Journal Pre-proof

Climate change-driven geographical shifts in Aspergillus species habitat and the implications for plant and human health

Christopher Uzzell, Jennifer Shelton, Norman van Rhijn

PII: S2589-0042(26)00286-5

DOI: https://doi.org/10.1016/j.isci.2026.114911

Reference: ISCI 114911

To appear in: *iScience*

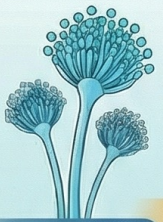
Received Date: 17 July 2025

Revised Date: 13 November 2025

Accepted Date: 2 February 2026

Please cite this article as: Uzzell, C., Shelton, J., van Rhijn, N., Climate change-driven geographical shifts in Aspergillus species habitat and the implications for plant and human health, *iScience* (2026), doi: https://doi.org/10.1016/j.isci.2026.114911.

THE FUNGAL LANDSCAPE TODAY



Avg. Temp: 12.2°C

Different Species, Different Climates.

A. fumigatus thrives in temperate zones.

Avg. Temp: 16.3°C

A. niger dominates warmer regions.

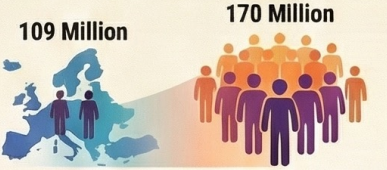
Avg. Temp: 17.8°C

A. flavus dominates

A SHIFTING WORLD: FUTURE PROJECTIONS & IMPACTS

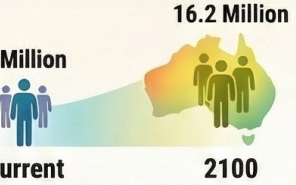
Pathogens on the Move: Under all climate scenarios, suitable habitats for all three species are predicted to shift northward.

Human Exposure Will Change Dramatically by 2100



Europe (*A. niger*)

While global exposure may drop, some regions will face increased risk, especially under severe warming.



Australia (*A. flavus*)

While global exposure may drop, some regions will face increased risk, especially under severe warming.

Climate change-driven geographical shifts in Aspergillus *species habitat and the implications for plant and human health*

Christopher Uzzell[1], Jennifer Shelton[2], Norman van Rhijn[3,4,5]*

[1] Liverpool School of Tropical Medicine, Liverpool, United Kingdom

[2] UK Centre for Ecology & Hydrology, Wallingford, United Kingdom

[3] Manchester Fungal Infection Group, Division of Evolution, Infection, and Genomics, Faculty of Biology, Medicine and Health, University of Manchester, Manchester, United Kingdom

[4] Microbial Evolution Research Manchester, Division of Evolution, Infection, and Genomics, Faculty of Biology, Medicine and Health, University of Manchester, Manchester, United Kingdom

[5]Lead contact

* To whom correspondence should be addressed: Dr. Norman van Rhijn, norman.vanrhijn@manchester.ac.uk

SUMMARY

Aspergillus species cause severe infections and are widespread environmental saprotrophs. Climate change is expected to alter the ecological niches and spread of fungal pathogens. Here, we use a global metabarcoding dataset and Maximum Entropy (MaxEnt) modelling to predict the current and future environmental suitability of three pathogenic *Aspergilli* : *A. fumigatus sensu lato*, *A. flavus sensu lato*, and *A. niger sensu lato*. We show that suitability of *A. fumigatus* is higher in temperate climates, while *A. flavus* and *A. niger* are more suitable in warmer regions. Future climate scenarios suggest a northward shifts of habitat suitability for all three

species, particularly under severe warming. We combine our MaxEnt model with spatial models of crop growing areas and human population and show that geographical shift will occur on *Aspergillus* species along different climate scenarios. These predictions can guide experimental validation efforts and provide a base model for further refinement for other pathogenic fungi.

Keywords:

Climate change, aspergillus, aspergillosis, fungal disease, MaxENT modelling, flavus, niger, fumigatus

Introduction

The filamentous fungal *Aspergillus* species are the prime example of a cross-kingdom pathogen. They are capable of infecting humans, other mammals, birds, honeybees and corals, they spoil crops pre- and post-harvest, and they render crops unsafe for consumption by production of mycotoxins [1,2]. They also play a crucial role in the environment as saprotrophs; recycling nutrients in decaying matter back into the soil [3]. Furthermore, frontline drugs used to treat clinical and veterinary aspergillosis, namely azoles, are also found in agricultural pesticides used to protect crops against fungal disease [4-6]. The structural similarity between clinical azoles and agricultural azoles has led to a rise in patients with azole-resistant infections after inhaling *Aspergillus* spores that have developed resistance following environmental exposure to azoles [7-9].

Due to their lifecycle; reproducing asexually and sexually in soil and sporulating to release 1000s of microscopic spores, *Aspergillus* spores are ubiquitous in air [10,11].

They are found indoors and outdoors, are detectable on a global scale, and it is estimated that we each inhale several hundred spores per day [12,13]. The small size of these spores (2-3 µm) allows them to bypass mucociliary clearance and reach the lung alveoli, where they are subsequently cleared by the innate immune system [14]. However, in individuals with a compromised immune system, or who have been exposed to a high number of spores, spores can establish and grow in a pre-existing cavity in the lung resulting in chronic pulmonary aspergillosis (CPA) [15,16]. If the immune system fails to prevent spores from entering the bloodstream via the lungs the infection results in a life-threatening disease called invasive aspergillosis (IA) [17]. It is estimated that 1.8 million people globally develop CPA, with 340,000 annual deaths, and 2.1 million people globally develop IA, with 1.8 million annual deaths [18].

There are a number of *Aspergillus* species more commonly associated with aspergillosis infections in humans and animals: *A. fumigatus, A. flavus, A. niger*, *A. terreus* and *A. nidulans* [19]. In the Northern Hemisphere, the majority of aspergillosis infections are caused by *A. fumigatus* [20-23], which in part contributed to the World Health Organisation (WHO) adding *A. fumigatus* to its fungal priority pathogens list (FPPL) [24]. However, in others parts of the world, other *Aspergillus* species are often reported as the leading cause of aspergillosis [25-27]. It is likely that environmental conditions, such as temperature, humidity and rainfall, favour the proliferation of different *Aspergillus* species in different climates [28-31]. It has been hypothesised that climate change will bring about an increase in human fungal infections in multiple ways including: i) by increasing the range of currently-pathogenic species, and ii) by increasing the thermotolerance of fungal species allowing more to survive at mammalian body temperature [32-36]. It follows that climate change may alter the distribution of currently-pathogenic *Aspergillus* species, or enable other *Aspergillus*

73 species to become pathogenic, leading to late or under diagnosis of aspergillosis
74 infections caused by unexpected species.

75 The same logic applies to *Aspergillus* species that cause crop losses, either through
76 spoilage or mycotoxin contamination [37]. We are currently facing the challenge of
77 feeding a predicted population of 9.7 billion by 2050, yet we still lose 20% of crop yields
78 pre-harvest and a further 10% post-harvest to pathogens [38,39]. Black *Aspergillus*
79 species, such as *A. niger*, and *Aspergillus* section *Flavi*, which includes *A. flavus*, are
80 the most often reported plant-pathogenic *Aspergilli* [40]. It is estimated that aflatoxin
81 contamination could cost the corn industry in the United States alone between
82 US$52.1 million and US$1.68 billion, with the upper estimate for if climate change
83 causes more regular aflatoxin contamination in the Corn Belt as was experienced in
84 2012 [41].

85 Studies of other fungal pathogens have underscored the significance of environmental
86 conditions in shaping host-pathogen dynamics. *Cryptococcus neoformans* is a
87 significant fungal pathogen of humans that is conditioned to grow in warmer
88 environments. Some strains of this organism have acquired enhanced
89 thermotolerance which enhances their virulence [42,43]. Likewise, *Fusarium* species that
90 damage both plants and humans, adaptively respond to climate variations with
91 increases in toxin production and fungicide resistance under warmer temperatures
92 [44,45]. It is timely that we build a global picture of *Aspergillus* species distribution: to
93 understand what it looks like now and predict what it might look like in the future, based
94 on the known impacts of climate variables on spore proliferation. In this study, we use
95 a literature review and the GlobalFungi database to ascertain the current distribution
96 of three pathogenic *Aspergillus* species: *A. fumigatus, A. flavus* and *A. niger* and

MaxEnt modelling to predict how the distribution of these species might alter in future climate scenarios.

Results

A Maximum Entropy model shows the geographic expansion of *Aspergillus* species

It has been hypothesised that fungal pathogens will expand their geographical range due to climatic changes within the next 100 years. However, currently there is little data to support these statements as experimental validation would rely on long term standardised global sampling efforts. Therefore, we approached this hypothesis using available metabarcoding sequencing data from GlobalFungi [46] and Maximum Entropy modelling. We focused on three fungal pathogens within the *Aspergillus* genus as these are causative agents of human infections but also plant infections. From the GlobalFungi database we obtained metabarcodes which both included ribosomal ITS1 and ITS2 data. These metabarcodes are only able to accurately define the three *Aspergillus* species up to their section level; *Aspergillus* Section *Fumigati*, *Aspergillus* section *Nigri* and *Aspergillus* Section *Flavi* [47,48]. However, speciation within these sections relies on multiple genetic markers (calmodulin and beta-tubulin) which are not available within the GlobalFungi dataset. Therefore, in here we refer to these further as *Aspergillus fumigatus sensu lato*, *Aspergillus niger sensu lato* and *Aspergillus flavus sensu lato*. We obtained data from 2599 samples, 5124 samples and 4015 samples for *Aspergillus niger*, *Aspergillus flavus* and *Aspergillus fumigatus*, respectively. After quality control, 1021, 871 and 319 datapoints were considered of high quality and contained all required metadata for *Aspergillus niger*, *Aspergillus*

flavus and *Aspergillus fumigatus*, respectively (**Fig S1**). We only included datapoints from natural soil samples (non-experimental). Several unique biomes were not represented in this data, as sampling data of these regions is sparse. Data from the Amazon region, the Sahara, and northern Russia and Alaska was not available and therefore we can't make any accurate predictions for these regions. Latitude and longitude data of occurrences were used in the MaxEnt model together with bioclimatic variables. We assessed correlation between bioclimate variables to reduce the variables, autocorrelation and overfitting in the model (**Fig S2**). ROC curves were obtained to quantify the models predictive ability relative to a random prediction (**Fig S3**). For *A. flavus* the AUC of the ROC curve was 0.804, for *A. fumigatus* 0.874 and for *A. niger* 0.776 showing that the MaxEnt model predicts suitable habitat better than a random model. Furthermore, the jackknife test on the regularised training data showed that the annual mean temperature was considered the most important variable when taken in isolation for all three fungi (**Fig S3**). In a multivariate model that included the 7 bioclim variables, omission of the annual mean temperature reduced the fit of the model of *A. flavus* and *A. fumigatus* habitat, while omission of precipitation of the coldest month most reduced the fit of the model for *A. niger* habitat.

