The proportion of soil-borne pathogens increases with warming at the global scale

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Understanding the present and future distribution of soil-borne plant pathogens is critical for supporting food and fibre production in a warmer world. Using data from a global field survey and a nine-year field experiment, we show that warmer temperatures increase the relative abundance of soil-borne potential fungal plant pathogens. Moreover, we provide a global atlas of these organisms along with future distribution projections under different climate change and land use scenarios. These projections show an overall increase in the relative abundance of potential plant pathogens worldwide. This work advances understanding of the global distribution of potential fungal plant pathogens and their sensitivity to ongoing climate and land-use changes, which is fundamental to reduce their incidence and impacts on terrestrial ecosystems globally.

Around 15% of the global crop production is lost to biological threats[1-5], a percentage that is expected to increase with ongoing global warming and the associated intensification of pest incidence[1]. This will jeopardize food security and reduce the productivity and health of terrestrial plant communities worldwide[4]. Many of the most aggressive plant pathogens are soil-borne fungi (e.g., *Alternaria alternata* or *Fusarium oxysporum*)[6-8] that threaten food security as the chemical fungicides currently used against them are mostly ineffective[6-8]. In recent years, information on the distribution of plant diseases has increasingly become available at the local and regional scale (e.g., via PlantWise, https://www.plantwise.org). Moreover, the fundamental study in ref.[9], provided important insights on the distribution of global fungi. Yet, global atlases of the current and future distribution of plant pathogens under contrasting global change scenarios, and based on multiple contrasting climates and vegetation types, are still lacking.

Soils from natural ecosystems provide an array of potential reservoirs for fungal pathogens surrounding croplands worldwide, challenging their productivity[6-8]. Moreover, natural ecosystems, which provide essential services (e.g. timber and livestock production)[10-11] to billions of people, are also highly sensitive to the incidence of fungal pests[1-6,10]. Understanding the current and future distribution of plant pathogens in natural ecosystems and the environmental factors influencing them is critical for forecasting their impact on human well-being and ecosystem sustainability under projected climate and land-use change scenarios. This could readily be seen as temperatures continue to rise along this century[3,12], which might have an impact upon the proportion of potential plant pathogens worldwide. Temperature is known to determine the distribution of soil microbial communities[9,13] as well as to influence the distributions of fast-growing opportunistic fungal and animal pests[14]. Even so, the potential role of warming in the relative abundance of fungal plant pathogens in the soil reservoir remains largely unexplored.

Here, we used a global field survey[15] conducted across 235 natural ecosystems from six continents (Supplementary Fig. 1) and a nine-year warming field experiment[16] to evaluate how temperature[17] regulates the relative abundance of soil-borne potential fungal plant pathogens (potential plant pathogens hereafter). This global survey was previously used to identify the top dominant fungal phylotypes in soils across the globe[15]. Here, we generated global atlases for the current and future distribution of potential plant pathogens under contrasting global change scenarios, and explored causal relationships between their relative abundance and warming. Our global field survey (Methods) included a wide variety of vegetation, climates and soil types, and covered ~73% of the environmental conditions found on Earth (Supplementary Appendix 1).

Using amplicon sequencing for the ITS gene, we identified 2,735 fungal phylotypes classified as potential plant pathogens out of the 23,399 fungal phylotypes found in our global survey (Supplementary Data 1)[6]. Together, potential pathogenic phylotypes represented between

0.5 and 46.5% (with the average at 14.4%) of all ITS sequences at a given site (Fig. 1A), and included multiple potential plant pathogens with single (plant pathogens only, 37.1% of all pathogenic phylotypes; e.g., *Venturia* spp.) and mixed (plant pathogen and endophyte and/or saprotrophic fungi, 62.8% of all pathogenic phylotypes; e.g., *Fusarium* spp.) trophic modes (Supplementary Fig. 2; Supplementary Data 1). Our results thus indicate that soil-borne potential plant pathogens can be relatively abundant in soils from natural ecosystems worldwide. This was particularly the case in tropical and dry forests, but not in boreal and cold forests (Fig. 1B). On average, surveyed soils were dominated by a few genera of potential plant pathogens, including *Alternaria*, *Fusarium*, *Venturia* and *Phoma* (Fig. 1C; Supplementary Data 1 for a complete list), which together accounted for almost half (43.0%) of the retrieved ITS sequences classified as potential plant pathogens. Many of these soil-borne fungal taxa include economically important potential pathogens, as they are likely to affect the health and productivity of many important crops (e.g., wheat, sunflowers, cabbages, tomatoes, and potatoes), gardening and cosmetic/medicinal plants (e.g., *Hibiscus*, *Aloe vera*), and wild species that are an important food source for livestock[6-8,18-19].

