China and the NCP. We studied the contribution of climatic, other spatial factors (e.g. related to the dispersal ability of fungi or geographic barriers), and crop area density to explain prevalence at these fungi at different scales. In particular, our specific aims were to 1) identify the major soil-borne fungal pathogens that could potentially affect maize, wheat and soybean in the NCP; 2) evaluate the prevalence of these pathogens in the NCP as compared to their distribution at increasingly larger scales (i.e. within China and globally); and 3) identify the main predictors influencing the distribution of these pathogens, with a particular emphasis on the availability of the specific host crop species (evaluated through regional crop area density).

Methods

Selection of focal pathogens

We first compiled a list of potential pathogenic fungal species with relevance for the production of wheat, maize or soybean based on the following criteria: (1) they have been reported in the literature as causal agents of disease in at least one of these crop species, (2) they are soil-borne (i.e. transmitted via soil), and (3) the diseases that they cause have been reported to cause agricultural yield losses in the NCP.

We used two approaches to select potential pathogens fulfilling those criteria. First, we identified important pathogens worldwide for the three focal crops by searching in the 'Fungal-Host Distributions' database of the US Department of Agriculture (USDA; Farr & Rossman 2021) in December 2021, using "*Triticum aestivum*" (wheat), "*Zea mays*" (maize) and "*Glycine max*" (soybean) as search terms in the 'Host Name' field. We retained for further analysis only those pathogens with relatively widespread global distributions, i.e. detected in at least 20 countries.

In the second approach, we looked for specific literature reporting pathogens of the focal crops in the NCP in December 2021, by searching in the China National Knowledge Infrastructure database (CNKI, https://www.cnki.net) and in Web of Science (WoS, https://www.webofscience.com/wos/woscc/basic-search). We used the query string "('wheat' OR 'maize' OR 'soybean') AND 'disease' AND 'China'". We reviewed these publications and retained those reporting pathogens in the NCP. In a second round of literature searches, we queried the CNKI database using the string "pathogen species" AND "yield losses", and retained the publications related to the yield losses in the NCP caused by those pathogens.

We combined the information obtained from the two approaches described above to compile a final list of soil-borne fungal pathogen species of potential relevance for the main crops produced in the NCP (Table 1). To determine the phylogenetic relationships among the selected pathogens, we built a Maximum Likelihood phylogenetic tree based on representative sequences retrieved from the NCBI GenBank database (http://www.ncbi.nlm.nih.gov; Table S1) using the software MEGA7 v7.0.26 (Kumar et al., 2016).

Retrieval of pathogen distribution, climatic, spatial and host availability data

We retrieved data on the global distribution of the selected pathogen species from the GlobalFungi database (https://globalfungi.com; Větrovský et al., 2020), which compiles high-throughput ITS (internal transcribed spacer) amplicon sequencing data from studies conducted across the globe and published between 2009 and 2022. These include quantitative datasets on the worldwide distribution of fungal taxa based on molecular sequencing of DNA barcode regions from environmental samples, enabling the characterization of whole fungal communities with a certain degree of taxonomic precision (Nilsson et al., 2019). By compiling these amplicon sequencing data, the database enables tracking of fungal taxa worldwide in environmental samples, such as soil or plant tissues (Bálint et al., 2016; Nilsson et al., 2019). We searched for each species in the GlobalFungi database and downloaded their global occurrence data and associated metadata, including geographical co-ordinates, biome (e.g. originating from cropland or other natural habitats), climatic variables (mean annual temperature, MAT; mean annual precipitation, MAP), and relative abundance per study in December 2021.

