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A multi-scale analysis of airborne *Alternaria* spore dispersal: influence of meteorology, land cover and air pollution

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A B S T R A C T

Alternaria is a fungal phytopathogen affecting over 4,000 species and causing 20% of agricultural production losses. About 9% of people in Europe are sensitized to its allergens. Understanding spore concentration variability under different environmental conditions can optimize fungicide use and improve allergy diagnosis and treatment. This study examines the spatio-temporal abundance of airborne *Alternaria* spores across varying climate and pollution regimes, hypothesizing that regional land cover is the main predictor of spore concentrations.

In 2015, airborne *Alternaria* spores were monitored at 23 sites in Bavaria using Hirst-type spore traps. Concentrations were assessed on a bihourly scale and differences between bioclimatic zones were analysed using regression (GLM, GLZ), variance (ANOVA, ANCOVA) and cluster analyses, controlling for meteorology, air quality and land use. Machine learning techniques, including random forest, regression tree and XGBoost, were also implemented to detect complex, non-linear patterns, while stepwise regression was used to identify the most influential predictors.

The seasonal fungal index (SFI) of *Alternaria* spores varied considerably between locations. Cluster analysis identified five main groups based on the maximum concentration and monthly distribution. The highest SFI values were in the north, including Bayreuth, Bamberg and Hof, but with shorter season. SFI decreased toward the south with lower temperatures, but seasons lengthened. One-third of spores appeared after 6 pm, with half of daily peaks post-8 pm. At higher altitudes, spore circulation was more variable, with peaks mostly at night. NO_2 and air temperature had a greater impact on spore levels than land use.

Our results indicate that in a world with warmer nights and higher pollution fungal spores may enhance growth and sporulation, increasing the risk of exposure to both human health and agricultural productivity, highlighting the need for monitoring and potential mitigation of fungal pathogens.

1. Introduction

Fungal spores, particularly those from the *Alternaria* genus of the Pleosporaceae family, are significant components of the air, being responsible for both environmental and public health concerns. There are 299 species in the genus, common globally, and comprising a natural

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part of fungal flora almost everywhere (Kirk, 2008). The majority of *Alternaria* species act as phytopathogens, negatively affecting the quality and quantity of various crops (Disalov *et al.*, 2018; Singh Saharan *et al.*, 2016). These organisms are responsible for a range of plant diseases, including leaf spots, blights, and rots, leading to significant pre- and post-harvest losses in many economically important crops. For instance, *Alternaria alternata* and *Alternaria solani* cause early blight in tomatoes and potatoes, which may reduce yields by up to 50–80% in severe cases (Schmey *et al.*, 2024). In cereals like wheat and barley, *Alternaria* spp. are associated with black point disease and kernel discolouration, reducing grain quality, germination rates, and market value (Leslie *et al.*, 2021). Furthermore, *Alternaria* infections can produce harmful mycotoxins, such as alternariol (AOH), which might contaminate food and feed, posing risks to food safety and human health (EFSA, 2011). In addition, *Alternaria* conidia have a high allergenic potential and exposure to them can lead to permanent respiratory diseases such as asthma, rhinoconjunctivitis and allergic rhinitis (Abel-Fernández *et al.*, 2023; Atkinson *et al.*, 2006). Moreover, recent research confirms that *Alternaria* spores peak in late summer, or exhibit a bi- and multimodal dispersal pattern, triggering asthma exacerbations, summer asthma, especially in sensitised individuals (Abel-Fernández *et al.*, 2023; Myszkowska *et al.*, 2023; Olsen *et al.*, 2023). Sensitisation to *Alternaria* spp. fungal spores in individuals with suspected inhalant allergy exceeded 8.9% in Europe (Heinzerling *et al.*, 2009). Understanding the temporal and spatial distribution of *Alternaria* spores is crucial for developing effective public health strategies, especially in urban areas where the risk of exposure may be higher due to environmental conditions and land use practices (Abel-Fernández *et al.*, 2023).

Several studies have highlighted the importance of meteorological parameters, such as temperature and humidity, as well as environmental factors like air pollutants, in influencing the concentration and dispersion of *Alternaria* spores in the air (Damialis and Gioulekas, 2006; Grinn-Gofroń *et al.*, 2019; Grinn-Gofroń and Bosiacka, 2015; Picornell *et al.*, 2022; Skjøth *et al.*, 2016a). These factors not only affect *Alternaria* sporulation but also spore survival and transport through the atmosphere. Temperature, for instance, can impact the growth rates of *Alternaria* species and the timing of spore release (Grewling *et al.*, 2019; Grinn-Gofroń *et al.*, 2019), with higher temperature promoting the faster growth of *Alternaria* mycelium but also the higher spore production (Damialis *et al.*, 2015a). Additionally, humidity plays a critical role in spore germination and viability (Attri *et al.*, 2024). The concentration of *Alternaria* spores in the air could also be influenced by pollutants, which may affect their production, release, or atmospheric persistence. However, the direct impact of air pollution on airborne spore concentration and on physical dispersion process have not been well documented in the literature. Air quality variables such as nitrogen dioxide (NO_2) and ozone (O_3) can alter the structural integrity of fungal spores, potentially increasing their allergenic properties (Grewling *et al.*, 2019) or enhancing the sporulation and release of *Alternaria* spores, leading to higher airborne concentrations under certain conditions, particularly in urban areas (Grinn-Gofroń *et al.*, 2011). These interactions may contribute to elevated airborne *Alternaria* concentrations leading to associated impact on respiratory health and reduced crop yields, although observed correlations remain weak.

In addition to meteorological factors, land use and land cover (LULC) patterns have emerged as significant determinants of *Alternaria* spore distribution (Apangu *et al.*, 2020; Olsen *et al.*, 2019; Skjøth *et al.*, 2012). Urbanization, agricultural practices, and vegetation cover can influence the sources and sinks of airborne spores, leading to spatial variability in spore concentrations. The abundance of *Alternaria* spores in the air seems to be linked to the growth and decomposition of the biomass in which they are hosted (Escuredo *et al.*, 2011; Fernández-Rodríguez *et al.*, 2015) and to the increased harvest activities in grain crop fields (Corden *et al.*, 2003; Skjøth *et al.*, 2016b). Since nutrient availability depends on the cropping systems and vegetation types, the *Alternaria* spores detected in the air are also expected to vary. However, urban landscapes may show different distribution patterns due to the effects of built environments and pollution (Abel-Fernández *et al.*, 2023).