We then used Structural Equation Modelling (SEM; Supplementary Figs. 3-5; Supplementary Tables 1-8) to identify the direct and indirect (e.g., via changes in soil properties and vegetation) associations between temperature and the relative abundance of potential plant pathogens across the globe. We found that mean annual temperature (MAT) had the largest positive and significant direct association with the relative abundance of soil pathogens globally (Fig. 1D; see all considered associations in Supplementary Fig. 3 and Supplementary Table 2). We also detected multiple indirect effects of MAT on the relative abundance of soil-borne potential plant pathogens via changes in vegetation types (forests and grasslands; Fig. 1D). Similar results were observed when calculating the relative abundance of potential plant pathogens from rarefied abundance (Supplementary Tables 3 and 8), when considering the relative abundance of potential plant pathogens with single and mixed trophic modes (Supplementary Tables 4-5 and 8), and when focusing on probable and highly probable pathogens only (Supplementary Tables 6-8). Our analyses further indicated that MAT was the most important factor influencing the relative abundance of soil-borne potential plant pathogens globally when considering both direct and indirect effects simultaneously (total standardised effects; Fig. 1E and Supplementary Fig. 4). We also found that MAT had a total positive effect on the relative abundance of fungal pathogens when focusing on the most abundant potential pathogen genera (*Alternaria*, *Fusarium*, *Venturia* and *Phoma*; Supplementary Fig. 5). Additional correlation analyses suggested that MAT is positively associated with the relative abundance of multiple genera classified as potential plant pathogens, which were found to be ubiquitous in soils across the globe (>50% of all locations) (Fig. 2; Supplementary Data 1). Likewise, ecosystem type (e.g. forests and grasslands) and plant cover were significantly associated with the relative abundance of plant pathogens. These findings suggest that changes in land use –as those predicted with global change[20]– might also alter the relative abundance of soil-borne potential pathogens globally. Other predominant environmental factors associated with specific pathogen genera include precipitation and soil pH (Fig. 2).

Together, findings from our observational survey[15] suggest that increasing temperature may cause increases in the presence of potential fungal plant pathogens in soils, which might act as reservoirs of infection. Natural areas are often surrounded by croplands across the globe, and there is significant "spill over" of soil microbes between them[21]. Given the high dispersal abilities of fungi[22-23], our results suggest that warming-induced increases in the relative abundance of potential plant pathogens in soils from natural ecosystems will increase the risk of infection by

these fungi in adjacent croplands[24-26]. These impacts are likely to have implications for sustaining a growing human population, which is predicted to reach 9.8 billion people in 2050[27]. Furthermore, it can create significant constraints for livelihood in least developed countries, where the majority of people rely to a large degree on livestock and natural products supported by natural ecosystems[10].

To experimentally corroborate the observed global patterns, we used a nine-year field warming experiment located at the centre of the Iberian Peninsula[16], where natural ecosystems are expected to be markedly affected by global warming if emissions are not significantly controlled[17]. Note that these data were not included in our global survey and were analysed independently. This experiment evaluates the effects of warming (~2°C; Supplementary Fig. 6) on key ecosystem attributes in a semiarid grassland with well-developed biocrusts (soil surface communities dominated by lichens, mosses, fungi, and cyanobacteria)[16]. Warming almost tripled the relative abundance of potential plant pathogens in soil (Fig. 3), providing additional experimental evidence of the positive effect of temperature on the relative abundance of these organisms. Additionally, warming increased the relative (measured via amplicon-sequencing) and total (measured via quantitative PCR) abundance of *Alternaria*, the most common pathogenic fungal genus found in our global survey (Fig. 1) by sevenfold and twofold, respectively (Fig. 3). Warming also increased the relative abundance of the globally dominant *Fusarium* genus (Fig. 1) by almost five times (Supplementary Fig. 7), and also affected other common pathogens such as *Cladosporium* spp., where relative abundance increased by 20-fold (see Supplementary Fig. 7 for more examples).