Table 1 List of target soil-borne fungal pathogens and their host specificity (i.e. wheat, maize, and soybean), based on database or literature searches

Pathogen	Class	Wheat	Maize	Soybean	Sources[1]
Fusarium asiaticum	Sordariomycetes	√			Zhang et al., 2012; Qi 2015; Gao 2016
Fusarium culmorum	Sordariomycetes	√			USDA; Ren 2011; Zhou et al., 2019
Fusarium graminearum	Sordariomycetes	√	√	√	USDA; Sun et al., 2014; Zhou 2014
Fusarium oxysporum	Sordariomycetes	√	√	√	USDA; Zhang 2012; He 2016
Fusarium proliferatum	Sordariomycetes	√	√	√	Yang, 2012; Sun et al., 2014; Wang, 2019
Fusarium fujikuroi	Sordariomycetes		√		Shan 2017
Fusarium solani	Sordariomycetes			√	USDA; Yang, 2012; Wang, 2019
Fusarium avenaceum	Sordariomycetes	√		√	USDA; Zhang 2012
Colletotrichum truncatum	Sordariomycetes			√	USDA
Phomopsis longicolla	Sordariomycetes			√	Wang, 2019; Ye et al., 2020
Macrophomina phaseolina	Dothideomycetes			√	USDA; Zhang et al., 2009; Wang, 2019
Zymoseptoria tritici	Dothideomycetes	√			USDA
Cercospora kikuchii	Dothideomycetes			√	USDA
Cercospora sojina	Dothideomycetes			√	USDA
Exserohilum turcicum	Dothideomycetes		√		USDA
Pyrenophora tritici-repentis	Dothideomycetes	√			USDA
Curvularia lunata	Dothideomycetes		√		USDA
Bipolaris zeicola	Dothideomycetes		√		USDA
Bipolaris sorokiniana	Dothideomycetes	√			USDA; Zhou 2014; Xu et al., 2018; Kang et al., 2020
Bipolaris maydis	Dothideomycetes		√		USDA
Physoderma maydis	Blastocladiomycetes		√		USDA
Rhizoctonia solani	Basidiomycetes		√	√	USDA; Ye et al., 2020
*Urocystis tritici**	Ustilaginomycetes	√	√		USDA
*Sporisorium reilianum**	Microbotryomycetes		√		USDA; Ma 2006
*Ustilago maydis**	Ustilaginomycetes		√		USDA

[1] Only a selection of references is shown. The full list is provided in Table S2. *All species are necrotrophs, except the last three, which are biotrophs

We obtained data about agricultural production of the three focal crop species per country, including crop area density (cultivated area of crops) for each target crop, land area and cropland area from FAOSTAT (https://www.fao.org/faostat/en/#data; FAOSTAT, 2022). In January 2022, we downloaded the data of host variables from the 'Crops and livestock products' database of the FAOSTAT, using "all countries" in the countries field; "Area harvested" in the elements field; "Wheat", "Maize" and "Soybean" in the items field; and "from 2000 to 2020" in the Years field. We also downloaded the data of land area and cropland area in the 'Land Use' database of the FAOSTAT, using "all countries" in the countries field; "Area" in the elements field; "Land area" and "Cropland" in the items field; and "from 2000 to 2020" in the years field.

We mainly targeted the effects of climatic, spatial and host availability variables on soil-borne fungal pathogen distributions, but we also accounted for additional variables that may affect pathogen distribution. We controlled for 1) differences in sampling effort across biomes (i.e. leading to a higher probability of detecting the focal fungi in countries with more studies at cropland biome) by calculating the proportion of cropland studies as the number of studies at cropland biome divided by the total number of studies in a given country; 2) for the country area (i.e. higher chances to detect the fungi in larger countries) by calculating the proportion of cropland area per country with respect to the total land area of each country; and 3) for other spatially-structured, unmeasured sources of variation that could explain patterns in the dataset. We accounted for the latter spatial factors using Principal Co-ordinates of Neighbor Matrices (PCNM; Dray et al., 2006) using package vegan v2.6–2 (Oksanen et al., 2020), which summarize spatial patterns of variation at different scales, that could represent factors either intrinsic to the organisms (e.g. dispersal), geographic (e.g. geographic barriers), or environmental (e.g. climatic variables other than those explicitly considered; Dray et al., 2006; Griffith & Peres-Neto, 2006; Peres-Neto & Legendre, 2010).