In addition, we extracted the data from the SoilGrid database on pH, sand, clay and silt particles, organic carbon stocks and density, total nitrogen, water retention, bulk density, cation exchange capacity to give further granularity to the metabarcoding data [49]. This revealed different patterns for each species could be found in cation exchange capacity where *A. flavus* was present in higher cmol(c)/kg soil compared to the other two species (**Fig S4**). In addition, *A. flavus* was found more in soil with lower carbon and nitrogen content, and in soil with higher proportion of sand particles, which is in line with published literature [50,51]. *A. fumigatus* was more commonly found in soils

containing higher levels of nitrogen and carbon stocks, higher proportion of clay particles as well as lower pH soils. These findings are also in line with previously published reports [52-54].

The MaxEnt model resulted in a world map with the suitability profile for each of these fungi (**Figure 1A**). Not completely unsurprisingly, *A. fumigatus* was most suitable in the northern hemisphere in temperate climates and *A. flavus* was more suitable for tropical regions. As relative abundance within each sample was not taken into consideration, we divided habitat into two categories: suitable and unsuitable. We used the maximum test sensitivity plus specific (MTSPS) as a threshold for suitable and non-suitable, which is generally used to classify suitability in MaxENT modelling [55,56]. A cut-off above 0.64, 0.61 and 0.68 was considered suitable habitat for *A. flavus*, *A. niger* and *A. fumigatus*, respectively. To validate our model, we collected published data on culture-based experimentation where culturing from soil was performed which allowed identification of the three *Aspergillus* species. We chose for soil culture experiments only as *Aspergilli* species are ubiquitously found in air. This resulted in 29 studies from different countries which identified all three *Aspergillus* species from soils. A positive correlation could be found between suitability from the MaxEnt model and frequency of each species from culture-based experimentation found in each study ($r(91) = 0.44$, $p = 0.114 \times 10^{-5}$) (**Figure 1B**).

Within our species distribution model environmental variables that significantly differed between the *Aspergillus* species included the annual mean temperature, annual precipitation and precipitation seasonality (**Figure 1C**). *A. flavus* and *A. niger* showed presence at a significantly higher annual mean temperature compared to A. fumigatus, at 17.8 and 16.5 and 12.3 average Celsius, respectively (one-way ANOVA with multiple comparison, $p<0.05$) (**Fig S5**). Significantly higher precipitation was

associated with presence of *A. fumigatus* compared to *A. flavus* and *A. niger*, while higher seasonality of precipitation was associated with *A. flavus* and *A. niger* (**Fig S5**).

Expanding geographic ranges can impact the spectrum of aspergillosis disease in plants and humans

Next, we wanted to model the environmental suitability changing over time due to climatic changes. We used the Shared Socioeconcomic Pathways (SSP) models SSP126, SSP245 and SSP585 within three time horizons (2041-2060, 2061-2080, 2081-2100) to assess the changes in suitability for the three *Aspergillus* species. The SSP126 models is the low emissions scenario, where the focus lays on a future with sustainability-focused development, where CO_2 emissions decline after 2025 and limit global warming to below 2 ° C. The SSP245 models is the intermediate emissions scenario where CO_2 emissions peak around 2040 and then decline slowly, with global warming reaching 2.5-3 °C by 2100. The SSP585 is the high emissions models where fossil-fuel driven development is central, and CO_2 emissions keep rising. This scenario would see warming of 4 °C or more by 2100. Of these SSP models and time horizons all bioclimatic variables contributing to the model were included. Using the MaxEnt model, we generated a habitat suitable/non-suitable map for these climate change models until 2100 (**Fig S6**).

For *A. flavus* the current suitable habitat contains much of middle of south Africa, Brazil and part of Mexico, large parts of South America, India, Pakistan, China and South-East Asia as well as Oceania. Under the low climate change model (SSP126), little will change for habitat suitability of *A. flavus* until 2100 and most regions will remain suitable, while only small pockets of land will become more suitable (**Fig S6**). Under

the moderate model (SSP245) (**Figure 2**), habitat suitability in Australia will largely disappear by 2100 while new suitable habitats are seen in north China and across Russia and part of northern America. Under the severe model (SSP585) by 2100 many of the suitable habitats will disappear, mainly on the African continent and across Brazil (**Fig S6**). Large parts of Australia will become unsuitable. However, larger parts of north China and Russia will become suitable as well as other parts of the northern hemisphere such as Scandinavia and Alaska. This is supported looking at suitability across latitude where 40 to 80 degrees latitude will become more suitable while 20 to -20 latitude will become less suitable (**Fig S7**).

Aspergillus fumigatus suitable habitat is currently mostly on the northern hemisphere in Europe, United States and parts of China. However, in the southern hemisphere parts of Brazil and Africa are also considered suitable as is New Zealand and some coastal regions in Australia. Under the low climate change model and moderate models (SSP126 and SSP245) only small parts of the northern hemisphere will become suitable for *A. fumigatus* and little change will be on the southern hemisphere suitable areas (**Figure 2**). However, under the severe model (SSP585) *A. fumigatus* suitable habitats will almost exclusively be on the northern hemisphere and pushed more towards the north pole (**Fig S6**). Still New Zealand, coastal Australia, parts of Argentina and Peru will be suitable as these remain more temperature climates. This is supported by suitability across latitudes as a strong decrease of suitability is observed from 40 to -40 degrees latitude (**Fig S7**).

Aspergillus niger habitat is currently suitable across many regions of the world, including all continents and many countries on the northern and southern hemisphere. None of the climate models will have a drastic impact on the northern hemisphere suitability for *A. niger*. The suitability for the southern hemisphere, in particular Africa

will change only in the land inwards region under the severe climate model (SSP585) but is predicted to remain suitable along the coastal regions (**Fig S6**). Suitability along latitude supports this as only marginally decreases are seen from 0 degrees to -40 latitude and some small increases from 50 – 80 degrees latitude (**Fig S7**).

Both *A. flavus* and *A. niger* are the causative agents of plant infections of many different crops. Using our MaxEnt model and land usage from CROPGRIDS [57] we established the habitat suitability of these two plant pathogens across 7 different crops; apple, grape, maize, rice, soybean, sugarcane and wheat for the severe climate model (SSP585) (**Figure 3A**). Across all crops, a reduction in habitat suitability across the growing areas was observed. Most interestingly, a steep decline was observed for *A. flavus* on maize habitat and rice. The maize growth area and habitat overlap was estimated to be 19.1 million km^2 currently, but would reduce to 13.3 million km^2 in 2050, 9.9 million km^2 in 2070 and 6.8 million km^2 in 2090. This steep decline was not observed for *A. niger* of which growth area and habitat overlap was estimated at 23.8 million km^2 currently, to 20.9 million km^2 in 2050, 19.1 million km^2 in 2070 and 16.8 million km^2 in 2090. For rice crops a similar trend was observed in which the *A. flavus* habitat was estimated at 8.8 million km^2 currently, but would reduce to 4.8 million km^2 in 2050, 3.2 million km^2 in 2070 and 2.0 million km^2 in 2090, while for *A. niger* it was estimated at 10.9 million km^2 currently, to 8.2 million km^2 in 2050, 7.3 million km^2 in 2070 and 6.4 million km^2 in 2090.

A detailed spatial overview of these overlaps was generated which revealed that for maize growing areas and *A. flavus* habitat the main regions which showed a reduced overlap were located across South America and Africa (**Figure 3B**). However, habitat suitability in the Northern Hemisphere was mostly retained. A similar trend was observed for *A. niger* but with a smaller effect. Some maize growing regions in Africa

and South America would not be considered suitable, but habitat across the Northern Hemisphere, including India and Mexico was maintained. *A. flavus* habitat within rice growing regions was severely reduced and would in 2100 only be maintained into China and small regions in Africa (**Fig S8**). However, for *A. niger* larger regions across South America (Brazil) and West-Africa would be retained by 2100.

Next, we wanted to know if a change in habitat could result in a change in causative agents of aspergillosis in the clinic. To assess the link between environment and clinical distribution of *Aspergillus* species we found literature where at least one report containing relative prevalence in invasive aspergillosis of *A. niger, A. flavus* and *A. fumigatus* and at least one report from these Aspergilli and their relative prevalence in soils (**Figure 4A**). This resulted in 14 countries in which we could find literature with these data. This showed that species distribution from clinical samples (invasive pulmonary aspergillosis) generally correlated with the species distribution (*A. flavus* $r(12) = 0.74$, $p = 0.002$, *A. fumigatus* $r(12) = 0.66$, $p=0.011$, *A. niger* $r(12) = 0.40$, $p=0.058$) in the environment.

Given that habitat suitability and causative agents of invasive aspergillosis are correlated, we sought to model how many more people will be living in suitable areas for these *Aspergillus* species. We combined our MaxEnt model with a 1km spatial model of population density across the same climate models (SSP126, SSP245 and SSP585) [58]. Currently, 846 million, 1.98 billion and 905 million people live in suitable habitat for *A. flavus*, *A. fumigatus* and *A. niger*, respectively (**Figure 4B**). Generally, less people will live in suitable habitat for all three fungi. The largest effect is in suitable habitat for *A. fumigatus* as this will be reduced to 650 million (SSP585 2081-2100) – 1.1 billion (SSP126 2081-2100), a reduction of 45-75%. The smallest effect will be on number of people living in suitable areas for *A. niger*. Under the least severe climate

model (SSP126) this will reduce to 562 million by 2100 (38% reduction), while under the most severe climate model (SSP585) 345 million people will live in suitable areas for *A. niger* by 2100 (a 62% reduction).