Global atlases, similar to those that have been available for plants and animals for centuries, now exist for some bacterial[28] and fungal (e.g., mycorrhizal fungi)[15,29] taxa. However, although regional and local information on plant diseases is starting to be increasingly available (https://www.plantwise.org), global atlases for the current and future distribution of potential plant pathogens under contrasting global change scenarios are lacking. Based on the consistent results from the global survey and experiment, we generated a global atlas depicting the current distribution of potential plant pathogens globally (Figs. 4A and Supplementary Figs. 8-9; see Supplementary Appendix 2 for a cross-validation on this map using an independent database[9]). We also generated a similar map for the relative abundance of potential pathogens with single tropic mode (plant pathogens only) (Supplementary Fig. 9); this map is highly correlated to that including all potential plant pathogens together (Fig. 4A; Pearson´s r = 0.83; $P < 0.0001$). These atlases show that the highest relative abundance of these pathogens can be found in warm areas such as dryland and tropical ecosystems (Fig. 4A; Supplementary Fig. 9; Supplementary Appendixes 1-2). Analyses conducted for dominant potential plant pathogens revealed that while *Venturia* has a more homogeneous spread across the globe, with especial relevance across the Northern Hemisphere, fungi from the genera *Fusarium, Phoma*, and *Alternaria* are more prevalent in tropical forests and drylands (Supplementary Fig. 10). These results are consistent with findings from croplands, where disease severity associated with these fungi is often more significant in warmer climates[7,30].

To provide new insights on other potential locations on Earth that might be more vulnerable to these organisms in the future, we forecasted the relative abundance of potential plant pathogens under global change scenarios (RCP2.6-SSP1, RCP6.0-SSP4, RCP8.5-SSP5 up to 2050; Fig. 4B and Supplementary Fig. 10). These analyses show an increase of the relative abundance of potential plant pathogens in most regions of the world regardless of the climate and land-use scenarios considered (Fig. 4B). Such an increase is supported by our experimental results showing a positive correlation of the abundance of these pathogens with warming effects like those expected

by global climate models. Although caution should be taken regarding the local accuracy of our model (see Supplementary Appendix 1), the impacts of warming are particularly evident in soils across the Northern Hemisphere, towards the Arctic, as well as in South Africa, where all scenarios show a systematic temperature rise (Fig. 4). Land use was especially important for some potential pathogenic genera such as *Fusarium*, which were found to be negatively correlated with plant cover (Fig. 2), and thus might increase with forecasted increases in aridity[11]. Together, our analyses show those locations of Earth where potential plant pathogens are expected to become more common in the near future. However, we would also like to stress here that we have not measured pathogen infection or disease of hosts, and that the importance of pathogens in determining vegetation structure might differ in warm vs. cold ecosystems, which might limit the implications of our results in boreal and artic ecosystems. In addition, our study has a global focus and does not provide high resolution information on the fine-scale (e.g. at the scale of meters or centimeters) distributions of fungal pathogens, which are affected by factors not included in our analyses such as microclimatic variations. Therefore, future work needs to be done to identify the fine-scale distribution of plant pathogens in specific localities.

Our results, based on a global survey and a nine-year field experiment, highlight the significance of soils from natural ecosystems as an important reservoir for potential fungal plant pathogens, and underscore temperature as a major environmental factor driving their global distribution. They indicate that the proportion of potential plant pathogens will likely increase in most regions of the world regardless of the climate and land use scenarios considered. Our findings advance our understanding of the distribution and sensitivities to climate and land-use change of potential fungal plant pathogens in a warmer and human-dominated world. They can also be used to make better predictions on how ongoing global environmental change will affect their distribution and impact on food production and human livelihoods worldwide.

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Methods
Global survey
Study sites and soil sampling
We used data from a global field survey[15] to identify the ecological drivers and the current and future distribution of potential soil-borne plant pathogens in soils worldwide. Briefly, bulk soils (top 7.5cm) were collected from 235 ecosystems located in 18 countries from six continents (Supplementary Fig. 1) and covering nine biomes (temperate, tropical and dry forests, cold, temperate, tropical and arid grasslands, shrubland, boreal) between 2003 and 2015. Locations were

selected to provide a solid representation for most environmental conditions (e.g., climate, soil and vegetation types) found on Earth (Supplementary Appendix 1). For example, mean annual precipitation and temperature in these locations ranged from 67 to 3085mm and from -11.4º to 26.5ºC, respectively. Given the global distribution of croplands, most natural ecosystems are surrounded to certain level by agricultural fields. Soil samples were sieved upon arrival to the laboratory (2mm mesh). Then, a portion of soil was immediately frozen at -20 ºC for molecular analyses, while the rest of the soil was air-dried, and stored for a month, before physicochemical analyses.