Several studies have been conducted to predict human exposure to this aeroallergen and to prevent its negative effects on the susceptible population (Damialis and Gioulekas, 2006; De Linares *et al.*, 2010; Grinn-Gofroń *et al.*, 2019; Myszkowska *et al.*, 2023; Picornell *et al.*, 2022). These studies revealed that some sampling sites tend to have a single season of *Alternaria* spores, while other sites tend to have two seasons within the same year or even exhibiting a multi-modal annual cycle. However, the reasons for these different seasonal patterns remain unclear and potentially lie on the multiple and complex sources of *Alternaria* spores, as well as complicated interactions in regional weather patterns. Furthermore, spatial and temporal studies on *Alternaria* in Europe are insufficient, mostly focusing on one or two locations only, or with relatively short spore time-series: as Damialis *et al.* (2015a) have pointed out, only few aerobiological stations worldwide monitor fungal spore concentration of various taxa on a regular basis for more than 15 years, even though they do so consistently for airborne pollen. Even continent-wide studies, such as the comprehensive analysis by Skjøth *et al.* (2016b), provide valuable insights into *Alternaria* spore abundance and distribution across Europe, however could not possibly encompass all biogeographical and bioclimatic areas. From such, larger-scale international studies, we do know that variability due to location and meteorological parameters play a key role and, hence, this paucity of information on temporal and spatial patterns of fungal spores leaves an important gap with respect to biodiversity and health (Berman, 2011).

Given their economic impact and the potential health risks, a regional assessment of fungal spore concentrations and how they vary in time and space is essential, for both public health and in agricultural management. Pollen information in Bavaria, Germany has been thoroughly investigated (Jung *et al.*, 2022; Menzel *et al.*, 2021; Oteros *et al.*, 2019, 2015; Rojo *et al.*, 2019a) but limited information exists on airborne fungal spores (González-Alonso *et al.*, 2023). Given that such temperate and continental climates of central Europe have not been focusing on fungal research of this kind, such a study will provide novel insight on such an environment.

Although research on the atmospheric distribution of fungal spores exists (Janssen *et al.*, 2021), it remains an underexplored field. By integrating recent advances in atmospheric science, environmental monitoring and geographic information systems (GIS), this study aims to provide a comprehensive understanding of the factors driving *Alternaria* spore dynamics. Ultimately, these insights will contribute to better risk assessment and mitigation strategies for fungal spore exposure at multi-resolution temporal and spatial scales.

2. Methodology

2.1. Sites location and spore sampling

Alternaria spore sampling was carried out using a dense network of 23 Hirst-type volumetric samplers (Hirst, 1952) installed across Bavaria, Germany, throughout the year 2015 (Fig. 1).

Coordinates, altitude and demographic characteristics of the study sites are given in **Table S1**. Each device operated according to EN 16828:2020, the European standard method for airborne biological particle sampling and according the minimum requirements by (Galán *et al.*, 2014). Traps were installed at a standardized height of 12 meters above ground level, specifically 1.5 m above rooftop level and at least 2 m from the roof edge, to reduce microclimatic variability and maintain homogeneity across sites (Rojo *et al.*, 2020).

The majority (21) of the monitoring stations were managed by the Center of Allergy and Environment (ZAUM) as part of the 'ePIN testnetz' project (Oteros *et al.*, 2019) with additional data contributed by the Technical University of Munich (Freising) and the University of Augsburg (Augsburg).

All traps operated continuously from the beginning of May until late

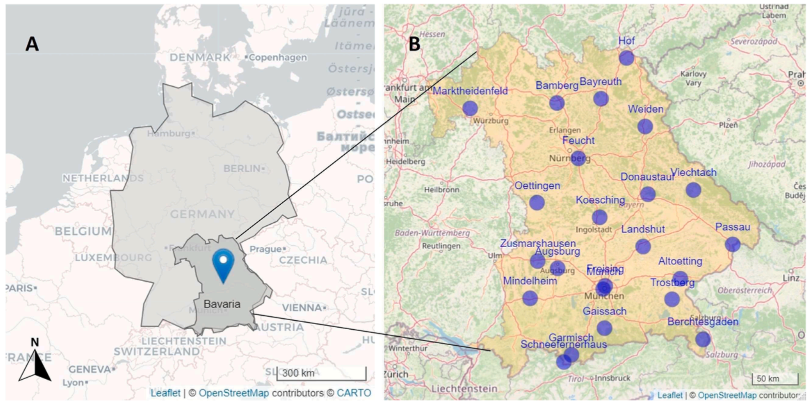

Fig. 1. Study area. Map of Bavaria (dark grey, panel A) in south eastern Germany, sowing the location of the 23 study sites (purple dots, panel B) used in this study. The study sites represent a range of environmental conditions across the region.

September 2015. Air was sampled at a flow rate of 10 L/min, and calibrated using a single, standardized flowmeter, minimizing intra-instrument variability.(Suarez-Suarez *et al.,* 2023).

Sample preparation and analysis were centralized in a single laboratory using a uniform Standard Operating Procedure (SOP). Slides were prepared using Melinex tape coated with silicone adhesive and stained using fuchsin in glycerin jelly. Counting was conducted by light microscopy at 40 × magnification, identifying spores to the genus level (*Alternaria*), based on conidial shape, septation and pigmentation. The observations under the microscope were performed along 12 transverse transects per slide, following (Damialis *et al.,* 2007). Spore counts were recorded with a 2-hour resolution and aggregated into daily mean concentrations expressed as spores per cubic meter of air (spores/m^3). All timestamps refer to Central European Summer Time (CEST) to match the period of data collection.

2.2. Season definitions and statistical analyses

The *Alternaria* spore season was defined following the method proposed by Galan *et al.* (2001) originally developed for olive pollen and later also applied in other airborne particle types. The start and end of the spore season were determined as the first and last occurrences of three consecutive days with daily concentration exceeding 1 spore/m^3. The Seasonal Fungal Index (SFI), a standard metric in Aerobiology, quantifies the total seasonal spore exposure, was calculated as the sum of daily *Alternaria* concentrations per cubic meter of air (spores/m^3) over the defined seasonal period.

In order to evaluate the similarity in *Alternaria* spore profiles across sites, an agglomerative hierarchical clustering analysis was performed using Ward Linkage method. Each site's daily spore concentration time series was initially treated as a separate (singleton) cluster. We then computed the Euclidean distance of each pair and successively merged the most similar clusters. This multidimensional technique enabled the determination of the groups (clusters) of sites with the greatest similarity in seasonal *Alternaria* dynamics. Differences in spore concentrations among the resulting clusters were tested using the Kruskal-Wallis Test, followed by Post-hoc pairwise comparisons using Dunn's Test.

The multivariate data analyses were performed using the computing environment R (Posit team, 2023; R Core Team, 2022) and the packages *MASS* (Venables and Ripley, 2002), *factoextra* (Kassambara and Mundt, 2017) and *AeRobiology* (Rojo *et al.,* 2019b).

2.3. Weather conditions and air quality variables

Daily and hourly meteorological parameters, including precipitation (mm), maximum, minimum and average temperature (°C), as well as average relative humidity (% RH), were provided by the CDC (Climate Data Center) of the German Meteorological Service (DWD). Each weather station has been selected according to the shortest distance to each spore sampler. Additional weather data, including surface solar radiation (J/m^2) and wind speed (m/s), were obtained from the Copernicus ERA5 reanalysis dataset (Hersbach et al., 2023), with values retrieved specifically for the coordinates of each sampling site.