However, a more detailed analysis of people living in suitable areas across different continents shows other patterns of potential exposure to these *Aspergillus* species (**Figure 4C**). The largest reduction of people living in suitable areas for all three *Aspergillus* species are in Africa, Asia and South America. In Asia a steep reduction of people living in suitable habitat is noticeable; for *A. flavus* from 278 million to 38 million (SSP585) – 98 million (SSP126), *A. fumigatus* from 1.5 billion to 392 million (SSP585) – 686 million (SSP126) and *A. niger* from 115 million to 14.5 million (SSP585) to 49 million (SSP126). In Africa lower numbers of people are already living in suitable areas for *A. fumigatu**s*** (45 million) compared to *A. flavus* (283 million) and *A. niger* (398 million), but a reduction in people living in suitable habitats for *A. flavus* (34 – 216 million) and *A. niger* (83 – 278 million) is predicted, especially in the more severe SSP585 model. In Europe, consistent number of people living in *A. flavus* (80 million currently versus 75 million) and increase in people living in *A. niger* (109 million currently versus 170 million) suitable habitat will only be seen in the SSP585 model. Interestingly, an increase in people living in *A. flavus* suitable habitat across Australia is observed across all three climate models; 5 million currently, 10.2 million in SSP126, 12.8 million in SSP245 and 16.2 million people in the SSP585 model (**Figure 4C**).

In summary, we have generated a MaxEnt model for three *Aspergillus* species that are of relevance in plant infections and infections of humans and animals. We have shown that this model correlates with experimental culture-based data available and that our model can be used to predict potential future outcomes along different climate scenarios. This model showed that all three *Aspergillus* species will move more

polewards and become more prevalent in the Northern hemisphere while the less suitable habitat will be presented across the Southern Hemisphere. We show this can potentially impact plant infections and human infections and provide data that can be used to inform future surveillance strategies.

Discussion

In this study we have used a MaxEnt modelling approach to assess how the geographical distributions of three *Aspergillus* species; *A. fumigatus*, *A. flavus*, and *A. niger*, are likely to shift in response to climate change. This MaxEnt model, supported by global metabarcoding data and climate variables, highlight trends in current and future environmental suitability for these species. Notably, *A. flavus* and *A. niger* are more prevalent in tropical and subtropical climates with higher mean temperatures, whereas *A. fumigatus* shows greater suitability in cooler, temperate regions as has been previously reported in the literature [12,27,30,59]. *A. fumigatus* has been previously found in low concentrations in soils in New Zealand, a temperature zone in the southern hemisphere and soils in Iceland, highlighting its potential to establish more northward and further expand [60,61]. Our literature review supports a positive correlation between environmental suitability and clinical prevalence of *Aspergillus* species, suggesting that shifts in habitat suitability may result in changing patterns of aspergillosis worldwide [62,63]. This is particularly concerning given the role of *A. flavus* and *A. niger* in both invasive human infections and crop contamination, especially as their environmental niches expand or shift.

Whilst this study focuses MaxEnt species distribution modelling, we acknowledge that alternative modelling approaches are available, including generalised linear models

(GLM) [64], gradient boosted models (GBM). [65,66] and random forest (FR) machine learning approaches [67-69]. However, MaxEnt offers several advantages [70], including its ability to handle presence-only data effectively [71]; is robust with relatively small sample sizes; incorporates regularisation techniques to avoid model overfitting and produces transparent and interpretable outputs. [72]. It is also widely used and well validated having been effectively tested across taxa and geographies [73-77]. In addition, here we have used one climate model, the HadGEM3-GC31-LL model [78]. Over 40 different climate models are currently available with slightly different outcomes across the tested timelines [79]. The HadGEM3-GC31-LL has shown a high climate sensitivity in the CMIP6 models, which has been debated if these are inconsistent with evidence from historical records [80,81]. Further research using other modelling approaches are required to come to a better understanding of the sensitivity of our analysis.

The MaxEnt modelling approach offers great potential in habitat suitable assessment, several methodological limitations are acknowledged. Firstly, highly customised MaxEnt models may become overly complex, leading to potential overfitting thus resulting in weakened predictive accuracy and ability to extrapolate to under sampled areas or new time horizons [82,83]. Moreover, MaxEnt also assumes that the presence data used in the model are geographically representative of the true species distribution. However, occurrence records typically exhibit spatial bias due to uneven sampling and/or reporting efforts, which we highlighted as no samples were available for example the Amazon, north Russia, Alaska and the Sahara dessert [84-86]. Finally, MaxEnt uses a presence-only modelling framework, therefore generating relative, rather than, absolute suitability. Therefore, consideration and careful interpretation is required when comparing between multiple species or across environments. MaxEnt and other modelling approaches do not account for biotic interactions,

344 microenvironmental variability, or genetic adaptation. For example, we do not account
345 for the potential evolution of thermotolerance, virulence or fungicide resistance, which
346 could drastically alter species distributions or ability to cause infections [87-89].

347 In addition, although we focused on climate variables, other abiotic factors, such as
348 soil composition, pH, and anthropogenic land use, undoubtedly influence *Aspergillus*
349 ecology [90]. *A. fumigatus*, in particular, is strongly associated with thermogenic
350 environments rich in decaying organic matter, such as compost heaps, where
351 temperatures can exceed 50°C during active decomposition [91,92]. Surveys across the
352 UK found elevated levels of *A. fumigatus* across compost bags, heaps and garden
353 plots treated with compost which was associated with antifungal resistant isolates [54,93].
354 These conditions provide a unique niche for *A. fumigatus*, enabling high sporulation
355 and aerial dispersal, especially when compost is disturbed [92,94]. In contrast, *A.*
356 *flavus* and *A. niger* are more frequently isolated from multiple types of soils, with high
357 organic content, lower nitrogen levels, and acidic to neutral pH [95,96]. Soil pH has been
358 shown to influence fungal community structure, with *A. niger* thriving in acidic
359 conditions [97,98]**.** Another layer of uncertainty stems from population projections in
360 suitable habitats. While we estimate increasing exposure risk in some regions, these
361 are modelled on current species-environment relationships and may not capture future
362 human behaviour, people at risk of developing fungal infections, or agricultural
363 changes that would render plants at risk of infection.

364 In addition to long-term climatic changes, seasonal variation and extreme weather
365 events are likely to play an important role in shaping the distribution
366 of *Aspergillus* species [99]. Seasonal dynamics influence growth and spore release,
367 particularly through cycles of rainfall and temperature shifts as is seen with other

fungal pathogens [100-102]. The MaxEnt model identified precipitation seasonality as a key predictor of habitat suitability, particularly for *A. flavus* and *A. niger*, suggesting these species are more present in areas with increased wet-dry cycles. Furthermore, extreme weather events such as droughts, floods, and heatwaves, which are expected to increase in frequency and intensity, can contribute to higher levels of fungal spores within the air [92,103]. Past studies have observed spikes in aspergillosis cases following natural disasters [104,105].

While our MaxEnt model provides a prediction of suitable habitat overlap within crop growing regions, it does not account for climate change directly impacting the crop growing regions. Several modelling attempts have shown that regions will become unsuitable to grow rice [106-108], wheat [109,110] and maize [111,112] under different climate scenarios. In addition, differential virulence of species and the occurrence of *Aspergillus* species across different crops and their disease has not been accounted for. While this would ideally be done, current epidemiological data from across the world remains sparse. Future work combining crop models, virulence data and epidemiology would provide a more detailed approached to model plant infections in a changing world.

Historically, invasive aspergillosis was primarily a concern for immunocompromised individuals, such as transplant recipients or those undergoing chemotherapy [113]. Our MaxEnt model does not take into account the changing patient population or emerging novel risk factors for aspergillosis. Examples of recently associated risk factors include COVID-19 and severe influenza, leading to COVID-19-associated pulmonary aspergillosis (CAPA) and influenza-associated pulmonary aspergillosis (IAPA), collectively termed viral-associated pulmonary aspergillosis (VAPA) [114,115]. These

diseases have been increasingly recognised in intensive care settings, where patients often experience prolonged ventilation and receive corticosteroids or other immunomodulatory treatments [116].

Despite these caveats, this work represents a valuable step in modelling the climate-driven shifts in *Aspergillus* ecology. By combining environmental metagenomic sequencing and modelling with clinical and environmental prevalence data, we highlight the importance of proactive monitoring in a changing world. The expanding and shifting range of these fungal pathogens, exacerbated by climate change, reinforces the urgency of a One Health approach to infectious disease surveillance.

Resource Availability

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Norman van Rhijn (Norman.vanrhijn@manchester.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- This paper analyses existing, publicly available data, accessible at https://globalfungi.com. Other databases used have been mentioned in the relevant section in the STAR methods.
- This paper does not report original code.

- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

Limitations of Study

This study has several limitations that should be considered when interpreting the findings. First, species occurrence data were derived primarily from global metabarcoding datasets, which rely on ITS sequencing that do not reliably resolve *Aspergillus* species beyond the section level, introducing uncertainty in species-level attribution, particularly within sections Nigri and Flavi. In addition, the presence-only nature of MaxEnt modelling produces relative suitability rather than true probability of occurrence and is sensitive to spatial sampling bias, which is evident in the underrepresentation of large regions such as the Amazon basin, Sahara, northern Russia, and the Arctic regions. Also, biotic interactions, microclimatic conditions, land management practices, and point-source habitats such as composting sites are not explicitly modelled, despite their known importance for *Aspergillus* ecology. Future projections rely on a single global climate model and do not capture inter-model variability present across CMIP6 ensembles, which can influence regional predictions. Finally, while the spatial modelling framework provides quantitative projections of potential future habitat suitability, it remains a theoretical representation of complex ecological systems, and the actual real-world impact on *Aspergillus* exposure, disease burden, and crop losses will ultimately depend on future environmental, biological, agricultural, and societal factors that require surveillance and experimental validation.

Acknowledgments

We thank M. Bromley and M. Brockhurst (UoM) for their insightful feedback on this work. This work was supported by the Wellcome Trust (grant: 226408/Z/22/Z).

Author Contributions

C.U. conceptualization, formal analysis, investigation, methodology, and writing—original draft. J.S. formal analysis, investigation, methodology, and writing—original draft N.v.R conceptualization, formal analysis, funding acquisition, supervision, and writing—original draft.

Declaration of Interests

The authors declare no competing interests.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Google Gemini and NotebookLLM in order to correct typos and grammar errors and generative the basis of the graphical abstract, respectively. After using this tool, the authors reviewed and edited the content and necessary and take full responsibility for the content of the publication.