Environmental factors

Our field global survey[15] included 12 environmental variables, which were obtained either in the field or from satellites/databases. Elevation and climatic variables, including mean annual temperature (MAT), mean annual precipitation (MAP) and temperature and precipitation seasonality, were collected from the Worldclim database (https://www.worldclim.org; (~1km resolution)[31]. Note that air and soil (https://neo.sci.gsfc.nasa.gov/) temperature are highly correlated at the global scale (Pearson r = 0.81, P = 0.0011) and that we used air temperature because current and future global models for this variable are more robust. Plant cover (2001-2015) was obtained using remote sensing data from the Moderate Resolution Imaging Spectroradiometer (MODIS) at ~1km resolution[32]. Soil properties (texture [% of clay + silt], pH and total organic C) were determined from topsoil (top 7.5cm) samples collected from each location using standardized protocols[33]. To avoid biases associated with having multiple laboratories analyzing soils from different sites, all samples were analyzed at the Universidad Rey Juan Carlos (Spain). Soil pH was measured with a pH meter, in a 1: 2.5 mass: volume soil and water suspension. Soil texture (% of fine fractions: clay + silt) was determined as detailed in ref.[33]. The concentration of soil total organic carbon (C) was determined using a wet chemistry method[34].

Statistical analyses

Structural Equation Modelling

We used Structural Equation Modelling (SEM)[35] to identify the direct and indirect effects of climate, vegetation and soil properties as drivers of the relative abundance potential plant pathogens (see our *a priori* model in Supplementary Fig. 3). The most common vegetation types in our database (forests and grasslands) were included in our SEM as categorical variables with two levels: 1 (a given ecosystem type) and 0 (remaining ecosystem types). Since some of the variables introduced were not normally distributed, the probability that a path coefficient differs from zero was tested using bootstrap tests[36]. Bootstrapping is preferred to the classical maximum-likelihood estimation in these cases, because in bootstrapping, probability assessments are not based on an assumption that the data match a particular theoretical distribution. Thus, data are randomly sampled with replacement in order to arrive at estimates of standard errors that are empirically associated with the distribution of the data in the sample. We conducted models for the relative abundance (%) of all soil-borne fungal plant pathogens (un-rarefied and rarefied, 4500 reads/sample; see the *Molecular analyses* section below), plant pathogens with single (plant pathogens only) and mixed trophic mode (plant pathogen and endophyte and/or saprotrophic fungi) and plant pathogens classified as probable and highly probable plant pathogens (excluding possible pathogens)[6]. Moreover, we conducted models for the most abundant pathogen genera (*Alternaria*, *Fusarium*, *Venturia*, and *Phoma*). Environmental data included in our model (Supplementary Table 1) did not suffer from multicollinearity (Pearson´s r < 0.7 in all cases; Supplementary Table 10).

We then tested the goodness of fit of our model. To do so, we used the Chi-square test (χ^2; the model has a good fit when $0 \leq \chi^2 \leq 2$ and $0.05 < p \leq 1.00$) and the root mean square error of approximation (RMSEA; the model has a good fit when RMSEA $0 \leq$ RMSEA ≤ 0.05 and $0.10 < p \leq 1.00$)[36]. Finally, we confirmed the fit of the model using the Bollen-Stine bootstrap test (the model has a good fit when $0.10 <$ bootstrap $p \leq 1.00$). Our model showed a solid goodness-of-fit, and therefore, a satisfactory fit to our data (Fig. 1D). SEM models were conducted with the software AMOS 20 (IBM SPSS Inc, Chicago, IL, USA).

Correlation analyses

We conducted Spearman correlation analyses to further evaluate the associations between climate, vegetation, soil properties and the relative abundance of the most ubiquitous putative fungal plant pathogens (i.e. those genera found in >50% of all locations surveyed). Spearman rank correlations measure the strength and direction of association between two ranked variables. They do not require normality of data, and linearity is not a strict assumption of these analyses. We used a False Discovery Rate approach to determine adjusted p-values for all correlations to control for spurious (false positives) correlations. We used the R package "fdrtool"[37] to conduct these analyses.