Analysis of pathogen distributions

All analyses of pathogen distributions were conducted in R v4.1.2 (R Core Team, 2021), using the package rnaturalearth v0.1.0 (South, 2017) to collect additional geographical information on the samples' origin, such as the country (for globe and China) and province (for the NCP), and the centroid co-ordinates per country or province. In each case, the relative pathogen abundance per study was calculated as the number of reads for the target fungus divided by the total number of reads per study. However, since this metric is prone to bias due to methodological differences across studies, we mainly used prevalence data, defined as the proportion of studies per country/province where the target pathogen was detected. For this, the number of studies in each country where the pathogen was detected was divided by the total number of studies in that area. Thus, the higher the prevalence of the pathogen at a given scale (e.g. global, China, the NCP), the higher the probability of detecting that pathogen at that scale.

We identified pathogens with a particularly high representation in the NCP compared to the rest of China or the globe by comparing their normalized prevalence across the three areas. We defined normalized prevalence as the ratio of prevalence per pathogen with respect to the maximum prevalence per scale (i.e. ranging from zero to one, respectively indicating no or maximum prevalence in the area). We considered pathogens to be overrepresented in the NCP with respect to the rest of China or the world when the normalized prevalence observed at NCP was at least three times larger than in the other areas. We arbitrarily selected this cut-off value based on the distribution of the prevalence data, because it yielded a conservative selection of pathogens with the highest representation at NCP.

Statistical analysis

All statistical analyses were performed with R. To test if the prevalence of each pathogen followed a proportional distribution across the three scales considered (global, China and NCP), between-group significant differences in pathogen prevalence were tested using pairwise Pearson's Chi-squared (R package fifer v1.2; Fife & Fife, 2017). We used linear models to estimate the effects of climatic, spatial and host availability variables on pathogen distributions, and the proportion of cropland area and the proportion of cropland studies were considered as covariates. The climatic predictors used were retrieved from the GlobalFungi dataset, including mean annual temperature (MAT) and mean annual precipitation (MAP) averaged per country/province. The spatial factors captured were those derived from PCNM variables based on the samples in the dataset (see above). For host availability, the mean annual harvest area (crop area density) of each target crop per country retrieved from FAOSTAT was considered. Firstly, for each selected pathogen, stepwise model selections using package MASS v7.3–54 (Venables & Ripley, 2013) were first performed to select only the PCNM variables that are significantly associated with pathogen prevalence, to avoid inflation of models caused by inclusion of too many PCNM variables (Gilbert & Bennett, 2010). Next, linear models were fitted to estimate the effects of climatic, the selected spatial, host availability and covariates variable on pathogen prevalence data. The analysis pipeline in this study can be found in Fig. S1

Results and discussion

Description of the datasets

The USDA database searches resulted in 819 records of pathogen species for wheat, 989 for maize and 597 for soybean, globally. From these, we selected 12 widespread pathogen species for wheat, 18 for maize and 10 for soybean for subsequent analyses (Table S2).

The two literature searches (one in WoS and one in CNKI) initially resulted in 100 publications describing pathogens of wheat in the NCP, 174 of maize, and 136 of soybean. After further analysis of the literature records, we identified 20 publications on wheat, 5 on maize and 6 on soybean from which we recorded the pathogen species and related information concerning the detection method (either isolation or direct sequencing), the host, the type of disease and the relative abundance. Finally, 23 publications related to yield loss caused by those pathogens in the NCP were retrieved from the second search in WoS and CNKI (Table S2). The references in this dataset were also listed in Table S3.

A final list of 25 target soil-borne fungal pathogens representing six taxonomic classes, and their host specificity towards each of the focal crop species, was compiled by collating the results from the above approaches (Table 1). Seven soil-borne fungal pathogens affecting yield were found for wheat, nine for maize and six for soybean (Table 1). Three out of 25 target pathogens were biotrophs, i.e. *Urocystis tritici*, *Sporisorium reilianum* and *Ustilago maydis* (Table 1).

Distribution of selected soil-borne fungal pathogens at global and regional scales

To investigate the distribution patterns of the 25 selected soil-borne pathogen species, we retrieved data from the GlobalFungi database representing 36,684 records of sampling sites across 367 studies (Table S4). The distribution of 20 pathogen species showed widespread occurrences, in most cases spanning the globe (more than three continents; Fig. 1a, b, S2), while five species (*Phomopsis longicolla*, *Bipolaris maydis, Physoderma maydis, Sporisorium reilianum* and *Ustilago maydis*) were concentrated in China and the NCP (Fig. 1d, e, S2). There were clear biases in the representation of geographical areas globally, e.g. with only a few records of sampling sites originating from Africa compared to Europe or Asia (Fig. 1c, f).