STAR methods

Key resources table

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
GlobalFungi v5	Vetrovsky et al 2020	globalfungi.com
WorldClim 2	Fick and Hijmans 2017	worldclim.org

HadGEM3-GC31-LL	O'Neill et al 2016	https://www.wdc-climate.de/ui/cmip6?in
CROPGRIDS	Tang et al 2024	https://figshare.com/articles/dataset/CR
Population distributions under SSP models	Wang et al 2022	https://figshare.com/articles/dataset/Pr grid_population_distributions_from_202
Software and algorithms		
SPSS Statistics 24	IBM	
ArcGIS Pro v3.4.2	Esri	
MaxEnt v3.4.4	https://biodiversityinformatics.amnh.org/open_source/maxent/	
RStudio v2024.09.0+375	Posit PBC	

METHOD DETAILS

Data acquisition

To gather metabarcoding sequencing data on *Aspergillus* species, the GlobalFungi database (release 5.0) was used [46]. Search by taxonomy on *Aspergillus fumigatus*, *Aspergillus flavus* and *Aspergillus niger* was used. Raw data containing sample ID, latitude and longitude, sample type and ITS total were exported following data quality control. Data from aquatic and air samples were removed as well as manipulated samples. To remove potential datapoints that resulted from low level contamination only datapoints with over 10 sequencing reads attributed to each species were maintained. Data were stored and analysed using IBM SPSS Statistics 24.

Current and future bioclimate variables were obtained from the WorldClim data archive [117]. Initially a total of 19 bioclimate variables were downloaded with a spatial resolution of 5 arc-min ($10km^2$) were selected for analysis. Initially, a baseline MaxEnt model was constructed with all 19 variables to assess contribution percentage, and Pearson correlation coefficients between variables were calculated. Variables demonstrating a correlation exceeding ± 0.8 were investigated and the variable with the lower contribution in the baseline model was excluded. Ultimately, seven WorldClim bioclimate variables - Annual Mean Temperature (bio_01), Mean Diurnal Range (bio_02), Temperature Annual Range (bio_07), Annual Precipitation (bio_12), Precipitation of Driest Month (bio_14), Precipitation Seasonality (bio_15) (which is calculated as the coefficient of variation of monthly precipitation) and Precipitation of Coldest Month (bio_19) were retained for MaxEnt modelling.

The future climate data used in this study comes from the Sixth iteration of the Coupled Model Intercomparison Project [118]. Specifically, we used the HadGEM3-GC31-LL future climate dataset for 3 shared socioeconomic pathways (SSPs; SSP 126, SSP 245 and SSP 585) for 3 future time horizons: 2014-2060, 2061-2080 and 2081-2100.

Data on future human population density was obtained from projections at a 30 arc-seconds (1km) spatial resolution until 2100 under different SSP models [58]. Data on spatial distribution of growing different crops (5.6km resolution) was obtained from CROPGRIDS [57]. A selection of crops to focus on was chosen at the top 10 highest value crops globally. Data intersections and maps were generated using ArcGIS Pro v3.4.2.

Literature review

A literature search was performed using several search terms for each individual country from the WHO country list; “country name” AND aspergillosis OR aspergillus, as well as “country name” AND aspergillus AND soil. Articles were manually curated and included when all three species were identified in the data, which allowed comparison of species prevalence. Articles referring to specific substrates (food items, fruits etc) were excluded and only data on soil species distributions were included for environmental prevalence of *Aspergillus* species. For clinical prevalence only data from invasive aspergillosis was used to make articles comparable.

QUANTIFICATION AND STATISTICAL ANALYSIS

Model generation

All pre-processing was undertaken in ArcGIS Pro 3.2. Occurrence data were cleaned, projected to a uniform coordinate system, and spatially thinned to reduce autocorrelation. Environmental predictor variables were reprojected, resampled, and clipped to a consistent spatial resolution and study extent.

Using MaxEnt v3.4.4, separate species-specific models were generated using GPS coordinates for *Aspergillus fumigatus*, *Aspergillus flavus* and *Aspergillus niger* individually. For each individual species model, 80% of occurrence records were used for model training and 20% for independent validation. Model complexity was explicitly defined by testing feature class (FC) combinations of L, H, LQ, LQH, and LQHPT with regularization multipliers (RM) of between 0.5 and 4 at 0.5 intervals. The maximum number of iterations was set to 500, and a convergence threshold of 0.00001 was applied to ensure model stability while minimising overfitting.

Each model used 10,000 background (pseudo-absence) points, spatially constrained by species-specific bias files to match the sampling structure of occurrence data.

Bootstrap replication (n = 10) was employed, and outputs were generated in Cloglog format to facilitate interpretation of habitat suitability as relative probability of presence. For each species, input variable importance was assessed via the Jackknife test, and response curves were examined to evaluate ecological relationships. Jackknife test of regularised training gain was assessed to quantify the importance of each environmental variable in isolation as well as when it is removed from the dataset. Model performance was quantified using the area under the receiver operating characteristic curve (AUC).

Following MaxEnt calibration, resulting suitability layers were imported into the ArcGIS Pro for further spatial analysis. Continuous Cloglog outputs were reclassified using the maximum training sensitivity plus specificity (MTSPS) threshold to delineate suitable habitat areas. In ArcGIS, the Reclassification Tool was used to divide habitats into non-suitable (0-MTSPS value) and suitable (MTSPS value-1). The future suitable habitats were generated by overlaying habitats using the “Intersect” function.

Maps and additional spatial analysis were executed using ArcGIS Pro v3.4.2. All other data was visualised using Rstudio (v 2024.09.0+375) and ggplot2.

Differences between bioclimatic variables were assessed via One-way ANOVA with post-hoc Tukey’s Honest Significant Difference. $P<0.05$ was considered significant.

Figure legends

Figure 1 MaxENT model accurate described *Aspergillus* global distributions. A Habitat suitability for three *Aspergillus* species from the MaxENT model. Least suitable is 0 and most suitable is 1. **B** Correlation plots of frequency of each *Aspergillus* species found in the literature compared to the median suitability for that particular country in

the MaxENT model. Shaded region represents the 95% confidence interval. **C** Boxplots showing environmental differences between *A. flavus, A. fumigatus and A. niger* among three environmental variables used for SDM. Species marked with the same letter are not significantly different at $P < 0.05$ with regards to each environmental variable. Boxplot shows the median and interquartile ranges. Whiskers represent lower and higher quartile range. a shows significance ($p<0.05$) versus the two other groups, b significance ($p<0.05$) versus *Aspergillus fumigatus* and c versus *Aspergilllus flavus* as determined by one-way ANOVA.

Figure 2 Climate change will shift distributions of *Aspergillus* species. The SSP245 model is shown here as a representative across three different time horizons (2041-2060, 2051-200 and 2081-2100). Red is considered suitable habitat according to the cut-off from the MTSPS analysis.

Figure 3 Suitable habitat will have lower overlap with crop growing regions. A Quantification of the km^2 overlap between crop growing regions from CROPGRIDS and the suitable habitat for *A. niger* and *A. flavus*. ND is not done as *Aspergillus niger* has not been reported to cause wheat infection. **B** Map overviews of *A. flavus* and *A. niger* across three different time horizons for the SSP585 model. Red is the overlap between habitat suitability and the crop growing region for maize.

Figure 4 The epidemiological landscape of invasive aspergillosis is predicted to shift due to climate change. A Correlation of the relative frequency of *Aspergillus* species found in the literature where one report of clinical frequencies and one of environmental frequencies could be found. Blue is *A. niger*, Orange *A. fumigatus* and grey *A. flavus*. Shaded bands are the 95% confidence intervals. **B** People living in suitable habitat for the three *Aspergillus* species until the 2100 time horizon. The solid

line is the moderate scenario SSP245, while the bands represent the SSP585 and SSP126 models. **C** People living in suitable habitat broken down into continents for the three *Aspergillus* species until the 2100 time horizon. Australia was considered separate in this analysis. The solid line is the moderate scenario SSP245, while the bands represent the SSP585 and SSP126 models.

References

1. Seyedmousavi, S., Bosco, S.d.M., De Hoog, S., Ebel, F., Elad, D., Gomes, R.R., Jacobsen, I.D., Jensen, H.E., Martel, A., and Mignon, B. (2018). Fungal infections in animals: a patchwork of different situations. Medical mycology *56*, S165-S187.
2. Navale, V., Vamkudoth, K.R., Ajmera, S., and Dhuri, V. (2021). Aspergillus derived mycotoxins in food and the environment: Prevalence, detection, and toxicity. Toxicology reports *8*, 1008-1030.
3. Fang, W., and Latgé, J.-P. (2018). Microbe profile: Aspergillus fumigatus: a saprotrophic and opportunistic fungal pathogen. Microbiology *164*, 1009-1011.
4. Snelders, E., Camps, S.M., Karawajczyk, A., Schaftenaar, G., Kema, G.H., Van der Lee, H.A., Klaassen, C.H., Melchers, W.J., and Verweij, P.E. (2012). Triazole fungicides can induce cross-resistance to medical triazoles in Aspergillus fumigatus. PloS one *7*, e31801.
5. Fisher, M.C., Hawkins, N.J., Sanglard, D., and Gurr, S.J. (2018). Worldwide emergence of resistance to antifungal drugs challenges human health and food security. Science *360*, 739-742.
6. van Rhijn, N., and Rhodes, J. (2025). Evolution of antifungal resistance in the environment. Nature Microbiology, 1-12.
7. Bueid, A., Howard, S.J., Moore, C.B., Richardson, M.D., Harrison, E., Bowyer, P., and Denning, D.W. (2010). Azole antifungal resistance in Aspergillus fumigatus: 2008 and 2009. Journal of Antimicrobial Chemotherapy *65*, 2116-2118.
8. Lestrade, P.P., Buil, J.B., van Der Beek, M.T., Kuijper, E.J., van Dijk, K., Kampinga, G.A., Rijnders, B.J., Vonk, A.G., de Greeff, S.C., and Schoffelen, A.F. (2020). Paradoxal trends in azole-resistant Aspergillus fumigatus in a national multicenter surveillance program, the Netherlands, 2013–2018. Emerging infectious diseases *26*, 1447.
9. van Rhijn, N., Arikan-Akdagli, S., Beardsley, J., Bongomin, F., Chakrabarti, A., Chen, S.C., Chiller, T., Colombo, A.L., Govender, N.P., and Alastruey-Izquierdo, A. (2024). Beyond bacteria: the growing threat of antifungal resistance. The Lancet *404*, 1017-1018.