Global mapping and predictions

We used the sampled dataset to generate global maps of likely distributions of these pathogens. In particular, we conducted ordinary least square models to project each map for current and future states of soil pathogens across the world. The implementation of these models was preceded by exploratory correlation analyses to identify the most important factors associated with the distributions of potential plant pathogens. These included: climate (DMAT: mean annual temperature; DMAP: mean annual precipitation), vegetation type (Dforest: forest; Dgrassland: grassland), elevation (Selev) and soil variables (Stext: soil texture; Scarbon: soil carbon; SpH: soil pH). 'S' and 'D' indicate the variables that were either kept constant for current and future conditions (S) or those that changed in future scenarios (D). Climatic seasonality data was not included in these analyses given the current levels of projection uncertainty associated with this type of data under contrasting global change scenarios[38].

For future projections of the relative abundance of potential plant pathogens, we used precipitation, temperature and land-use datasets from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP)[39], and the land-use Model Intercomparison Project (LUMIP)[40] activities from the Intergovernmental Panel for Climate Change (IPCC). This selection followed the protocol laid out in ref[41].

In terms of climate datasets, we used the bias-corrected historical and future ISMIP2a dataset[39,42] spanning the timeframe from 1951 to 2099. We considered three Representative Concentration Pathways: RCP2.6 (+0.4 to 1.6ºC by 2050), RCP6.0 (+0.8 to 1.8ºC by 2050), and RCP8.5 (+1.4 to 2.6ºC by 2050). The monthly means of daily temperatures and daily total precipitation greater than 1mm were calculated for the available period of these data. For the purpose of this study, we selected two projection steps: 2010 and 2050. To avoid outliers, we calculated 20-year climatologies using an analysis window centered in each year-step. The dataset created was used as a climate input for all model runs. For each SSPxRCP combination, we used two different general circulation models (GCM) (i.e., gfdl-esm2m, noresm1-m)[42].

For the land-use projections, we built on the dataset provided by the land-use Harmonized v2.0 project (http://luh.umd.edu/)[43]. This dataset was produced in the context of the World Climate Research Program Coupled Model Intercomparison Project 6 (CMIP6)[44-45], and contains a

harmonized set of land-use scenarios that are consistent between historical reconstructions and future projections. It reproduces annual land-use reconstructions for historical land-use forcing (covering the period 850-2015) and for different integrated assessment models (IAMs) and shared socioeconomic pathways (SSP, from 2015 to 2100) at 0.25 degree resolution. These pathways represent a range of plausible future scenarios based on different socioeconomic challenges for climate change mitigation (low in SSP1 [sustainability] and SSP 4 [Regional inequality]; high in SSP5 [Fossil-fuelled development]), and potential challenges for adaptation (low in SSP1 and SSP5; high in SSP4). A full description of each scenario is given in ref.[44]. Each SSP corresponds to a specific RCP; here we selected the combinations SSP1xRCP2.6, SSP4xRCP6.0, and SSP5xRCP8.5. For the static datasets, we resampled all soil data coming from soil grids[39] to 0.25 degree resolution to match the resolution of the non-static datasets. The same procedure was done with the elevation dataset[46].

Using an exploratory analysis, which loops through all potential variable combinations to maximize the predicted power of each equation, we obtained different equations for each of the analysis:

$$P_{Pathogens} = 0.905 + (0.014 \times D_{MAT}) + (- < 0.0011 \times D_{MAP}) + \left(0.194 \times D_{forest}\right)$$
$$+ \left(0.119 \times D_{grassland}\right) + (0.035 \times S_{text}) + (-0.295 \times S_{carbon}) + ($$
$$< 0.0011 \times S_{elev})$$

$$P_{Alternaria} = -0.194 + (0.012 \times D_{MAT}) + \left(-0.052 \times D_{forest}\right) + \left(0.010 \times D_{grassland}\right)$$
$$+ (-0.113 \times S_{text}) + \left(0.913 \times S_{pH}\right) + (-0.313 \times S_{carbon})$$
$$+ (< 0.0011 \times S_{elev})$$

$$P_{Fusarium} = -0.013 + (< 0.0012 \times D_{MAP}) + \left(0.117 \times D_{grassland}\right) + \left(0.409 \times S_{pH}\right)$$
$$+ (-0.310 \times S_{carbon}) + (< 0.0011 \times S_{elev})$$

$$P_{Phoma} = -0.483 + (0.009 \times D_{MAT}) + (- < 0.0011 \times D_{MAP}) + \left(0.175 \times D_{forest}\right)$$
$$+ \left(0.014 \times D_{grassland}\right) + \left(0.699 \times S_{pH}\right) + (-0.029 \times S_{text}) + (-$$
$$< 0.00104 \times S_{elev})$$

$$P_{Venturia} = 0.400 + (0.008 \times D_{MAT}) + (- < 0.0012 \times D_{MAP}) + \left(0.162 \times D_{forest}\right)$$
$$+ (0.041 \times S_{text}) + \left(-0.585 \times S_{pH}\right) + (0.173 \times S_{carbon})$$