To account for the variable representation of data points across geographic areas, we calculated prevalence as the proportion of studies per country or province (in China) in which each pathogen was detected. We found a low prevalence for all pathogens at the global scale as compared to scales encompassing all of China and, particularly, the NCP (Fig. 2). At the global scale, members of the Sordariomycetes showed a higher prevalence than fungi from other classes, a trend that was consistent at the scale of China but was somewhat lost in the NCP, which showed an elevated frequency of species in the Dothideomycetes, such as *Bipolaris sorokiniana* and *Cercospora sojina* (Fig. 2). A comparison of the prevalence patterns of pathogens across the three scales using Chi-square tests showed that no significant difference ($X^2 = 0.07–0.9$, $P = 1$). Based on a threshold of a ratio ≥ 3 between the normalized prevalence in the NCP respect to the global and China scales, we identified 13 pathogen species to be disproportionately overrepresented in the NCP: *Fusarium graminearum*, *Phomopsis longicolla*, *Cercospora kikuchii*, *C. sojina*, *Exserohilum turcicum*, *Pyrenophora tritici-repentis*, *Bipolaris zeicola*, *B. sorokiniana*, *B. maydis*, *Physoderma maydis*, *Urocystis tritici*, *Sporisorium reilianum* and *Ustilago maydis* (Fig. 2). In contrast, two pathogen species were found to have extremely low representation in the NCP,