As the aerobiological data did not follow a normal distribution (Shapiro-Wilk test, $P < .05$) a nonparametric Spearman's rank correlation analysis was used to examine the associations between daily and bi-hourly average spore concentrations and meteorological data as well as to verify the non-collinearity of the covariates in subsequent analysis. Several parameters were included: temperature (minimum, maximum and average T,°C), relatively air humidity (RH, %), precipitation (PP, mm), solar radiation (SR, J/m^2) and wind speed (WS, m/s).

Daily air quality data (NO_2, O_3, CO_2, $PM_{2.5}$, PM_{10}, all in µg/m^3) were obtained from Copernicus Atmosphere Monitoring Service (Copernicus Atmosphere, 2021; IEK, 2020), extracted specifically for the coordinates of each sampling site.

To ensure complete spatial coverage of meteorological variables, ERA5 data (precipitation (mm), maximum, minimum and average temperature (°C), and relative humidity (% RH)) were also used to fill gaps where no ground-based weather station was available within a 15 km radius of a sampling site (see **Fig. S1** and **Table S2** in the Supplementary Material). Where station data were available within this radius, they were prioritized for their higher local representativeness. This hybrid approach combines the spatial specificity of in situ observations with the temporal consistency and continuity of satellite-based reanalysis. Interpolated ERA5 values were compared against station data when possible to assess consistency and minimize potential biases. Full-factorial analysis of variance and covariance (ANOVA, ANCOVA, post-hoc Bonferroni test) and regression analysis (GLM, GLZ) were applied to assess the effects of meteorological and air quality variables influencing *Alternaria* spore seasonality. Additionally, we employed machine learning and statistical modelling techniques, including random forest, regression tree (Picornell *et al.,* 2022), and extreme gradient boosting (XGBoost), to capture complex, non-linear relationships, while stepwise regression identified the most significant predictors. These methods enabled us to evaluate the relative importance of environmental factors in shaping spore variability.

The analyses were performed using the computing environment R (Posit team, 2023; R Core Team, 2022) and the package *caret* (Kuhn, 2007).

2.4. Land cover and land use information

Each site was analysed according to nearby land cover from the Corine Land Cover (CLC, 2020) dataset. Shapefiles of the 23 sites were used as the baseline features for the reclassification. Additional input from OpenStreetMap (OSM) shapefile layer was considered. CLC is the most comprehensive international land cover dataset currently available (Thibaudon *et al.*, 2014) for this kind of study. The vegetation cover in a maximum of 30-km radius from each site was analysed, as previous studies showed (Skjøth *et al.*, 2016b, 2010). The description of the habitat can be found in https://land.copernicus.eu/user-corner/technical-library/corine-land-cover-nomenclature-guidelines/html.

The regional green space available per inhabitant (greenery/km^2) according to the actual type of use can be found in the Genesis database of the Bavarian State Statistical Office (https://www.statistikdaten.bayern.de/genesis/online/logon). The population figures used for this calculation are based on official census data estimates from the same statistical office, considering only residents in urban areas where each spore sampler is located. In total, the area of green space in Bavaria is 19,814 hectares at the end of 2019. Green spaces include, for example: parks or botanical gardens, but not natural green spaces, such as floodplains, which are recorded as vegetation areas.

3. Results

3.1. *Alternaria* season and spatial differences

The results showed a strong spatial variability in *Alternaria* exposure, with distinct high-risk regions (**Table S3,** Fig. 2). The timing and intensity of the seasons varied considerably across the 23 sites, with season lengths ranging from 51 days in Altoetting in south-eastern Bavaria to 107 days in Augsburg in the central south. Peak spore concentrations were also highly variable, with the highest daily peak recorded in Marktheidenfeld (865.98 spores/m^3), followed by Hof (744.33 spores/m^3) in the north and Koesching (560.82 spores/m^3) in central Bavaria. The SFI, representing cumulative spore exposure, showed the greatest values in Bamberg (16,646.39 spores/m^3), Marktheidenfeld (16,171.13 spores/m^3), and Hof (13,578.35 spores/m^3), indicating these areas in the north as hotspots for *Alternaria* exposure. Conversely, the lowest seasonal spore loads were observed in Viechtach (278.87 spores/m^3) and Garmisch (663.92 spores/m^3), sites in colder areas.

The number of days exceeding 100 spores/m^3, a threshold relevant for allergy risk (Bush and Portnoy, 2001; Green *et al.*, 2006), varied widely. Bamberg (57 days), Koesching and Oettingen (both 51 days) had the most days above this threshold, while several locations, including Garmisch, Gaissach, and Viechtach, recorded none. The seasonal peak date varied from early June (Viechtach, 4 June) to late August (Weiden, 23 August), reflecting regional differences in spore production, release and transport.

3.2. Cluster analysis

The result of the analysis is summarized as a dendrogram (**Fig. S2**), starting with 23 elements and ending with one (senseless) big cluster. The elbow plot recommends the existence of five main clusters. Fig. 3 shows the five defined clusters per their location: (1) a *Cold Cluster* with eight sites distributed in the colder areas (Alps and Bavarian Forest); (2) a *Central Cluster* with eight stations in total and distributed in the center

Fig. 2. Daily time series of *Alternaria* spore concentrations at each sampling location. The patterns of daily concentrations of airborne *Alternaria* (spores/m^3) during the peak of the season (from June 1st to August 31st) are shown for each monitoring station. Each panel corresponds to a different location, ordered by cluster grouping and then alphabetically. The x-axis represents the date, while the y-axis shows daily spore concentrations. Although the full sampling period extended from May 1st to September 30th, this figure focuses on the core season, as values before and after this window were close to zero at most sites.