10. Latgé, J.-P., and Chamilos, G. (2019). Aspergillus fumigatus and Aspergillosis in 2019. Clinical microbiology reviews *33*, 10.1128/cmr. 00140-00118.
11. Danion, F., van Rhijn, N., Dufour, A.C., Legendre, R., Sismeiro, O., Varet, H., Olivo-Marin, J.-C., Mouyna, I., Chamilos, G., and Bromley, M. (2021). Aspergillus fumigatus, one uninucleate species with disparate offspring. Journal of Fungi *7*, 30.
12. Klich, M.A. (2002). Biogeography of Aspergillus species in soil and litter. Mycologia *94*, 21-27.
13. Kwon-Chung, K.J., and Sugui, J.A. (2013). Aspergillus fumigatus—what makes the species a ubiquitous human fungal pathogen? PLoS pathogens *9*, e1003743.
14. Bertuzzi, M., Hayes, G.E., Icheoku, U.J., Van Rhijn, N., Denning, D.W., Osherov, N., and Bignell, E.M. (2018). Anti-Aspergillus activities of the respiratory epithelium in health and disease. Journal of Fungi *4*, 8.
15. Sabino, R., Veríssimo, C., Viegas, C., Viegas, S., Brandão, J., Alves-Correia, M., Borrego, L.-M., Clemons, K.V., Stevens, D.A., and Richardson, M. (2019). The role of occupational Aspergillus exposure in the development of diseases. Medical mycology *57*, S196-S205.
16. Richardson, M., Bowyer, P., and Sabino, R. (2019). The human lung and Aspergillus: You are what you breathe in? Medical mycology *57*, S145-S154.
17. Dagenais, T.R., and Keller, N.P. (2009). Pathogenesis of Aspergillus fumigatus in invasive aspergillosis. Clinical microbiology reviews *22*, 447-465.
18. Denning, D.W. (2024). Global incidence and mortality of severe fungal disease. The Lancet Infectious Diseases *24*, e428-e438.
19. Stemler, J., Többen, C., Lass-Flörl, C., Steinmann, J., Ackermann, K., Rath, P.-M., Simon, M., Cornely, O.A., and Koehler, P. (2023). Diagnosis and Treatment of invasive aspergillosis caused by non-fumigatus Aspergillus spp. Journal of Fungi *9*, 500.
20. Bilal, H., Zhang, D., Shafiq, M., Khan, M.N., Khan, S., Cai, L., Khan, R.U., Hu, H., and Zeng, Y. (2023). Epidemiology and antifungal susceptibilities of clinically isolated Aspergillus species in South China. Epidemiology & Infection *151*, e184.
21. Katriina, P., Veli-Jukka, A., and Ulla, H. (2023). The clinical significance of Aspergillus-positive respiratory samples. Mycoses *66*, 387-395.
22. Prigitano, A., Esposto, M., Grancini, A., Passera, M., Paolucci, M., Stanzani, M., Sartor, A., Candoni, A., Pitzurra, L., and Innocenti, P. (2020). Prospective multicentre study on azole resistance in Aspergillus isolates from surveillance cultures in haematological patients in Italy. Journal of global antimicrobial resistance *22*, 231-237.
23. Perfect, J., Cox, G., Lee, J., Kauffman, C., De Repentigny, L., Chapman, S., Morrison, V.A., Pappas, P., Hiemenz, J., and Stevens, D. (2001). The impact of culture isolation of Aspergillus species: a hospital-based survey of aspergillosis. Clinical Infectious Diseases *33*, 1824-1833.
24. Organization, W.H. (2022). WHO fungal priority pathogens list to guide research, development and public health action (World Health Organization).
25. Tzar, M.N., Mustakim, S., Yusoff, H., and Tap, R.M. (2024). Antifungal susceptibility of molecularly confirmed Aspergillus species from clinical samples. The Malaysian Journal of Pathology *46*, 71-78.
26. Itor, E.A., Noubom, M., Nangwat, C., Ngueguim, D.A., Kountchou, C.L., Thierry, N.K., Paul, D.J., and Bonglavnyuy, T.C. (2020). Clinical and microbiological

epidemiology of otomycosis in the centre region of Cameroon. Eur J Clin Biomed Sci *6*, 78-83.

27. Rudramurthy, S.M., Paul, R.A., Chakrabarti, A., Mouton, J.W., and Meis, J.F. (2019). Invasive aspergillosis by Aspergillus flavus: epidemiology, diagnosis, antifungal resistance, and management. Journal of Fungi *5*, 55.
28. Molnár, K., Rácz, C., Dövényi-Nagy, T., Bakó, K., Pusztahelyi, T., Kovács, S., Adácsi, C., Pócsi, I., and Dobos, A. (2023). The effect of environmental factors on mould counts and AFB1 toxin production by Aspergillus flavus in maize. Toxins *15*, 227.
29. Monda, E., Masanga, J., and Alakonya, A. (2020). Variation in occurrence and aflatoxigenicity of Aspergillus flavus from two climatically varied regions in Kenya. Toxins *12*, 34.
30. Cogliati, M., Buil, J.B., Esposto, M.C., Prigitano, A., Romanò, L., and Melchers, W.J. (2025). Evaluation of environmental factors related to Aspergillus fumigatus azole resistance in the Netherlands. Science of the Total Environment *958*, 177923.
31. Van Rhijn, N., Coleman, J., Collier, L., Moore, C., Richardson, M.D., Bright-Thomas, R.J., and Jones, A.M. (2021). Meteorological factors influence the presence of fungi in the air; A 14-month surveillance study at an adult Cystic Fibrosis center. Frontiers in cellular and infection microbiology *11*, 759944.
32. Garcia-Solache, M.A., and Casadevall, A. (2010). Global warming will bring new fungal diseases for mammals. MBio *1*, 10.1128/mbio. 00061-00010.
33. Van Rhijn, N., and Bromley, M. (2021). The consequences of our changing environment on life threatening and debilitating fungal diseases in humans. Journal of Fungi *7*, 367.
34. Nnadi, N.E., and Carter, D.A. (2021). Climate change and the emergence of fungal pathogens. PLoS pathogens *17*, e1009503.
35. Seidel, D., Wurster, S., Jenks, J.D., Sati, H., Gangneux, J.-P., Egger, M., Alastruey-Izquierdo, A., Ford, N.P., Chowdhary, A., and Sprute, R. (2024). Impact of climate change and natural disasters on fungal infections. The Lancet Microbe *5*, e594-e605.
36. Bottery, M., Sedik, S., Schwartz, I., Hoenigl, M., and Van Rhijn, N. (2025). Climate change: shifting boundaries of fungal disease in Europe and beyond. Thorax.
37. Casu, A., Camardo Leggieri, M., Toscano, P., and Battilani, P. (2024). Changing climate, shifting mycotoxins: A comprehensive review of climate change impact on mycotoxin contamination. Comprehensive Reviews in Food Science and Food Safety *23*, e13323.
38. Nations, U. (2019). Department of economic and social affairs, population division (2019). World Population Prospects 2019: Data Booket. ST/ESA/SER. A/424.
39. Bebber, D.P., and Gurr, S.J. (2015). Crop-destroying fungal and oomycete pathogens challenge food security. Fungal Genetics and Biology *74*, 62-64.
40. Zakaria, L. (2024). An overview of Aspergillus species associated with plant diseases. Pathogens *13*, 813.
41. Mitchell, N.J., Bowers, E., Hurburgh, C., and Wu, F. (2016). Potential economic losses to the US corn industry from aflatoxin contamination. Food Additives & Contaminants: Part A *33*, 540-550.
42. Gusa, A., Williams, J.D., Cho, J.-E., Averette, A.F., Sun, S., Shouse, E.M., Heitman, J., Alspaugh, J.A., and Jinks-Robertson, S. (2020). Transposon

mobilization in the human fungal pathogen Cryptococcus is mutagenic during infection and promotes drug resistance in vitro. Proceedings of the National Academy of Sciences *117*, 9973-9980.

43. Gusa, A., Yadav, V., Roth, C., Williams, J.D., Shouse, E.M., Magwene, P., Heitman, J., and Jinks-Robertson, S. (2023). Genome-wide analysis of heat stress-stimulated transposon mobility in the human fungal pathogen Cryptococcus deneoformans. Proceedings of the National Academy of Sciences *120*, e2209831120.
44. Parikka, P., Hakala, K., and Tiilikkala, K. (2012). Expected shifts in Fusarium species' composition on cereal grain in Northern Europe due to climatic change. Food Additives & Contaminants: Part A *29*, 1543-1555.
45. Timmusk, S., Nevo, E., Ayele, F., Noe, S., and Niinemets, Ü. (2020). Fighting Fusarium pathogens in the era of climate change: A conceptual approach. Pathogens *9*, 419.
46. Větrovský, T., Morais, D., Kohout, P., Lepinay, C., Algora, C., Awokunle Hollá, S., Bahnmann, B.D., Bílohnědá, K., Brabcová, V., and D'Alò, F. (2020). GlobalFungi, a global database of fungal occurrences from high-throughput-sequencing metabarcoding studies. Scientific Data *7*, 228.
47. Henry, T., Iwen, P.C., and Hinrichs, S.H. (2000). Identification of Aspergillus species using internal transcribed spacer regions 1 and 2. Journal of clinical microbiology *38*, 1510-1515.
48. Visagie, C., Houbraken, J., Overy, D., Sklenář, F., Bensch, K., Frisvad, J., Mack, J., Perrone, G., Samson, R., and van Vuuren, N. (2025). From chaos to tranquillity: a modern approach to the identification, nomenclature and phylogeny of Aspergillus, Penicillium and other Eurotiales, including an updated accepted species list. Studies in Mycology.
49. Poggio, L., De Sousa, L.M., Batjes, N.H., Heuvelink, G.B., Kempen, B., Ribeiro, E., and Rossiter, D. (2021). SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. Soil *7*, 217-240.
50. Migahed, F.F. (2003). Distribution of fungi in the sandy soil of Egyptian beaches. Mycobiology *31*, 61-67.
51. Zakaria, L. (2018). Microscopic characteristics as preliminary identification of Aspergillus spp. from beach sand. Malaysian Journal of Microscopy *14*.
52. Nayak, S., Samanta, S., and Mukherjee, A.K. (2020). Beneficial role of Aspergillus sp. in agricultural soil and environment. Frontiers in soil and environmental microbiology, 17-36.
53. Nwagu, T., and Okolo, B. (2011). Growth profile and amylolytic activity of a thermophilic fungus Aspergillus fumigatus isolated from soil. Asian Journal of Biotechnology *3*, 46-57.
54. Shelton, J.M., Collins, R., Uzzell, C.B., Alghamdi, A., Dyer, P.S., Singer, A.C., and Fisher, M.C. (2022). Citizen science surveillance of triazole-resistant Aspergillus fumigatus in United Kingdom residential garden soils. Applied and environmental microbiology *88*, e02061-02021.
55. Liu, C., Newell, G., and White, M. (2016). On the selection of thresholds for predicting species occurrence with presence-only data. Ecology and evolution *6*, 337-348.
56. Wang, X., Li, Z., Zhang, L., Wang, Y., Liu, Y., and Ma, Y. (2024). The optimized Maxent model reveals the pattern of distribution and changes in the suitable cultivation areas for Reaumuria songarica being driven by climate change. Ecology and Evolution *14*, e70015.