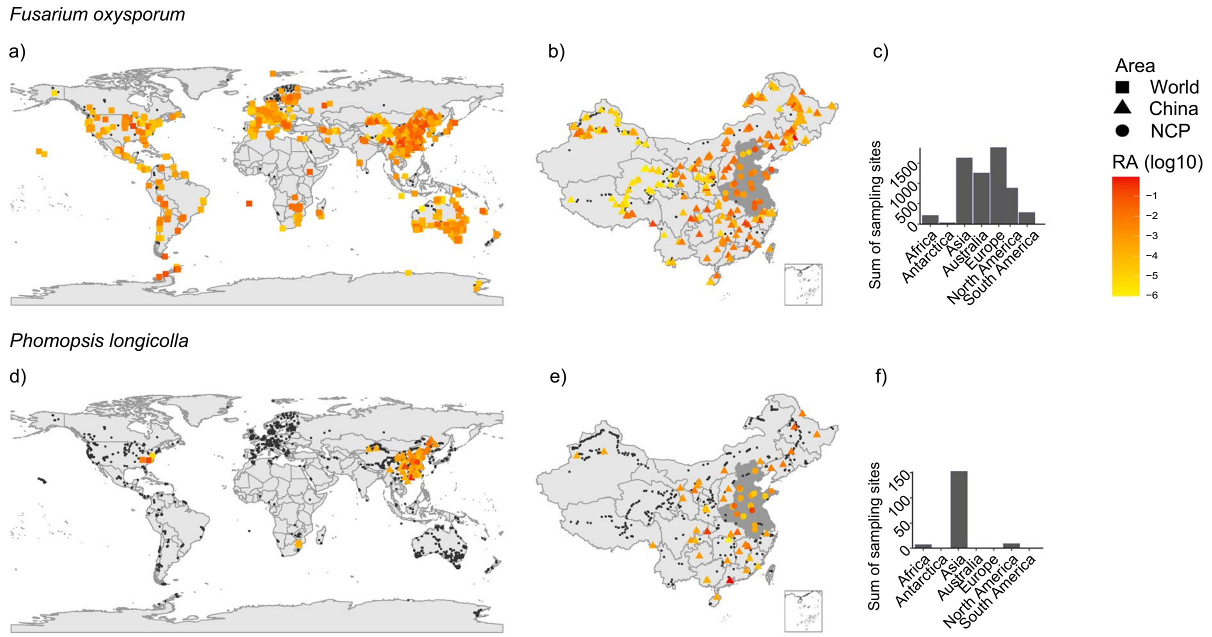

Fig. 1 Examples of the distribution of soil-borne fungal pathogens at the three different scales (Global, China and the North China Plain). The maps show the detection across the GlobalFungi dataset of two species selected as examples based on their contrasting distribution ranges: *Fusarium oxysporum* (**a**-**c**) and *Phomopsis longicolla* (**d**-**f**) (For the distributions of the remaining 23 pathogens selected in this study, see Figure S2). In each map, points indicate sampling sites, with black points and heat-coloured points indicating absence or presence of the target fungal species, respectively. In coloured points, the colour correlates with the relative abundance (RA) of the pathogen species ($\log_{10}$-scale, see colour key). Note that the North China Plain is highlighted in dark grey in the maps of China (**b**, **e**). The bar plots in c and f show the sum of records of sampling sites detecting *Fusarium oxysporum* (**c**) and *Phomopsis longicolla* (**f**) across continents (note the different scales in the y axes)

Fusarium culmorum and *Zymoseptoria tritici*, for which the ratios were zero.

Ecological determinants of pathogen prevalence

We estimated the contribution of variables indicative of climatic, spatial and host availability conditions to the global levels of prevalence of the target soil-borne fungal pathogens using linear regression models (Fig. 3). We did not find a general pattern in the association of fungal groups (i.e. phylogenetically related species or with similar host preferences) with particular sets of climatic and spatial factors, even though more species were affected by spatial factors (e.g. geographical barriers, dispersal limitation, or historical factors) than by climatic conditions (Fig. 3). Likewise, we did not find a relationship between pathogen prevalence and the availability of the respective host crop species, estimated as the crop area density (Fig. 3). Of all pathogen species, only *Urocystis tritici* and *Sporisorium reilianum* (both biotrophic Basidiomycota) were positively related to regional crop area density of their respective host crops. In the case of *Fusarium proliferatum*, its prevalence was related to crop area density of its host wheat but not of its other hosts maize and soybean, whereas *Cercospora kikuchii* was related to crop area density of its host soybean, but also of the non-host wheat (Fig. 3).

Discussion

We identified 25 soil-borne fungal pathogen species that could potentially affect the productivity of the three main crops produced in the NCP, wheat, maize and soybean. Twenty of these pathogens had widespread distributions across the globe, but 13 species showed prevalence patterns associated with the NCP. An investigation of the underlying ecological factors that could drive the global distribution of these