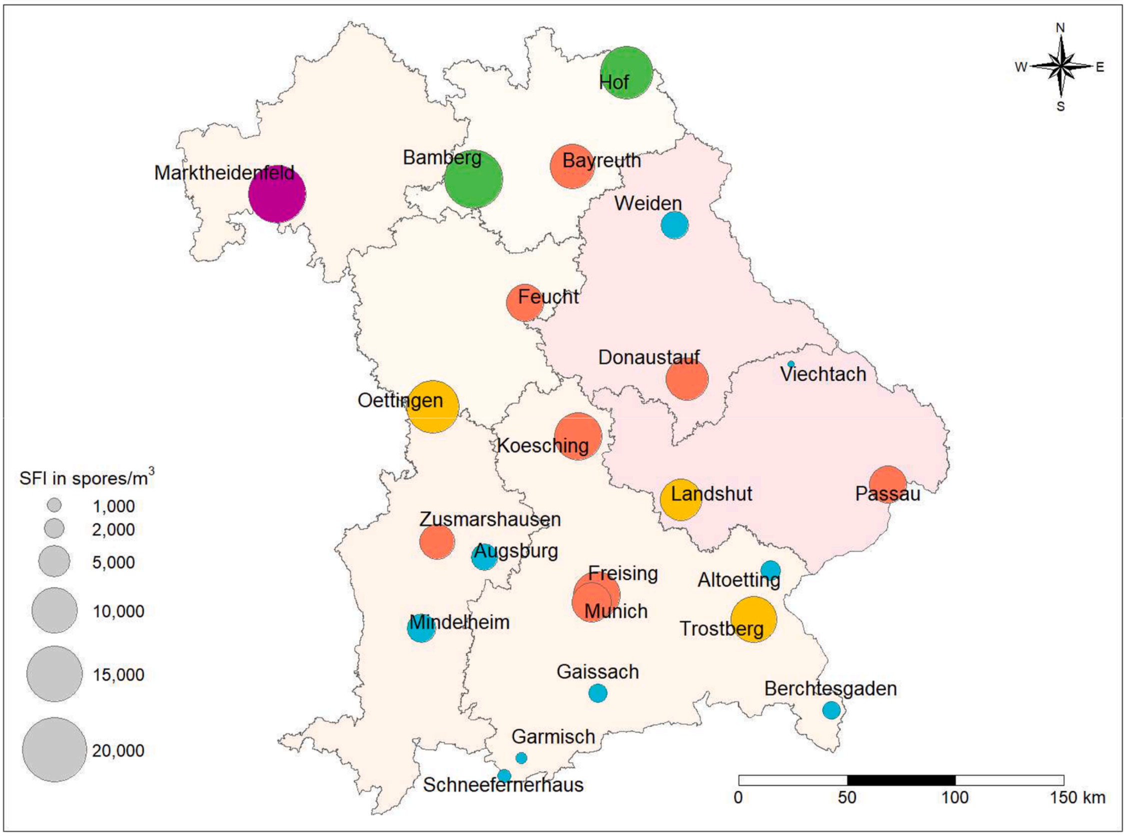

Fig. 3. Hierarchical clustering of *Alternaria* spore concentrations in Bavaria. Study area in Bavaria showing the results of hierarchical clustering using Ward's method applied to the complete daily *Alternaria* spore concentration dataset and based on temporal trends across monitoring sites. Each colour represents one of the five cluster identified in the analysis. Within each cluster, a circular marker (bubble) is displayed, with its size (see legend) proportional to the Seasonal Fungal Index (SFI) of *Alternaria* at each site. The legend includes representative bubble sizes for the SFI values of <5,000, <10,000, <15,000, and <20,000 spores/m^3, allowing for a visual comparison of cumulative spore loads across regions.

of Bavaria; (3) an *Outlier Cluster* with three stations also in the center of Bavaria; (4) a *Franconian Cluster* with only two stations distributed in the North and (5) a *High Cluster* with only one site situated in northwest characterised by the highest value in SFI but a relatively short spore season.

These clusters represent different spatiotemporal patterns of spore dynamics. Locations in cluster 1 comprised sites primarily situated in the southern region of Bavaria (Schneefernerhaus, Garmisch, Berchtesgaden, Gaissach, Augsburg and Mindelheim), as well as colder locations (Viechtach, Altoetting and Weiden) (Fig. 3). In these areas, the number of days with *Alternaria* concentrations exceeding 100 spores per cubic meter was minimal (Fig. 2, **Table S3**), yet the spore season tended to be notably longer. This extended duration may be influenced by more stable environmental conditions that support sustained, low-to-moderate spore presence over time. Cluster 2 was characterized by moderate overall spore concentrations, with a prolonged spore season and a relatively steady spore release pattern, typically lacking sharp peaks, with the exception of Koesching, which showed more variable behaviour. The highest spore concentrations were mainly observed in July (**Table S4**, Fig. 3). Cluster 3 was characterized by high SFI with late peak(s) in the center of the study area (Oettingen; Landshut and Trostberg). Locations in cluster 4 exhibited very high SFI and a prolonged spore season, with a multi-modal pattern in the north of Bavaria. Cluster 5, with only one site (Marktheidenfeld), showed the highest total spore concentration, with three very high peak values.

The Kruskal-Wallis Test revealed that the SFI differed significantly between some clusters ($p < 0.05$). Post-hoc pairwise comparisons using Dunn's Test to explore which clusters differed significantly in spore concentration, indicated significant differences between Cluster 1 and the other four clusters ($p < 0.002$). However, the test did not reveal significant differences between the other clusters. This could be due to several factors, including overlapping distributions of spore concentrations within clusters, which may not reflect significant central tendency differences such as medians. In addition, other important seasonal variables such as onset, peak value, and length are involved in defining the different clusters. An additional targeted analyses focusing on specific environmental factors will allow us to identify which environmental variables are most strongly associated with spore concentrations, and better understand the underlying processes affecting spore abundance.

3.3. Bi-hourly temporal differences in spore concentration

Spore concentrations typically follow a diurnal cycle (Fig. 4), which is often influenced by meteorological conditions such as temperature, humidity, and wind vectors. In many cases, *Alternaria* spores show a peak in the late afternoon or evening, i.e. Augsburg and Bamberg, however, with highly variable averages during the day.

A significant proportion of spores are often released after 6 PM (CEST, Central European Summer Time), with peak concentrations typically occurring between 8 PM and midnight and again in early morning, as observed in locations like Bayreuth and Marktheidenfeld. This pattern is likely driven by the lag effect of the peak temperature in early afternoon (and the lowest relative humidity too by that time), which are known to favour spore release and dispersion. During the morning and midday, spore concentrations tend to be lower in most of the sites. This could be due to increased turbulence and mixing in the atmosphere, which disperses spores more effectively, as well as drier conditions that may inhibit spore release. However, in colder locations