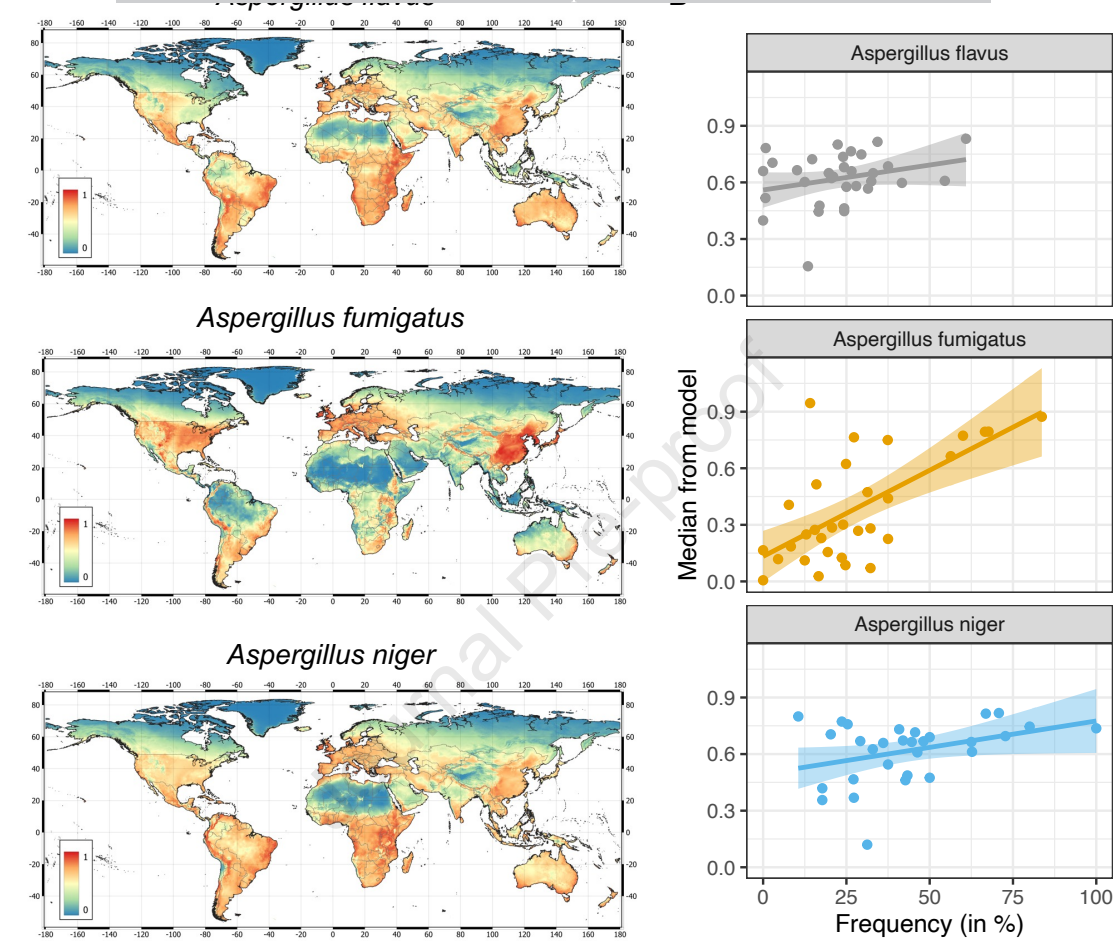
57. Tang, F.H., Nguyen, T.H., Conchedda, G., Casse, L., Tubiello, F.N., and Maggi, F. (2024). CROPGRIDS: a global geo-referenced dataset of 173 crops. Scientific Data *11*, 413.
58. Wang, X., Meng, X., and Long, Y. (2022). Projecting 1 km-grid population distributions from 2020 to 2100 globally under shared socioeconomic pathways. Scientific Data *9*, 563.
59. Korfanty, G., Heifetz, E., and Xu, J. (2023). Assessing thermal adaptation of a global sample of Aspergillus fumigatus: Implications for climate change effects. Frontiers in Public Health *11*, 1059238.
60. Korfanty, G.A., Dixon, M., Jia, H., Yoell, H., and Xu, J. (2021). Genetic diversity and dispersal of Aspergillus fumigatus in Arctic soils. Genes *13*, 19.
61. Korfanty, G.A., Teng, L., Pum, N., and Xu, J. (2019). Contemporary gene flow is a major force shaping the Aspergillus fumigatus population in Auckland, New Zealand. Mycopathologia *184*, 479-492.
62. Richardson, M., and Lass-Flörl, C. (2008). Changing epidemiology of systemic fungal infections. Clinical microbiology and infection *14*, 5-24.
63. Lass-Flörl, C., and Cuenca-Estrella, M. (2017). Changes in the epidemiological landscape of invasive mould infections and disease. Journal of Antimicrobial Chemotherapy *72*, i5-i11.
64. Guisan, A., Edwards Jr, T.C., and Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological modelling *157*, 89-100.
65. Yu, H., Cooper, A.R., and Infante, D.M. (2020). Improving species distribution model predictive accuracy using species abundance: Application with boosted regression trees. Ecological Modelling *432*, 109202.
66. Hallman, T.A., and Robinson, W.D. (2020). Comparing multi-and single-scale species distribution and abundance models built with the boosted regression tree algorithm. Landscape Ecology *35*, 1161-1174.
67. Evans, J.S., Murphy, M.A., Holden, Z.A., and Cushman, S.A. (2010). Modeling species distribution and change using random forest. In Predictive species and habitat modeling in landscape ecology: Concepts and applications, (Springer), pp. 139-159.
68. Bradter, U., Kunin, W.E., Altringham, J.D., Thom, T.J., and Benton, T.G. (2013). Identifying appropriate spatial scales of predictors in species distribution models with the random forest algorithm. Methods in Ecology and Evolution *4*, 167-174.
69. Valavi, R., Elith, J., Lahoz-Monfort, J.J., and Guillera-Arroita, G. (2021). Modelling species presence-only data with random forests. Ecography *44*, 1731-1742.
70. Phillips, S.J., and Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography *31*, 161-175.
71. Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H., and Veran, S. (2013). Presence-only modelling using MAXENT: when can we trust the inferences? Methods in Ecology and Evolution *4*, 236-243.
72. Hernandez, P.A., Graham, C.H., Master, L.L., and Albert, D.L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography *29*, 773-785.

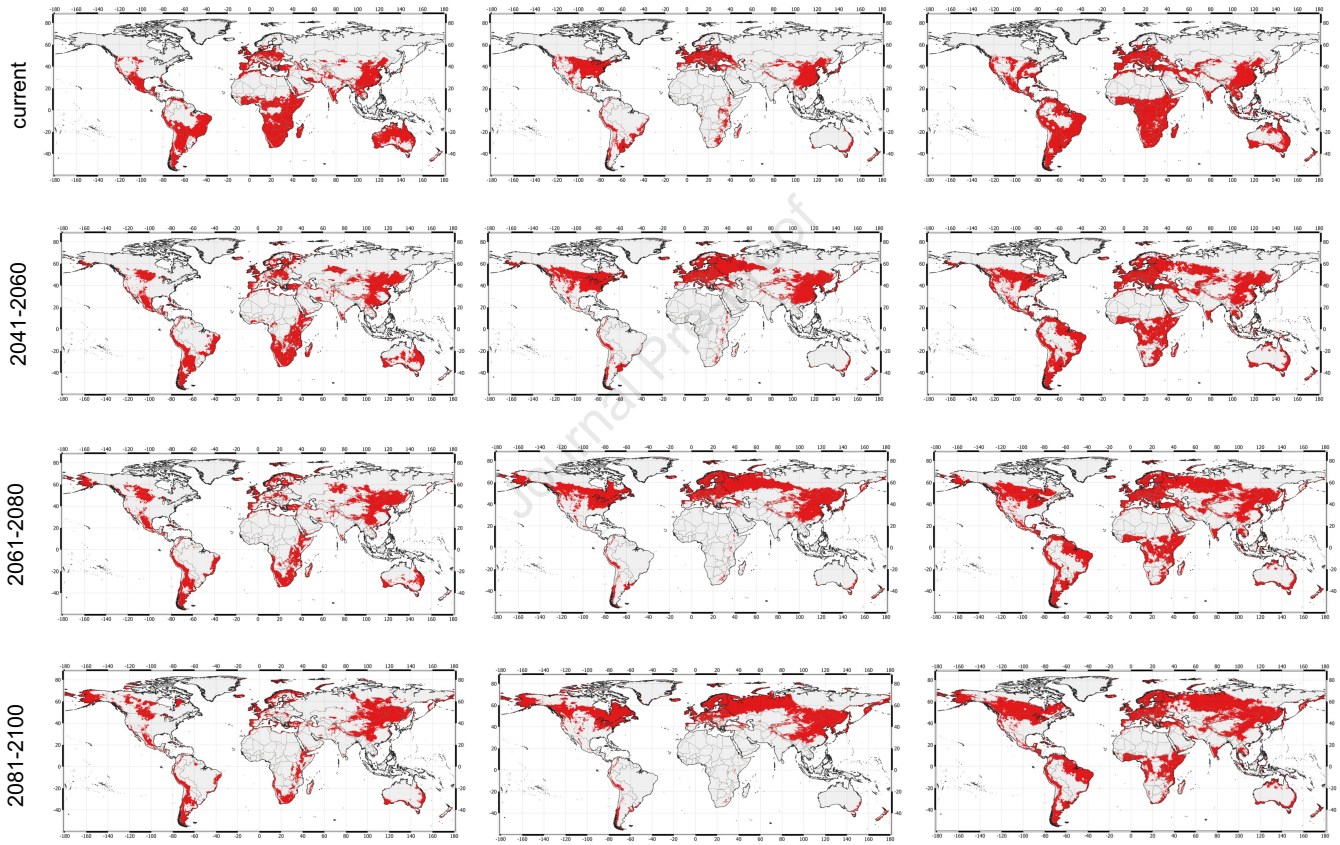
73. Alkhalifah, D.H.M., Damra, E., Khalaf, S.M., and Hozzein, W.N. (2022). Biogeography of black mold Aspergillus niger: Global situation and future perspective under several climate change scenarios using MaxEnt modeling. Diversity *14*, 845.
74. Yuan, H.-S., Wei, Y.-L., and Wang, X.-G. (2015). Maxent modeling for predicting the potential distribution of Sanghuang, an important group of medicinal fungi in China. Fungal Ecology *17*, 140-145.
75. Batista, E., Lopes, A., Miranda, P., and Alves, A. (2023). Can species distribution models be used for risk assessment analyses of fungal plant pathogens? A case study with three Botryosphaeriaceae species. European Journal of Plant Pathology *165*, 41-56.
76. Kaky, E., Nolan, V., Alatawi, A., and Gilbert, F. (2020). A comparison between Ensemble and MaxEnt species distribution modelling approaches for conservation: A case study with Egyptian medicinal plants. Ecological Informatics *60*, 101150.
77. Alqahtani, M.S., Shahin, G., Abdelalim, I.T., and Khalaf, S.M. (2025). Evaluation of ecological consequences on the global distribution of Staphylococcus aureus Rosenbach 1884 due to climate change, using Maxent modeling. Scientific Reports *15*, 1-10.
78. Jones, G.S., Andrews, M.B., Andrews, T., Blockley, E., Ciavarella, A., Christidis, N., Cotterill, D.F., Lott, F.C., Ridley, J., and Stott, P.A. (2024). The HadGEM3-GC3. 1 contribution to the CMIP6 detection and attribution model intercomparison project. Journal of Advances in Modeling Earth Systems *16*, e2023MS004135.
79. Tebaldi, C., Debeire, K., Eyring, V., Fischer, E., Fyfe, J., Friedlingstein, P., Knutti, R., Lowe, J., O'Neill, B., and Sanderson, B. (2021). Climate model projections from the scenario model intercomparison project (ScenarioMIP) of CMIP6. Earth System Dynamics *12*, 253-293.
80. Andrews, M.B., Ridley, J.K., Wood, R.A., Andrews, T., Blockley, E.W., Booth, B., Burke, E., Dittus, A.J., Florek, P., and Gray, L.J. (2020). Historical simulations with HadGEM3-GC3. 1 for CMIP6. Journal of Advances in Modeling Earth Systems *12*, e2019MS001995.
81. Jackson, L.S., Maycock, A.C., Andrews, T., Fredriksen, H.B., Smith, C.J., and Forster, P. (2022). Errors in simple climate model emulations of past and future global temperature change. Geophysical Research Letters *49*, e2022GL098808.
82. Radosavljevic, A., and Anderson, R.P. (2014). Making better Maxent models of species distributions: complexity, overfitting and evaluation. Journal of biogeography *41*, 629-643.
83. Anderson, R.P., and Gonzalez Jr, I. (2011). Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. Ecological Modelling *222*, 2796-2811.
84. Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A.K., and Augeri, D.M. (2013). The importance of correcting for sampling bias in MaxEnt species distribution models. Diversity and distributions *19*, 1366-1379.
85. Fourcade, Y., Engler, J.O., Rödder, D., and Secondi, J. (2014). Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PloS one *9*, e97122.