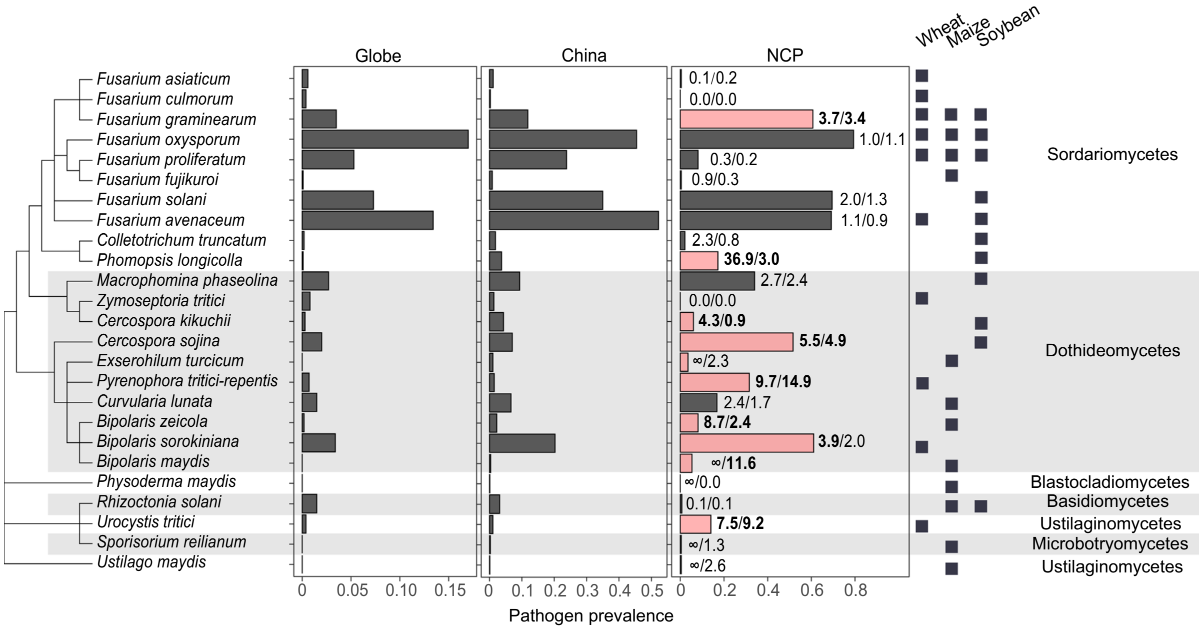

Fig. 2 Prevalence profile of the 25 selected soil-borne fungal pathogens at the three scales considered (Global, China, and North China Plain). Species and class names of the selected pathogens, and their phylogenetic relationships inferred by a Maximum Likelihood phylogeny are shown. The bar plots show the prevalence of soil-borne fungal pathogens at the global, China, and the NCP scale, defined as the proportion of studies per region where the target pathogen was detected (note the different scales in the x axes of each panel). The red bars highlight the pathogens identified as being overrepresented in the NCP as compared to the globe and China scales, based on ratios of normalized prevalence (prevalence of each pathogen divided by the maximum prevalence of a pathogen at each scale) above three (values next to bars, globe/China). The ∞ symbol indicates infinite ratio values, which occur when there are zero detections outside of China. The black squares rightwards to the bar plots show the pathogen's host specificity towards the three focal crops (wheat, maize and soybean), based on literature records

pathogens did not reveal consistent relationships between pathogen prevalence and climatic or spatial variables. In addition, the crop area density of the three main crops did not account for the prevalence of the pathogens, except for two specialist pathogens, *Urocystis tritici* and *Sporisorium reilianum*. Based on these data we conclude that other factors not accounted for in our study may be better predictors for the prevalence of potential fungal pathogens in wheat, maize, and soybean in the NCP.

Soil-borne pathogens: taxonomy and fungal lifestyles

Twenty of the 25 studied soil-borne pathogen species belong to the classes of Sordariomycetes and Dothideomycetes, which are known to contain a high proportion of plant pathogenic species (Hyde et al., 2013; Maharachchikumbura et al., 2016). Examples of these pathogenic species from Dothideomycetes are *Zymoseptoria tritici* (see Table S2; Torriani et al., 2015) and *Bipolaris maydis* (Table S2; Aregbesola et al., 2020); from the class Sordariomycetes—*Phomopsis longicolla* (Table S2; Mengistu et al., 2009). All these pathogens are frequently reported as ubiquitous pathogens in agriculture (Zhang et al., 2006; Haridas et al., 2020).

Based on our results of reviewing literature records, five out of the studied 25 pathogens were generalists (see Table 1). These species can infect a wide range of crops from different families (*F. graminearum*: Chongo et al., 2001; *F. oxysporum*, *F. proliferatum*, *F. avenaceum*: Aoki et al., 2014; O'Donnell et al., 2015; *R. solani*: Anderson, 1982). The other 20 pathogen species were reported to affect only single crops (Table 1; Wheat: Strelkov & Lamari, 2003; Jahani et al., 2014; Maize: Kumar et al., 2022; Xia et al., 2022; Soybean: Goodwin et al., 2001; Li et al., 2010). Of these 20 pathogens associated with single crops, 17 have necrotrophic