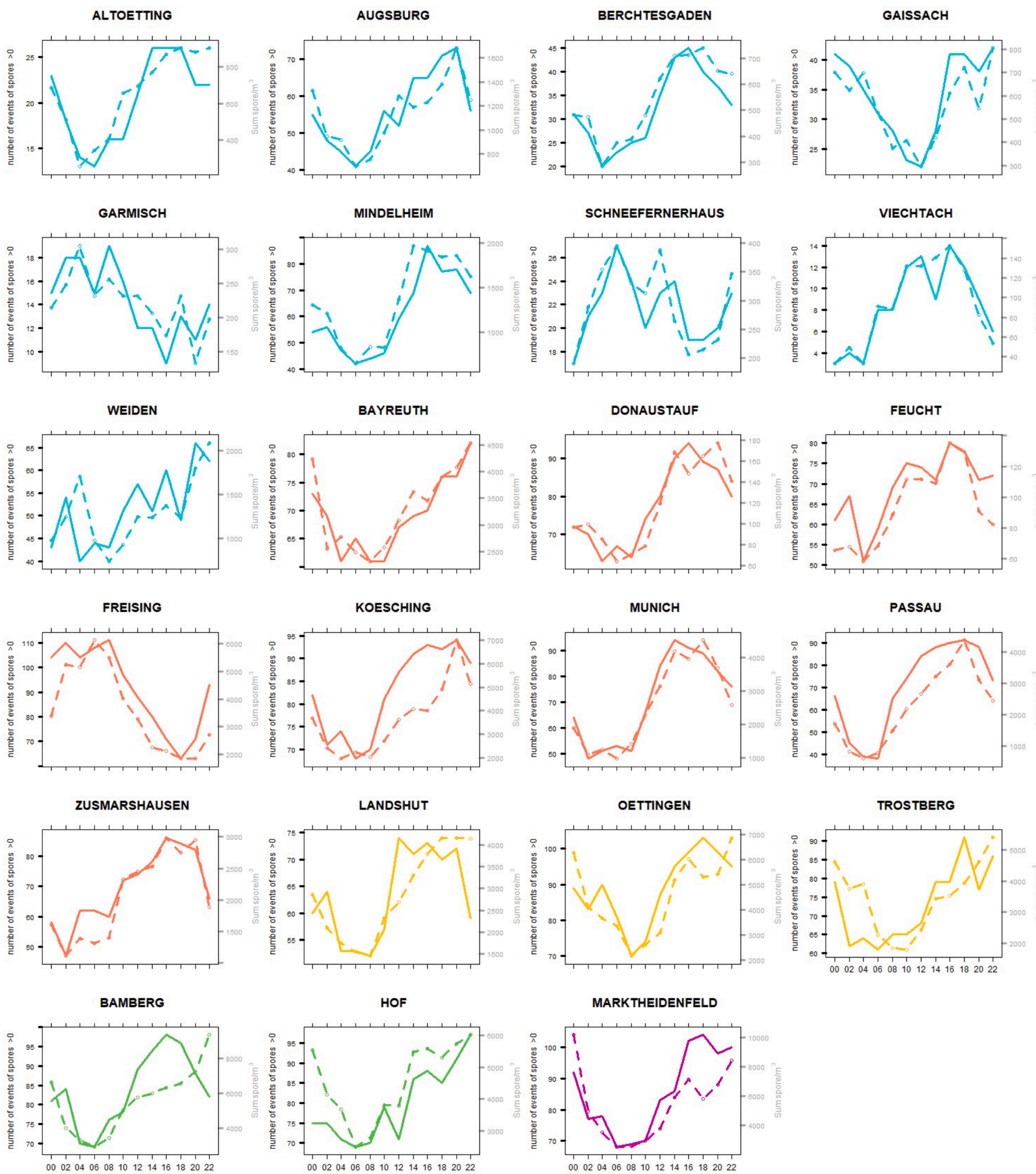

Fig. 4. Bi-Hourly spore distribution trends across sampling sites. Each panel shows the diurnal distribution of spores per sampling site during 2015 spore season (1st May to 30th September), with sites arranged alphabetically and coloured according to their cluster grouping (see Fig. 3). The X-axis displays the time of the day in 2-hours intervals (CEST, Central European Summer Time). The primary Y-axis (left in black) shows the frequency of spore occurrence for each bi-hourly interval (solid line), indicating when spores were most frequently present. The secondary Y′-axis (right in grey) displays the Seasonal Spore Integral per interval (dashed line), summarising the total spore load accumulated at each time point across the season. This dual-axis approach helps distinguish between the timing and intensity of spore presence.

at higher elevations, as Garmisch, Viechtach and Schneefernerhaus, the daily spore release pattern may become more variable, with peaks occurring at different times compared to lowland sites, and especially in the morning. This variation could be due to local meteorological conditions, such as temperature inversions or wind patterns that influence spore transport. The bi-hourly frequency of spore release and the SFI follow a similar trend (Fig. 4). However, in sites with higher SFI, such as Bamberg, Hof, and Marktheidenfeld, spore frequency is notably lower in the late evening and early morning.

3.4. Land cover, weather and air quality conditions

The abundance of the potential spore sources surrounding the sampling sites were analysed. The **Figure S3** represents the relative abundance (% of the total) of the main habitats (artificial land uses and vegetation) surrounding one site of each cluster and one from the Alps (Garmisch). The stations with the highest number of spores per year (Marktheidenfeld, Bamberg) are surrounded by more than 40% of non-irrigated arable land in all ring distances, i.e. cultivated land parcels under rainfed agricultural use for annually harvested non-perennial crops, usually under a crop rotation system, including fallow land within such a crop rotation. On the other hand, despite the fact that Munich and Freising are largely covered by urban habitat, especially in the smaller circle (5 km), the spore concentration is not the lowest, with a relative abundance of more than 5% at both sites. This indicates that the spores must have come from greater distances, 20 to 30 km, where the land use of non-irrigated arable land is more abundant.

Augsburg and Garmisch sites, with low spore concentration, are surrounded by pasture habitats (permanent grassland characterized by agricultural use or strong human disturbance). Floral composition is dominated by grasses and influenced by human activity) in more than 35% in ring of 10 km and 20 km.

On the other hand, the health risk that urban green spaces may imply to the population in the concept of *Alternaria* spore allergies is explored. Fig. 5 shows the correlation between km^2 of green space in each location with the total sum of spores collected during the study period. As we can see, once we do not consider Augsburg and Munich, where the amount of green space in relation to the total amount of the municipality is very high, the relationship between green space and the number of spores is significant (for all locations, see Supplementary Material, **Fig. S4**). Large green spaces, such as in Augsburg and Munich, do not have a high spore content (Fig. 2), which means that the spores are not found in the urban green spaces, but probably come either from other urban sources, or from the more distant cultivation and forest areas.

When analysing the influence of land use together with wind speed and direction, it is observed that the highest concentrations of spores in each cluster were associated mainly with westerly winds, while low concentrations of spores were associated with easterly winds. The analysis of variety and abundance of potential habitats suitable for *Alternaria* (within 30 km from the monitoring site) did not, however, show any striking differences between west and east areas (Fig. 6 **and Fig. S5**). The agricultural fields, meadows and pastures were equally distributed. The most distinct differences were observed w.r.t. forests which were much more abundant in the west.

The 23 sampling sites displayed different meteorological conditions during the study period (**Table S5**). Schneefernerhaus and Garmisch, at a high mountain level, registered a mean seasonal minimum temperature [Tmin] below 2°C, whereas in the northern areas of Bavaria, it is higher than 7°C. On the other hand, the maximum temperature [Tmax], registered values ranging between 12.0°C in Schneefernerhaus and 17.0°C in Marktheidenfeld. The precipitation sums also presented important differences, with the lowest values in Bamberg and Marktheidenfeld and highest in the Alps stations. The lowest values of air humidity were recorded in the center of the study area, in Munich, Freising and Landshut.