The equations mentioned above translate to different fit parameters: i) all potential plant pathogens (P*Pathogens*): R^2=0.16, $P<0.001$; ii) *Alternaria* (P*Alternaria*): R^2=0.27, $P<0.001$; iii) *Fusarium* (P*Fusarium*): R^2=0.18, $P<0.001$; iv) *Phoma* (P*Phoma*): R^2=0.37, $P<0.001$; and vi) *Venturia* (P*Venturia*): R^2=0.26, $P<0.05$. A map of the extrapolation uncertainty for our global database (235 locations) is available in Supplementary Fig. 8 (see also Supplementary Appendix 1). In addition, we further cross-validated our main map using an independent global database as explained in Supplementary Appendix 2 below.

Field experiment
Study site and soil sampling
We used a nine-year manipulative field experiment to provide further experimental evidence for a causal link between warming and the relative abundance of soil-borne fungal potential plant pathogens. This experiment is being conducted on a dryland ecosystem located in the center of the Iberian Peninsula (40°01'55.7"N 3°32'48.3"W; 590 m.a.s.l.). Mean annual temperature and rainfall are 15 °C and 349 mm, respectively and the soil is classified as Gypsiric Leptosol (IUSS Working

Group WRB, 2006). Perennial plant cover is lower than 40%, and is dominated by the perennial grass *Stipa tenacissima* L. Open areas between plant patches contain a well-developed biocrust community dominated by lichens such as *Diploschistes diacapsis*, *Squamarina lentigera* and *Psora decipiens*. Biocrust communities have been proposed as a system-model to test the effects of global change on ecosystem functioning under global change scenarios[47-50]. The experiment, described in ref.[16], was established in the study area in July 2008[50], and includes two levels of warming (ambient [control] vs. ~2ºC increase [warming])[16,50].

To achieve a temperature increase within the forecasts of climate change models for the study area[51], we built open top chambers (OTCs) of hexagonal design with sloping sides of 40 cm $\times$ 50 cm $\times$ 32 cm in 1.2 x 1.2 m plots (Supplementary Fig. 6). We used methacrylate to build our OTCs because this material does not substantially alter the characteristics of the light spectrum. Our warming treatment promoted an average increase of air and surface soil (0-2 cm) temperature of 1.94ºC and 2.55ºC, respectively. Warming effects were highest during the summer (June-September).

Soil samples (top 0-1 cm depth) were collected nine years after the beginning of the experiment from ten plots per combination of treatments. Three soil samples per plot were sampled with a 5 cm diameter core, which were then bulked to obtain a unique sample per plot. Soil was sieved (2 mm mesh) and separated into two fractions. A portion of soil was immediately frozen at -20 ºC for molecular analyses. Given the different soil sampling depth between our experimental and observational study, caution should potentially be applied when directly comparing the two datasets.

We used non-parametric PERMANOVA (Anderson 2001) to test for significant effects of warming on the (ITS amplicon sequencing and qPCR analyses) abundance of fungal plant pathogens (see the *Molecular analyses* section below). These analyses are robust to lack of normality in our data. Warming was considered a fixed factor in these analyses (n = 10). Non-metric PERMANOVA analyses were carried out using PRIMER v 6113 and PERMANOVA[+] (PRIMER-E, Plymouth, UK).

