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Abundance of *Ganoderma* sp. in Europe and SW Asia: modelling the pathogen infection levels in local trees using the proxy of airborne fungal spore concentrations

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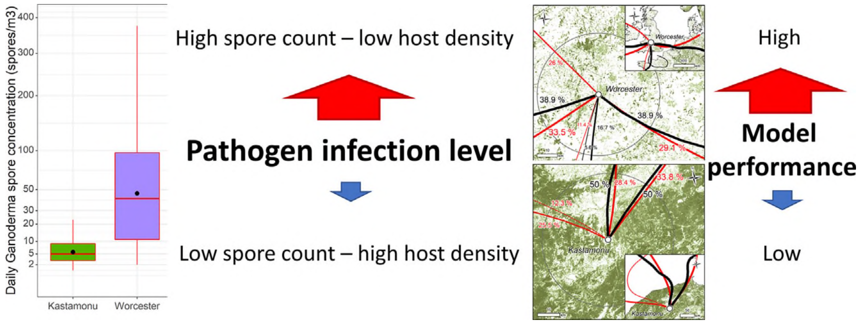
GRAPHICAL ABSTRACT



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1. Introduction

Ganoderma species are wood-decaying basidiomycete fungi with a cosmopolitan distribution, and they comprise common pathogens on deciduous and coniferous trees, as well as palms with stems without secondary growth. The fungi reproduce via airborne spores and grow in the non-living tissues. They usually attack dead, weakened or damaged trees, however, recent surveys of basidiomycete endophytes revealed that wood-decaying fungi, including *Ganoderma* species, can be found in wood of living trees too (Song et al., 2017). Pathogenicity studies revealed that the investigated *Ganoderma* species are capable of infecting healthy sapwood following trunk wounding, however, they are not usually pathogens in young, actively-growing trees that only possess sapwood (Loyd et al., 2018).

Ganoderma sp. enzymes allow them to break down wood components such as lignin and cellulose (Schwarze et al., 2000). Delignification and defibration caused by undisturbed rotting extend throughout the interior of the trunk making the tree susceptible to wind damage (Blanchette et al., 1985; Dill and Kraepelin, 1986). Based on the type of decay caused by *Ganoderma* species, they are classified as white rot fungi (the infected wood becomes wet, spongy or stringy and the colour changes to white or yellow). Several approaches are needed to control white rot infection. Most have been trialed in oil palm plantations due to serious economic losses (Flood et al., 2005; Paterson, 2007). Some control methods can be extrapolated to the deciduous and coniferous commercial forests, e.g. infection sources should be reduced at the time of clearing old stands by removing infected debris and *Ganoderma* sp. fruiting bodies (Panchal and Bridge, 2005), and all infected plant material should be treated with a specific type of biofungicide (Soepena et al., 2000). An important problem related to white rot control, however, is the lack of sufficient information on variation in *Ganoderma* species associated with disease and their mode of reproduction.

Ganoderma is taxonomically considered as the most difficult genus among all those in the Polyporales order and is in a state of taxonomical chaos (Ryvarden, 1985, 1991). Taxonomists have described 326 legitimate *Ganoderma* species and lower taxa (Robert et al., 2013). Among these only 7 species are accepted in the European polypore monographs: *G. adspersum, G. applanatum, G. carnosum, G. cupreolaccatum* (syn. *G. pfeifferi*), *G. lucidum, G. resinaceum* and *G. valesiacum* (e.g. Pegler and Young, 1973; Ryvarden and Gilbertson, 1993; Sokół, 2000; Wojewoda, 2003). *G. adspersum* occurs on *Alnus* sp., *Fraxinus* sp., *Carpinus* sp., *Morus* sp., *Quercus* sp., *Juglans* sp., *Ulmus* sp. and very rarely on conifers; *G. applanatum* occurs mainly on deciduous trees (*Alnus* sp., *Betula* sp., *Carpinus* sp., *Fagus* sp., *Quercus* sp., *Salix* sp., *Populus* sp.), less frequently on coniferous (*Abies* sp., *Picea* sp., very rare on *Pinus* sp.); *G. carnosum* infects mainly conifers (*Abies* sp., *Taxus* sp.) but rarely occurs on deciduous tree species; *G. cupreolaccatum* prefers to live on *Fagus* sp. and rarely on a variety of other deciduous trees (*Aesculus* sp., *Acer* sp., *Fraxinus* sp., *Prunus* sp., *Quercus* sp.); *G. lucidum* grows on *Quercus* sp., *Carpinus* sp., *Salix* sp., *Corylus* sp., *Acer* sp. and very rarely on conifers; *G. resinaceum* infects only deciduous trees (*Quercus* sp., *Salix* sp.); *G. valesiacum* is a Central European species occurring predominantly in montane to subalpine regions, in the natural stands of *Larix* sp. (Ryvarden and Gilbertson, 1993; Sokół, 2000; Szczepkowski and Piętka, 2003; Papp and Szabó, 2013; Lindequist et al., 2015).