The different methods applied to find the daily and hourly variables that affected spore concentration most, random forest, regression tree, xgboost and stepwise regression methods, showed that temperature was the most relevant variable for the *Alternaria* spore concentration (**Fig. S6, S7** and **S8**). Water availability was also a very significant variable, with humidity having a negative and significant influence. It is evident from Fig. 7 and **Figure S3** that higher minimum temperature locations, characterised by lower relative humidity, predominately in the northern region of Bavaria, exhibited a prolonged period and elevated levels of *Alternaria* spore detection.

Regarding the air quality variables, NO_2 (ANOVA, F = 76.29, $p < 0.001$) showed statistically significant association with daily *Alternaria* spore concentrations. Pairwise comparisons between the locations, based on the estimated marginal means, revealed that NO_2 concentrations and minimum temperature (Tmin) are the most influential

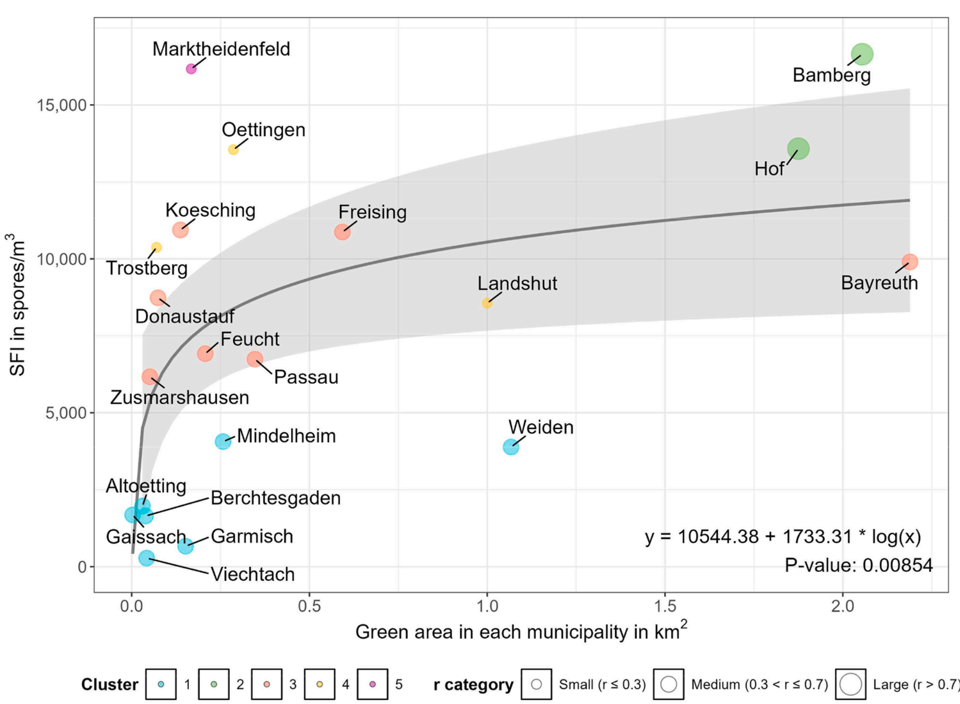

Fig. 5. Association between city green spaces and airborne *Alternaria* spores. Relationship between green urban areas (km^2) and Seasonal Fungal Index (SFI) at each location. The Munich and Augsburg sites were excluded from the analysis. Each colour represents a different cluster group identified through clustering analysis and the size of each point represents the Spearman correlation coefficient (r) between the green area and SFI for that location, with different sizes indicating varying strengths of the correlation.