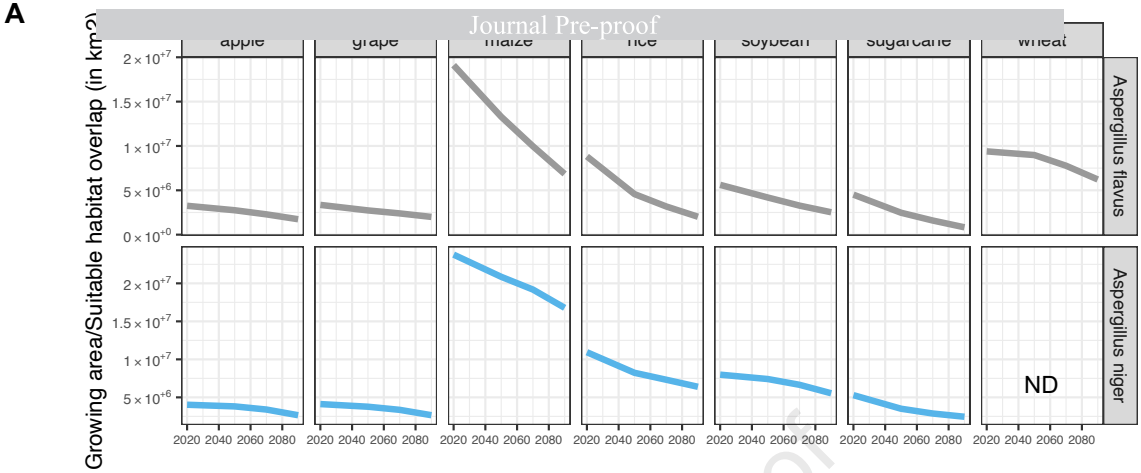
86. Syfert, M.M., Smith, M.J., and Coomes, D.A. (2013). The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. PloS one *8*, e55158.
87. Ragland, G.J., and Kingsolver, J.G. (2008). Evolution of thermotolerance in seasonal environments: the effects of annual temperature variation and life-history timing in Wyeomyia smithii. Evolution *62*, 1345-1357.
88. Caspeta, L., and Nielsen, J. (2015). Thermotolerant yeast strains adapted by laboratory evolution show trade-off at ancestral temperatures and preadaptation to other stresses. MBio *6*, 10.1128/mbio. 00431-00415.
89. De Crecy, E., Jaronski, S., Lyons, B., Lyons, T.J., and Keyhani, N.O. (2009). Directed evolution of a filamentous fungus for thermotolerance. BMC biotechnology *9*, 1-11.
90. Paulussen, C., Hallsworth, J.E., Álvarez-Pérez, S., Nierman, W.C., Hamill, P.G., Blain, D., Rediers, H., and Lievens, B. (2017). Ecology of aspergillosis: insights into the pathogenic potency of Aspergillus fumigatus and some other Aspergillus species. Microbial biotechnology *10*, 296-322.
91. Millner, P., Marsh, P., Snowden, R., and Parr, J. (1977). Occurrence of Aspergillus fumigatus during composting of sewage sludge. Applied and Environmental Microbiology *34*, 765-772.
92. Williams, B., Douglas, P., Barcelo, A.R., Hansell, A., and Hayes, E. (2019). Estimating Aspergillus fumigatus exposure from outdoor composting activities in England between 2005 and 14. Waste Management *84*, 235-244.
93. Rhodes, J., Abdolrasouli, A., Dunne, K., Sewell, T.R., Zhang, Y., Ballard, E., Brackin, A.P., van Rhijn, N., Chown, H., and Tsitsopoulou, A. (2022). Population genomics confirms acquisition of drug-resistant Aspergillus fumigatus infection by humans from the environment. Nature microbiology *7*, 663-674.
94. Millner, P.D., Bassett, D.A., and Marsh, P.B. (1980). Dispersal of Aspergillus fumigatus from sewage sludge compost piles subjected to mechanical agitation in open air. Applied and environmental microbiology *39*, 1000-1009.
95. Angle, J., Dunn, K., and Wagner, G. (1982). Effect of cultural practices on the soil population of Aspergillus flavus and Aspergillus parasiticus. Soil Science Society of America Journal *46*, 301-304.
96. Zablotowicz, R., Abbas, H., and Locke, M. (2007). Population ecology of Aspergillus flavus associated with Mississippi Delta soils. Food additives and contaminants *24*, 1102-1108.
97. Andersen, M.R., Lehmann, L., and Nielsen, J. (2009). Systemic analysis of the response of Aspergillus niger to ambient pH. Genome Biology *10*, 1-14.
98. Zheng, W., Yang, H., Xuan, G., Dai, L., Hu, Y., Hu, S., Zhong, S., Li, Z., Gao, M., and Wang, S. (2017). Longitudinal Study of the Effects of Environmental pH on the Mechanical Properties of Aspergillus niger. ACS Biomaterials Science & Engineering *3*, 2974-2979.
99. Knight, C.G., Nicolitch, O., Griffiths, R.I., Goodall, T., Jones, B., Weser, C., Langridge, H., Davison, J., Dellavalle, A., and Eisenhauer, N. (2024). Soil microbiomes show consistent and predictable responses to extreme events. Nature, 1-7.
100. Chow, N.A., Kangiser, D., Gade, L., McCotter, O.Z., Hurst, S., Salamone, A., Wohrle, R., Clifford, W., Kim, S., and Salah, Z. (2021). Factors influencing distribution of Coccidioides immitis in soil, Washington state, 2016. Msphere *6*, e00598-00521.