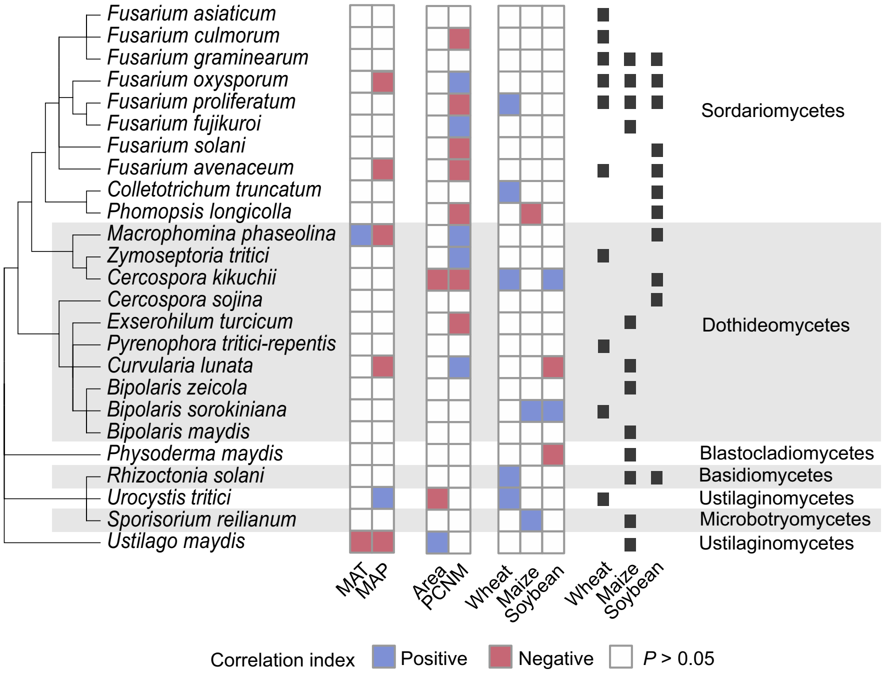

Fig. 3 Relationship between ecological drivers and the prevalence of selected soil-borne fungal pathogen species. The heatmaps summarize results from linear regressions between ecological drivers (i.e. climate, space, and host availability variables) and the prevalence per country of each fungal species. The colours within the cells represent significant positive or negative regression coefficients in the relationship between pathogen prevalence and each variable (see key), thus indicating positive or negative relationships, respectively. The contributions of different PCNMs were combined in a single column, for simplicity, indicative of a correlation between pathogens prevalence and spatial factors (see Table S5 for the effects of individual PCNMs). Species and class names of the selected pathogens, and their phylogenetic relationships are shown. The black squares on the right of the heatmaps show the pathogens' host specificity towards the three focal crops (wheat, maize, and soybean), based on literature records. Abbreviations: MAT, mean annual temperature; MAP, mean annual precipitation; PCNM, principal co-ordinates of neighbor matrices, calculated from the countries' centroid co-ordinates

lifestyles (Table 1), meaning that they can also survive and grow on crop debris or other organic matter in the soils (Glazebrook, 2005; Horbach et al., 2011). For example, Zhen et al. (2009) observed an increased soil-borne disease of wheat when higher amounts of straw amendments were used as inputs to improve soil structure.

Two important soil-borne pathogens for wheat in many regions across the world—*Fusarium culmorum* and *Zymoseptoria tritici* (Wagacha & Muthomi, 2007; Torriani et al., 2015; Li et al., 2016; Zhong et al., 2017) were found to be particularly underrepresented in the NCP (see Fig. 2). In the case of *F. culmorum*, this could be due to its apparent preference for high moisture, as it is observed in wheat fields under high moisture climates in Australia (Backhouse & Burgess, 2002). However, wheat in the NCP is grown with flood irrigation in the dry part of the season as most rain falls during summer monsoons after wheat harvest and before wheat sowing (Sun et al., 2010). *Z. tritici* is more problematic in temperate climates in Europe than in the NCP, probably for the same reason: the relatively dry growing conditions with little rainfall (Fones & Gurr, 2015; Boixel et al., 2022). It is important to acknowledge that certain regions of the world have been underrepresented in studies on global fungal distribution, which is a common limitation of studies focusing on microbial biogeography (Větrovský et al., 2019; Tedersoo et al., 2022; Makhalanyane et al., 2023). Future research should prioritize addressing this gap by expanding the geographic scope and increasing the inclusion of underexplored regions.