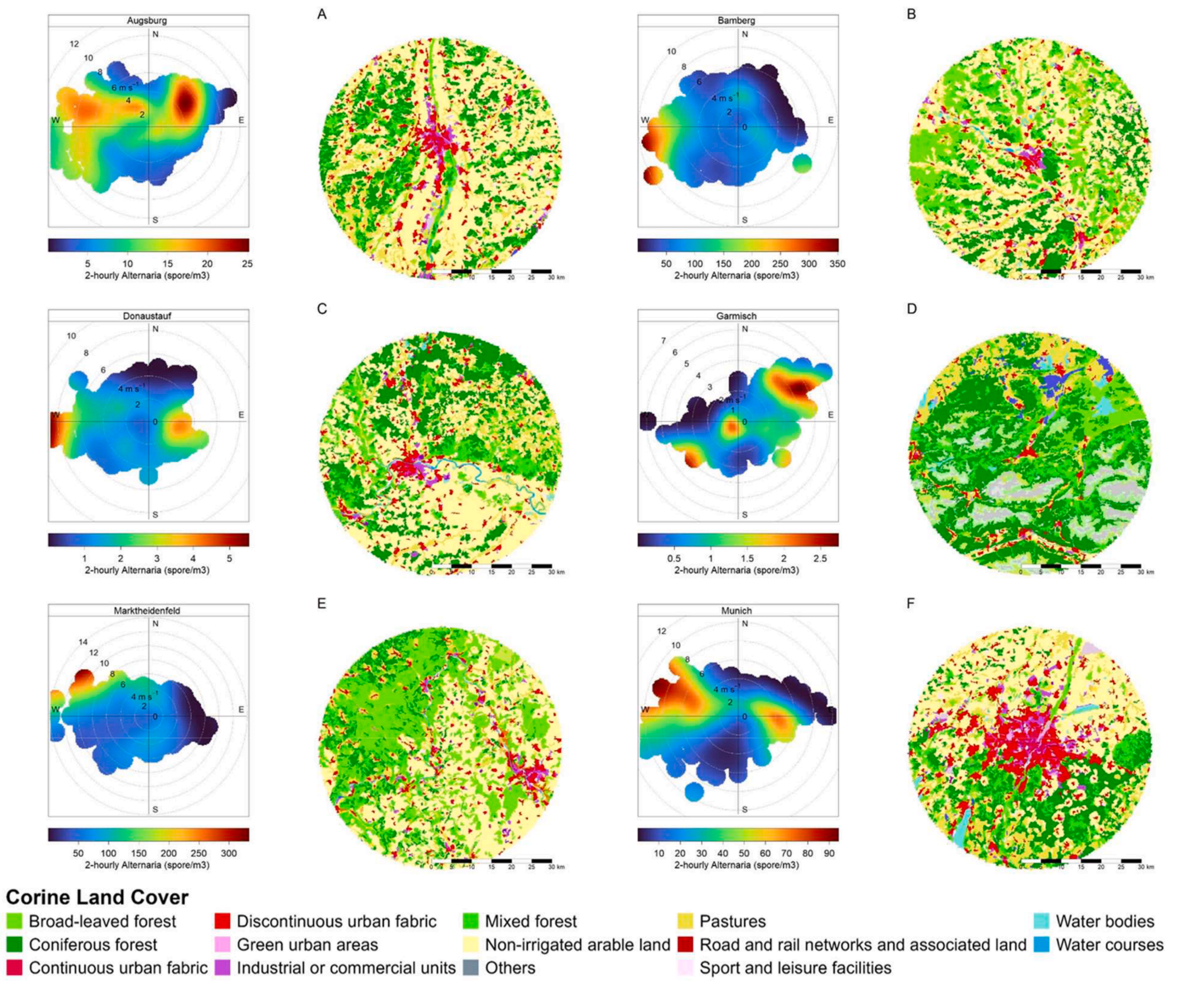

Fig. 6. Bi-**hourly *Alternaria* concentrations in polar coordinates and site location with land cover types.** *Alternaria* bi-hourly concentration in polar coordinates (left) showing concentration by wind speed and direction in one of the sites of each cluster and one from the Alps (Garmisch). Mean concentrations are calculated for wind speed-direction 'bins' (e.g. 0-1, 1-2 m/s and 0-10, 10-20 degrees etc.). Lower concentration of spores are in blue and the higher in red colour. On the right, the location of the spore-monitoring site and land cover types (based on Corine Land Cover data) within 30 km distance of the site. It is assumed that the amount of airborne particles recorded using volumetric trap is in general considered to reflect the overall particles load within a distance of about 30 km (Skjøth *et al.*, 2010).

variables affecting airborne *Alternaria* concentrations in the study area, with temperatures being almost always the top significant variable and NO_2 in the top five significant variables (**Fig. S8**). In factorial regression models (with weighted least-square difference fitting; Fig. 7), study sites were evenly separated based on different latitudes and longitudes, and it was found that at more northern sites, temperature was clearly the driving factor for higher SFI, but towards the south the interaction of both temperature and NO_2 gave this same increased SFI. In all combinations, both environmental parameters exhibited a significant effect (p<0.001), but with the variable importance of temperature being constantly more significant than that of NO_2.

The ANCOVA results highlighted significant differences among locations ($F= 24.96$, $p < 0.001$), and subsequent post-hoc analyses, adjusted using the Bonferroni correction to control for Type I error, confirmed the relevance of NO_2 and Tmin as key environmental factors driving *Alternaria* variability across the region.

4. Discussion

The distribution of *Alternaria* spores in the air, as observed in this study, underscores the complex interplay between meteorological conditions, atmospheric pollutants, and land use patterns across Europe. Our findings align with previous research (De Linares *et al.*, 2022; González-Alonso *et al.*, 2023; Kasprzyk *et al.*, 2015; Picornell *et al.*, 2022) that highlighted the critical role of environmental factors in shaping the temporal and spatial patterns of *Alternaria* spore concentrations. While our original hypothesis was that land uses would be the determining factor influencing airborne spore concentrations, the results proved that the interaction is complex with a variety of parameters contributing to the local and regional seasonal fungal amount in the air.

Influence of weather and air quality parameters

Minimum temperature and NO_2 levels were identified as the most significant determinants of *Alternaria* spore distribution. The positive correlation between minimum temperature and spore concentration observed in our study supports the notion that higher night-time temperatures facilitate *Alternaria* spore production and release (De Linares *et al.*, 2010; Grinn-Gofroń *et al.*, 2019). From a similar wide variety of environmental factors, but in one site, Thessaloniki, Greece, and in a

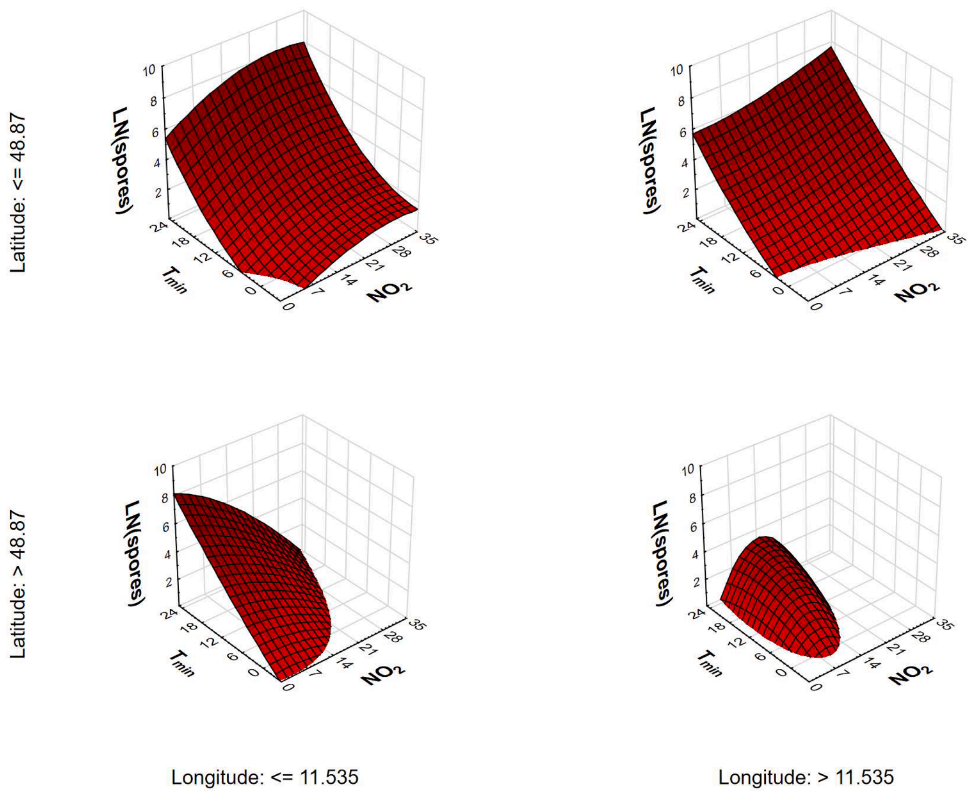

Fig. 7. Surface plot of spore concentration vs. temperature and NO_2 levels by location. Surface plot (weighted least-square difference (LSD) fitting) illustrating the logarithmic Seasonal Fungal Index (SFI) plotted against minimum temperature and NO_2 levels. The data are categorized according to four evenly distributed geographical positions, each defined by latitude and longitude coordinates.

completely different climate, (Damialis and Gioulekas, 2006) also evidenced that air temperature was the driving factor in the daily and monthly airborne spore variability. Furthermore, the diurnal variation in spore concentrations, with peaks in the late afternoon and early evening, likely reflects the combined effects of temperature and relative humidity, which are known to influence spore dispersal patterns. Despite the findings of previous studies which indicated that spore concentrations frequently reach their peak during the midday period, the minor discrepancy in the timing of these peaks observed with our results may be attributable to variations in regional climates or differences in local environmental factors, as well as lagged effects of air temperatures.