Molecular analyses

Amplicon sequencing

Amplicon sequencing analyses were used to determine the fungal communities in soils from the global survey and warming experiment. The extracted DNA samples were frozen and shipped to the Next Generation Genome Sequencing Facility of the University of Western Sydney (Australia). Fungal communities were determined by sequencing the Internal Transcribed Spacer (ITS) region 2 with primers FITS7 (GTGARTCATCGAATCTTTG) /ITS4 (TCCTCCGCTTATTGATATGC) on a Illumina MiSeq platform (2x300 PE). Bioinformatic processing was performed using a combination of USEARCH[52] and UNOISE3[53]. Operational taxonomic units or OTUs (phylotypes) were defined at 100% similarity thresholds using UNOISE3[53]. Phylotype identification was obtained against the UNITE fungal database (V7.2)[54]. The relative abundance (%) of each phylotype was calculated from the resulting OTU (phylotype) table. Plant pathogenic lifestyles for fungal communities were determined using the FUNGuild database (http://www.stbates.org/guilds/app.php; retrieved at September 2019)[6]. A complete list of the potential soil-borne fungal plant pathogens included in this study can be found at Supplementary Data 1 (supplementary Excel file). We obtained 12086669 (global survey; n = 235) and 787142 (field experiment; n = 20) ITS reads across the studied samples, being 14.4% and 21.6% of all the retrieved ITS reads classified as putative fungal plant pathogens in the global survey and field

experiment, respectively. The relative abundance of all soil-borne fungal plant pathogens (both exclusively pathogenic or with mixed life styles) was calculated in both cases using un-rarefied ITS OTU tables, as the sum of the relative abundance (%) of all ITS sequences classified as fungal plant pathogens (i.e., sum of all ITS reads classified as pathogens / all ITS reads x 100 at each soil sample). The total relative abundance of potential plant pathogens was highly correlated with the same variable calculated using a rarefied OTU table for the global field survey (4500 reads/sample; r = 0.998; *P* < <0.0011) and the field experiment (4500 reads/sample; r = 0.999; *P* < <0.0011), so the choice of not rarefying our data did not affect our conclusions. All *Gibberella* reads were considered as *Fusarium* in this study for consistency with the most recent classifications[55].

Additional taxonomic assignment analyses
To further confirm the robustness of the taxonomic assignments, for each phylotype identified as a putative plant pathogen, we performed a BLAST search (https://blast.ncbi.nlm.nih.gov/Blast.cgi) against the fungal ITS sequences from type material, and representative fungal genomes available in GenBank (https://www.ncbi.nlm.nih.gov/genbank/). We then selected the top 10 hits for each phylotype, and then re-parsed those matching species with FUNGuild. A total of 1574 and 586 OTUs matched, at a 97% identity cut-off, with ITS ex-type sequences and representative genomes, respectively (Supplementary Data 1), having pathogenic trophic modes (both exclusively pathogenic and mixed modes). The relative abundance of all plant pathogens identified using the UNITE fungal database (V7.2)[54] was highly correlated to the one calculated using GenBank from ITS ex-type (r = 0.96; *P* < <0.0011; 97% cut-off) and representative genomes (r = 0.71; *P* < <0.0011; 97% cut-off) (Supplementary Data 1). These analyses provide further support of our data.

qPCR analyses
qPCR analyses were done to further confirm results from our warming experiment. The absolute abundance of *Alternaria* –the most predominant fungal plant pathogen in our surveys– was estimated by a real-time quantitative polymerase chain reaction (qPCR) using primers Dir1ITSAlt (TGTCTTTTGCGTACTTCTTGTTTCCT) and Inv1ITSAlt (CGACTTGTGCTGCGCTC), which are commonly used to quantify pathogenic plant-associated *Alternaria* spp[56]. Mastermix reactions were prepared in a volume of 10 μl containing a 1.5 ng DNA template, 5 μl 2 × SensiFast SYBR Hi-ROX kit (Bioline, Australia), 2 μl water and 1 μl (5μmol/ μl) of each primer, respectively. Amplifications were performed in 96-well reaction plates using a Bio-RAD CFX96 real-time PCR system (Bio-Rad, Australia). Each plate included duplicate reactions per DNA sample, standards and a negative control sample (without DNA). Standard curves were generated using tenfold serial dilution of PCR-amplicons containing the *Alternaria* target region. The amplification program consisted of 1 cycle of 94°C for 4 min, followed by 35 cycles of 94°C for 30 s, 62°C for 25 s and 72°C for 20 s, and a final elongation step of 72 °C for 2 min. To determine the reaction specificity a melting curve analysis was subsequently performed by incubating the samples at 95°C for 2 min, annealing at 65°C for 5 s, followed by heating them slowly at 0.5°C/sec up to 95°C, while continuously monitoring the fluorescence signal.