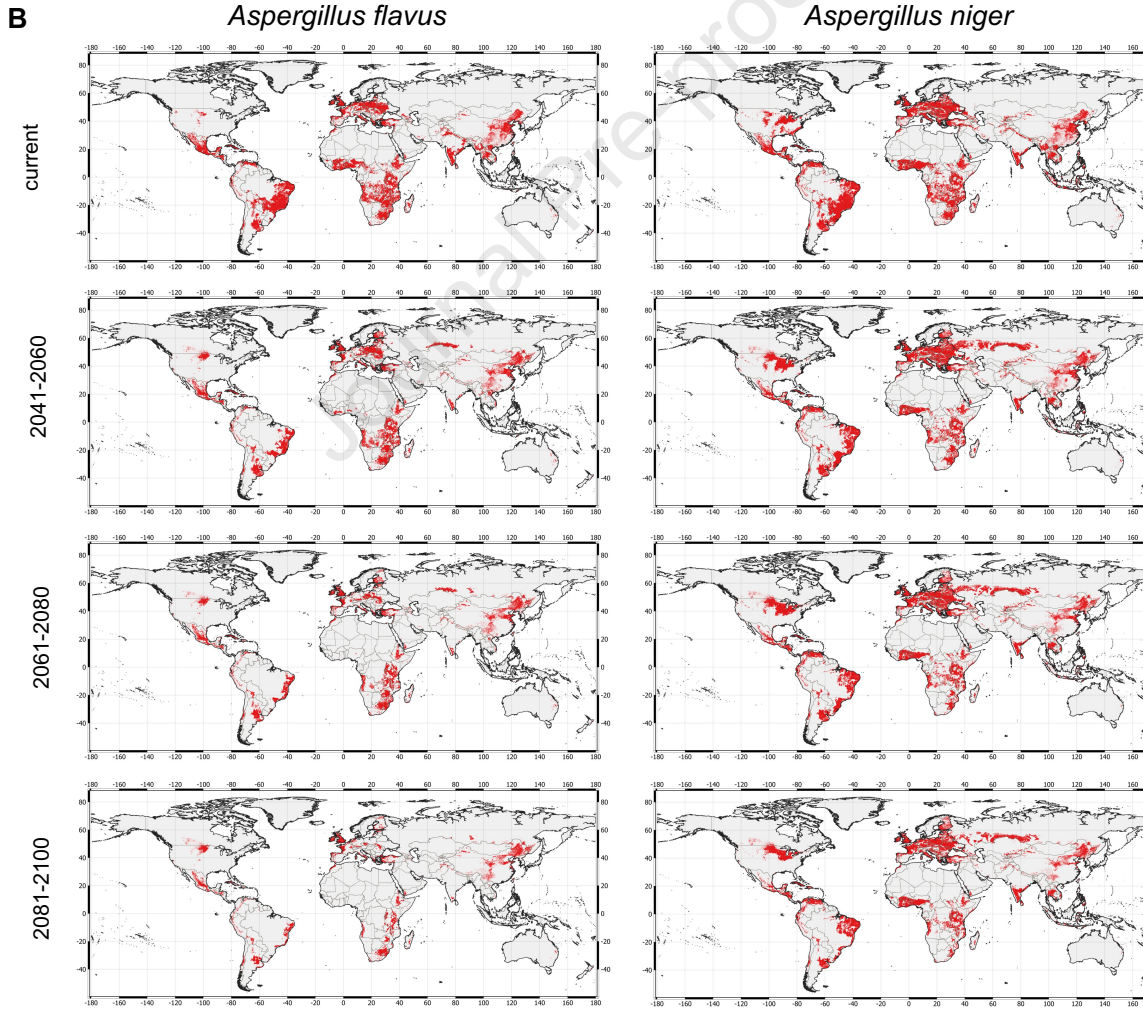
101. Gorris, M.E., Treseder, K.K., Zender, C.S., and Randerson, J.T. (2019). Expansion of coccidioidomycosis endemic regions in the United States in response to climate change. Geohealth *3*, 308-327.
102. Choi, Y.-J., and Oh, J.-W. (2024). The Impact of Climate Change on the Sporulation of Atmospheric Fungi. Immunology and Allergy Clinics *44*, 45-54.
103. Benedict, K., and Park, B.J. (2014). Invasive fungal infections after natural disasters. Emerging infectious diseases *20*, 349.
104. Omebeyinje, M.H., Adeluyi, A., Mitra, C., Chakraborty, P., Gandee, G.M., Patel, N., Verghese, B., Farrance, C.E., Hull, M., and Basu, P. (2021). Increased prevalence of indoor Aspergillus and Penicillium species is associated with indoor flooding and coastal proximity: a case study of 28 moldy buildings. Environmental Science: Processes & Impacts *23*, 1681-1687.
105. Jakšić, D., Sertić, M., Kocsubé, S., Kovačević, I., Kifer, D., Mornar, A., Nigović, B., and Šegvić Klarić, M. (2020). Post-flood impacts on occurrence and distribution of mycotoxin-producing Aspergilli from the sections Circumdati, Flavi, and Nigri in indoor environment. Journal of fungi *6*, 282.
106. Dang, A.T., Kumar, L., and Reid, M. (2020). Modelling the potential impacts of climate change on rice cultivation in Mekong Delta, Vietnam. Sustainability *12*, 9608.
107. Rokochynskiy, A., Turcheniuk, V., Prykhodko, N., Volk, P., Gerasimov, I., and Koç, C. (2020). Evaluation of climate change in the rice-growing zone of Ukraine and ways of adaptation to the predicted changes. Agricultural Research *9*, 631-639.
108. Chhogyel, N., Kumar, L., Bajgai, Y., and Jayasinghe, L.S. (2020). Prediction of Bhutan's ecological distribution of rice (Oryza sativa L.) under the impact of climate change through maximum entropy modelling. The Journal of Agricultural Science *158*, 25-37.
109. Fradgley, N.S., Bacon, J., Bentley, A.R., Costa-Neto, G., Cottrell, A., Crossa, J., Cuevas, J., Kerton, M., Pope, E., and Swarbreck, S.M. (2023). Prediction of near-term climate change impacts on UK wheat quality and the potential for adaptation through plant breeding. Global Change Biology *29*, 1296-1313.
110. Yue, Y., Zhang, P., and Shang, Y. (2019). The potential global distribution and dynamics of wheat under multiple climate change scenarios. Science of the Total Environment *688*, 1308-1318.
111. Gao, Y., Zhang, A., Yue, Y., Wang, J.a., and Su, P. (2021). Predicting shifts in land suitability for maize cultivation worldwide due to climate change: A modeling approach. Land *10*, 295.
112. Aguirre-Liguori, J.A., Ramírez-Barahona, S., Tiffin, P., and Eguiarte, L.E. (2019). Climate change is predicted to disrupt patterns of local adaptation in wild and cultivated maize. Proceedings of the Royal Society B *286*, 20190486.
113. Baddley, J.W. (2011). Clinical risk factors for invasive aspergillosis. Medical mycology *49*, S7-S12.
114. Arastehfar, A., Carvalho, A., van de Veerdonk, F.L., Jenks, J.D., Koehler, P., Krause, R., Cornely, O.A., S. Perlin, D., Lass-Flörl, C., and Hoenigl, M. (2020). COVID-19 associated pulmonary aspergillosis (CAPA)—from immunology to treatment. Journal of Fungi *6*, 91.
115. Rijnders, B.J., Schauwvlieghe, A.F., and Wauters, J. (2020). Influenza-associated pulmonary aspergillosis: a local or global lethal combination? Oxford University Press US.

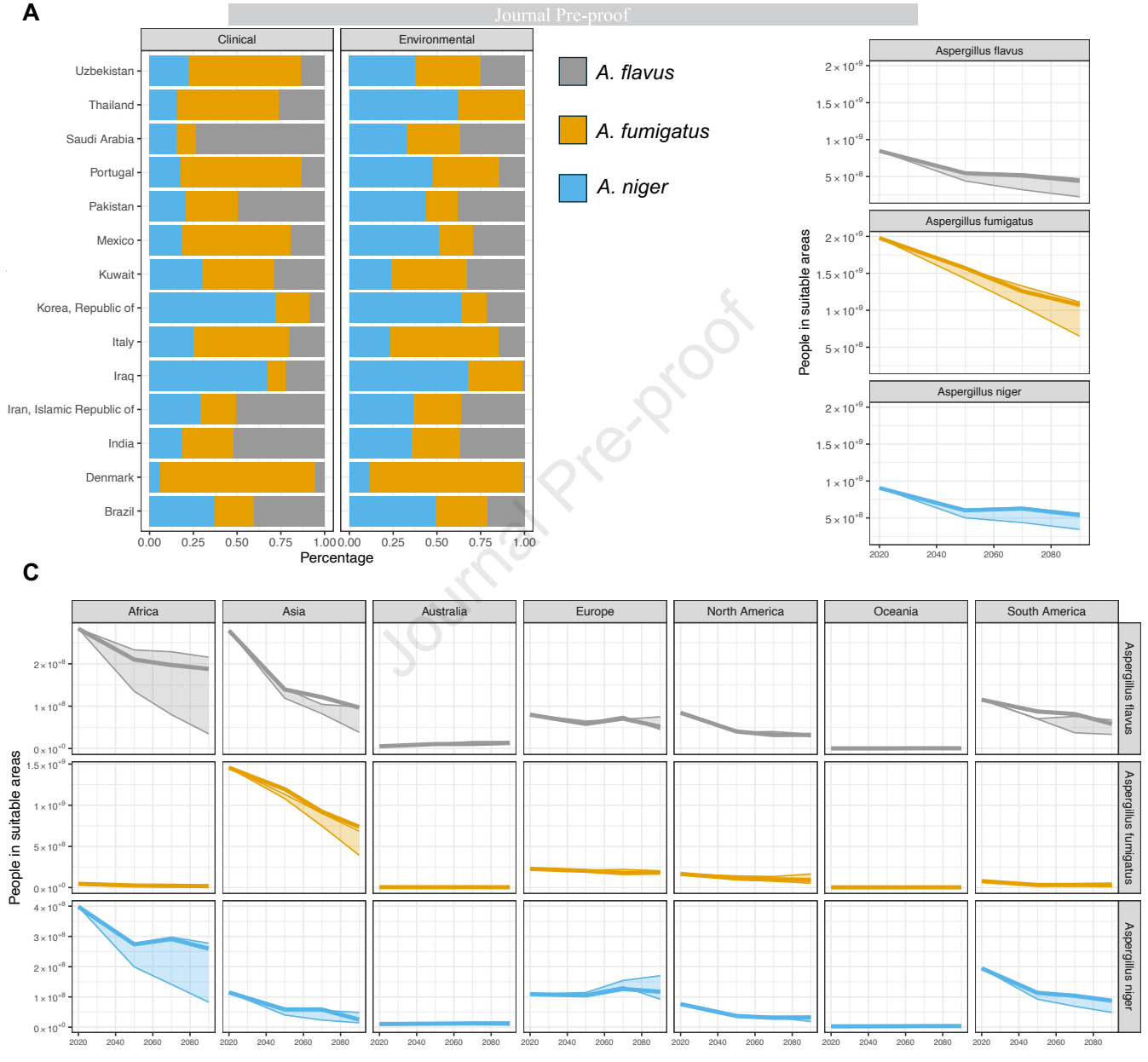
116. Permpalung, N., Chiang, T.P.-Y., Massie, A.B., Zhang, S.X., Avery, R.K., Nematollahi, S., Ostrander, D., Segev, D.L., and Marr, K.A. (2022). Coronavirus disease 2019–associated pulmonary aspergillosis in mechanically ventilated patients. Clinical Infectious Diseases *74*, 83-91.
117. Fick, S.E., and Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International journal of climatology *37*, 4302-4315.
118. O'Neill, B.C., Tebaldi, C., Van Vuuren, D.P., Eyring, V., Friedlingstein, P., Hurtt, G., Knutti, R., Kriegler, E., Lamarque, J.-F., and Lowe, J. (2016). The scenario model intercomparison project (ScenarioMIP) for CMIP6. Geoscientific Model Development *9*, 3461-3482.











Highlights

- MaxEnt models reveal poleward habitat shifts of *Aspergillus* spp. under climate change
- *A fumigatus* prefers temperate, while *A. flavus* and A*. niger* thrive in warmer climates
- Climate-driven habitat shifts reduce overlap with maize and rice crop-growing areas
- Clinical prevalence of aspergillosis mirrors environmental suitability patterns
- Over 2 billion people currently live in areas suitable for pathogenic *Aspergillus* species