In addition, a relevant meteorological phenomenon that may contribute to the observed late-day peaks in spore concentrations—particularly at sites in southern Bavaria and near the northern Alpine foothills—is the influence of mountain–valley breeze systems. Specifically, katabatic (downslope) flows typically develop in the late afternoon and evening as cooler, denser air descends from higher elevations into adjacent valleys and lower terrain. While this phenomenon is more intense in the coastal places (Damialis *et al.*, 2005), where thermocapacity between sea/lakes and land differs a lot, still such an airflow may facilitate the downward transport and accumulation of *Alternaria* spores from surrounding forested slopes and alpine meadows, enhancing evening concentrations in foothill and mid-elevation areas. Similar effects of mountain and valley breezes on the dynamics of airborne pollen have been documented in the Bavarian Alps (Wörl *et al.*, 2022) and other mountainous regions, including the Iberian Peninsula (Cariñanos *et al.*, 2025). Although this phenomenon was not explicitly modeled in the current study, it may partially explain the consistent late-day spore peaks observed at several southern and alpine-adjacent locations (e.g., Garmisch-Partenkirchen, Gaissach, Berchtesgaden) and should be explored in future research.

Humidity, another critical factor, exhibited a dual role. While higher humidity levels support the germination and viability of *Alternaria* spores, our data also indicate that extremely high humidity may reduce airborne spore concentrations due to the aggregation and deposition of spores. This finding highlights the non-linear relationship between humidity and spore dispersion, suggesting that there is an optimal humidity range that maximizes spore presence in the air. This observation is particularly relevant in the context of climate change, where altered precipitation patterns may lead to shifts in the seasonal and geographic distribution of fungal spores (Damialis *et al.*, 2015a).

NO_2, commonly associated with urban pollution, also demonstrated an association with *Alternaria* spore concentrations, as earlier studies have also reported (Grinn-Gofroń *et al.*, 2011). The elevated spore levels in areas with higher NO_2 suggest that this pollutant may either promote spore production or enhance the survival of airborne spores, at least within the range examined in this study. However, in contrast to pollen, few studies have investigated the influence of different pollutants on airborne spore concentrations. The exact mechanisms underlying this relationship remain unclear, but NO_2 may act as a stressor, leading to increased spore release as a survival response by the fungal species (Grewling *et al.*, 2019). These findings are consistent with preceding research showing that air pollutants can interact with biological particles, potentially exacerbating their health impacts (Lam *et al.*, 2021).

4.1. Geographical variability and land use patterns

As González-Alonso *et al.*, (2023) observed, there was significant geographical variability in *Alternaria* spore concentrations across Bavaria, Germany. Specifically, the study revealed higher counts in northern regions and lower counts in southern areas proximate to mountains, which also exhibited lower temperatures. While these patterns may reflect underlying differences in meteorological conditions, such as temperature and humidity, they also appear to be influenced by land use characteristics. . These findings align with the conclusion of the present study that land use patterns, in combination with meteorological variables, play a critical role in shaping the spatial distribution of *Alternaria* spores. In urban areas, characterized by high NO_2 levels and limited vegetation, distinct spore dynamics compared to rural and agricultural regions would be expected. However, previously published studies showed completely opposite results (Kasprzyk and Worek, 2006; Oliveira *et al.*, 2009), suggesting that the relationship is not uniform across regions. On the other hand, agricultural areas, especially those with extensive crop cultivation, were associated with higher *Alternaria* spore levels, likely due to the presence of host plants and decaying organic matter that serve as reservoirs for fungal growth (Apangu *et al.*, 2020). Therefore, we hypothesize here that the interplay between land uses (urban vs. rural environments) and meteorological conditions might be way more complex and context-specific, as many other parameters can contribute to the positive or negative contribution to airborne fungal spore concentration. Factors such as the use of pesticides and insecticides, irrigation practices, type of cultivated agricultural products (species and monocultures), seasonality of biotic and abiotic factors, including climatic type, altitude, latitude and longitude, even national strategies for agricultural development and forest sustainability, may all modulate airborne spore dynamics.

The spatial variability in spore concentrations across different land use types and varying climatic conditions, highlights the importance of considering local environmental conditions when assessing the health risks associated with *Alternaria* exposure. Moreover, the interaction between land use, meteorological and air quality factors, especially temperature and wind components (direction, speed and persistence), suggests that future changes in land use, driven by urbanization or agricultural practices, could significantly alter the landscape of fungal spore distribution in Europe.

4.2. Implications for public health, agricultural productivity and future research

The findings of this study have important implications for public health, particularly in the context of increasing urbanization and climate change. The identification of specific environmental conditions that exacerbate *Alternaria* spore concentrations can inform the development of targeted mitigation strategies, such as urban planning initiatives that reduce pollution levels. Additionally, public health advisories could be tailored to periods of high spore concentrations, helping to minimize exposure for vulnerable populations, such as those with asthma or other respiratory conditions.

The widespread occurrence and adaptability of *Alternaria* spp. to different environmental conditions make them persistent threats in agricultural systems worldwide. These strategies may include determining the best time for fungicide applications, selecting pathogen-resistant cultivars, and implementing cultural practices to reduce sources of fungal spores.

Future research should focus on the mechanistic understanding of the interactions between fungal spores and atmospheric pollutants, as well as the potential effects of long-term climate changes on *Alternaria* spore distribution. Continuous biomonitoring of airborne fungal spores (as in the case of airborne pollen) has to take place in a wide range of sites, so that we may comprehend the spatiotemporal dynamics of fungal biology and ecology. Limited research exists on the topic (Damialis *et al.*, 2015b), and interestingly, results seem different from those of airborne pollen, with climate-change-associated variables exhibiting an inverse impact on spore abundances for the majority of taxa. One may hypothesize that climate change effects may show a longer lag and a higher resilience of fungi, so far. Additional data and advanced modeling approaches that integrate meteorological data, pollution levels, and land use patterns could provide more accurate predictions of spore dynamics under various environmental scenarios.

In conclusion, this study demonstrates the significant impact of weather parameters, NO_2, and land use on the spatiotemporal distribution of *Alternaria* spores in Europe. By elucidating these relationships, we contribute to a better understanding of the environmental drivers of fungal spore exposure, which is essential for protecting public health and ensuring the quality and quantity of crops in an era of rapid environmental change.

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CRediT authorship contribution statement

Maria P. Plaza: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jose Oteros:** Writing – review & editing, Project administration, Data curation, Conceptualization. **Vivien Leier-Wirtz:** Writing – review & editing, Investigation, Data curation. **Franziska Kolek:** Writing – review & editing, Investigation, Data curation. **Annette Menzel:** Writing – review & editing, Investigation. **Jeroen T.M. Buters:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization. **Claudia Traidl-Hoffmann:** Writing – review & editing, Investigation, Funding acquisition. **Athanasios Damialis:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Maria P. Plaza reports financial support was provided by German Federal Ministry of Education and Research. Jeroen Buters reports financial support was provided by Bavarian State Ministry of Health and Care. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2025.110716.

Data availability

The authors do not have permission to share data.

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