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Author contributions

M.D-B. developed the original idea of the analyses presented in the manuscript. M.D-B, F.T.M., and B.K.S. led the global survey. F.T.M. designed the field warming experiment and has maintained it over the years. Lab analyses were done by M.D-B., C.C-D., E.E., F.T.M and B.K.S. Bioinformatic analyses were done by B.K.S., J.W and E.E. Statistical modelling, mapping and data interpretations were done by C.G., N.E. and M.D-B. The manuscript was written by M.D-B. with contributions from all co-authors.

Data accessibility

The data associated with the global field survey and the field experiment are publicly available in Figshare[57].

Code availability

Most numerical analyses included in this article do not have an associated code. Used codes are available in ref.[57].

Competing financial interests
The authors declare no conflict of interest.

Supplementary Information
Supplementary Appendixes 1 to 2
Supplementary Figures 1 to 11
Supplementary Tables 1 to 10

Figure captions

Figure 1 | Relative abundance, identity and ecological preferences of potential plant pathogens worldwide. Panel A represents the distribution of the relative abundance of total fungal pathogens across the 235 ecosystems surveyed. Panel B includes mean values (± SE) for the relative abundance (%) of potential plant pathogens across continents/biomes. Panel C shows the most common soil fungal pathogens identified (mean values ± SE). Panel D includes a structural equation model assessing the direct and indirect effects of environmental factors on the relative abundance of potential plant pathogens. We grouped the different categories of predictors (climate, soil properties, vegetation and spatial influence) in the same box for graphical simplicity (these boxes do not represent latent variables). Variable within these boxes are allowed to covary. Numbers adjacent to arrows are indicative of the effect size of the relationship. Only significant effects ($P < 0.05$) are plotted. Information on environmental factors included in our SEM, and on direct effects for other SEM arrows can be found in Supplementary Fig. 3 and Supplementary Tables 1-2. Supplementary Table 2 offers a complete view of our full SEM. The degree of freedom in this SEM came from the lack of relationship between PSEA and clay+silt (%). R^2 for other endogenous variables in Supplementary Table 8. Panel E represents the total standardised effects on SEM (sum of direct and indirect effects; STE; ± bootstrap CI 95%) on the relative abundance of potential plant pathogens. In panels A and C-E, n = 235 locations. n associated with panel B are shown in parentheses. F = Forests; G = Grasslands. MAT = mean annual temperature. MAP = mean annual precipitation. PSEA = precipitation seasonality. TSEA = temperature seasonality.

Figure 2 | Temperature is positively associated with the relative abundance of potential plant pathogens at the genus level. Spearman correlations between environmental factors and the relative abundance of ubiquitous fungal plant pathogens at the genus level (n = 235). Information on environmental factors included in this analysis can be found in Supplementary Table 1. MAT = mean annual temperature. MAP = mean annual precipitation. PSEA = precipitation seasonality. TSEA = temperature seasonality. Correlations with False Discovery Rate adjusted $P > 0.05$ are excluded (plotted in white).

Figure 3 | Experimental evidence that warming increases the relative and total abundance of potential plant pathogens. Warming effects on the relative (%) and absolute (gene copies g^{-1} soil) abundance of fungal pathogens in a nine-year field warming experiment. The solid lines show mean values (n = 10). P values as follows: ***$P < 0.001$; *$P < 0.05$. $^{\#}$log$_{10}$-transformed. See Supplementary Table 9 for further statistical details.

Figure 4 | Current relative abundance (A) and temporal projections (2050; B-C) of potential plant pathogens across the globe. A cross-validation of the map shown in A using an independent global survey is available in Supplementary Appendix 2. Panel B shows the agreement across the different scenarios considered (gain reflects areas where gain is predicted, loss reflects areas where loss is predicted, and mixed reflects areas where different scenarios predict gain or loss). Panel C shows the relative change for potential plant pathogens and that of the most abundant genera (*Alternaria*, *Fusarium*, *Venturia*, and *Phoma*) assessed for scenarios SSP1 (sustainability), SSP4 (Regional inequality), and SSP5 (Fossil-fueled development). The bars and barplots indicate the interquartile interval and median value for each scenario, respectively. A map of the extrapolation uncertainty for our global database (235 locations) is available in Supplementary Fig. 8 (see also

Supplementary Appendix 1). See also Supplementary Figs. 9-10 for an alternative panel (A), and
680 for maps of individual pathogen-associated genera.