Relationships between soil-borne fungal pathogens and host cultivated area

For two out of the 25 fungal species, the biotrophic species *Urocystis tritici* and *Sporisorium reilianum*, we found positively significant relationships between their prevalence and crop area density of their respective host crops, wheat and maize, respectively. These two fungal species are known as true specialists because they depend on their host species to complete their life cycles (*U. tritici*: Zhao et al., 2019; *S. reilianum*: Poloni & Schirawski, 2016), thus highlighting the importance of host density in driving pathogen pressure, which is consistent with predictions in plant epidemiology (Gilbert, 2002; Halliday et al., 2017; Parker et al., 2015).

For the remaining pathogen species (i.e. 23 out of 25) we did not find relationships between their prevalence and crop area density. One possible explanation could be that these soil-borne fungal pathogens have much broader host ranges than biotrophic species, thus their occurrence may depend less on the presence of specific plant species as they can colonize multiple hosts, often without inducing disease symptoms (Jibril et al., 2016; Lofgren et al., 2018; Maciá-Vicente et al., 2020; Newman & Derbyshire, 2020; Maciá-Vicente et al., 2020). It is well known that presumed non-host crop species may serve as pathogen reservoirs (Malcolm et al., 2013; Glynou et al., 2018; Lofgren et al., 2018). For example, *Macrophomina phaseolina* has been found to colonize more than 500 host species (Khan, 2007).

Rather than being the cause of the lack of correlations, it can also be that crop area density is not a good descriptor of pathogen occurrence. Xu et al. (in preparation) observed that in addition to wheat, maize and soybean, 28 other crops are grown in the NCP, such as stevia, chili pepper, cabbage and mung bean (see Table S6 for full list). In addition, the diversity of agricultural practices is immense, ranging from labour-driven systems managed by smallholders to very intensive, mechanized companies that optimize yields (Pan et al., 2014; Zhang et al., 2016; Liang et al., 2022). This diversity of crops and management practices may provide another reason for the small effects of specific host availability on the occurrence of soil-borne pathogens. Therefore, further research is needed to test the actual relationships between fungal pathogens, crops and management practices, in order to provide a baseline to start designing more sustainable cropping systems.

Environmental drivers of pathogen occurrence

Our work reveals inconsistent patterns in the effects of climatic conditions and spatial factors on the distribution of fungal pathogens. Previous studies have emphasized the roles of climate and spatial distance in shaping soil fungal communities (Peay et al., 2010; Tedersoo et al., 2014; Coleman-Derr et al., 2016; Glynou et al., 2016; Maciá-Vicente & Popa, 2022), and this also holds true for soil-borne fungal pathogens (van Agtmaal et al., 2017; Delgado-Baquerizo et al. 2020). However, our finding shows that the soil-borne fungal pathogen species at the three different scales were not consistently affected by environmental conditions. Instead, the distribution of each species responded differently to different sets of conditions, in line with multiple studies investigating the environmental drivers of individual plant-associated fungi (Glynou et al., 2016, 2018; Maciá-Vicente & Popa, 2022). This result is further supported by previous studies in the NCP showing that the occurrence of different pathogen species (*Fusarium* spp.) was affected differently by distinct environmental factors (Dong et al., 2016; Xu et al., 2018). The variation in response to environmental factors among these different pathogen species may be attributed to their genetic diversity, leading to different genotypes with varying sensitives to environmental factors (Jump et al., 2009; Mann et al., 2014).

Conclusions

Our study identified 13 out of 25 soil-borne fungal pathogens that exhibited a disproportionately high prevalence in the NCP, potentially leading to yield losses in wheat, maize, and soybean crops. We found inconsistent correlations between these 13 pathogen species and environmental factors, indicating individual ecological preferences across fungal species. Notably, two of these 13 species showed a significantly positive correlation with their respective host crop's area density. These findings highlight the importance of proactive management strategies to mitigate yield losses caused by these fungal pathogens in the NCP. Understanding the specific interactions between these pathogens and their host crops, as well as the environmental factors that determine their occurrence and function, will enable the development of targeted strategies for disease management. Overall, our study provides valuable insights for implementing approaches to enhance crop sustainability in the NCP. By establishing an inventory of pathogen prevalence in the region, our research serves as a foundation for developing sustainable agricultural systems that are more resilient against soil-borne fungal diseases in the future.

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Data Availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest All authors declare that they have no conflict of interest.

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