Ganoderma spores can be an important component of atmospheric bioaerosols. A single *G. applanatum* basidiocarp can produce 30 billion spores per day, over a period of six months (Meredith, 1973; Levetin, 1990). Airborne fungal spores are able to travel long distances via air mass transport (Edman et al., 2004; Sesartic and Dallafior, 2011), so studying *Ganoderma* spore concentrations in the air may be relevant from the forestry and the economic perspective on a large landscape scale. In England, the Forest Commission highlighted *Ganoderma* genus as an important pathogen (McKay, 2011). Similar negative impacts on forestry can be expected in other regions, but this has so far not been quantified.

A limited number of aerobiological studies have focused on characterizing daily and seasonal patterns of *Ganoderma* spore occurrence, and relationships between spore concentration and meteorological parameters, often in the context of the allergenic properties of *Ganoderma* spp. (Tarlo et al., 1979; Levetin, 1991; Craig and Levetin, 2000; Hasnain et al., 2004; Kadowaki et al., 2010; Grinn-Gofroń and Strzelczak, 2011; Kasprzyk et al., 2011; Grinn-Gofroń et al., 2015; Jędryczka et al., 2015; Sadyś et al., 2016).

Until now, the only research on the distribution of *Ganoderma* spores among different landscapes was conducted in the UK (Sadyś et al., 2014). Back-trajectories from that study showed export of these spores from forests to agricultural and urban areas, and the results suggested the main sources of this pathogen were located within a 200 km range from the trap site (Worcester, UK). No evidence of long-distance spore transport from the main continent was found.

In the present study, we hypothesize that *Ganoderma* spores originate from local sources, and therefore that spore concentrations can be predicted using local meteorological data. Moreover, if local fungal sources are crucial for spore concentration, the relative pathogen infection level can be determined by combining airborne spore concentrations and the area covered by potential tree hosts. To test these hypotheses we used aerobiological records from seven sites, representing five biogeographical regions and four climate types, and aimed to (1) estimate the host (tree) density at different distances from each trapping site; (2) determine the spore season parameters; (3) assess the relationships between primary meteorological variables and airborne spore concentrations (4) calculate the backward trajectories indicating pathways of possible *Ganoderma* spores transport to sites; and, (5) compute machine learning models for *Ganoderma* spore concentration in the air.

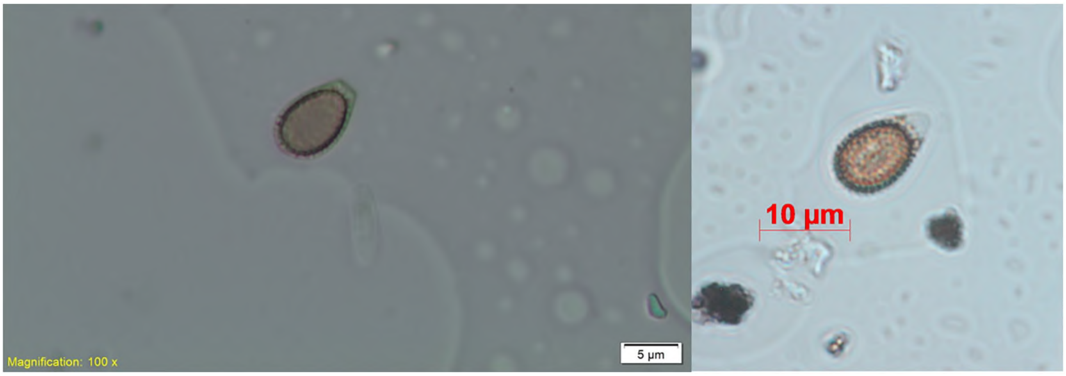


Fig. 1. *Ganoderma* spores under ×1000 (*left*) and ×400 magnification (*right*) (phot. M. Sadyś).

2. Material and methods

2.1. Spore identification, sampling and a comparison between receptor sites

Ganoderma spp. (hereafter *Ganoderma*) spores have either an egg or ovoid shape and they are approx. 4.5–8 × 8–13 μm in size (Pegler and Young, 1973; Fig. 1). *Ganoderma* can be distinguished from other bracket fungi because it possesses a double-walled basidiospore. The external spore wall is transparent and smooth, while the internal wall varies from dark brown to golden in colour. The wall layers are connected by pillars, which under the microscope may resemble dots. Another distinctive feature is a flattened basal apiculus, the projection on the spore from where it was attached to the fungus (Southworth, 1974).

Fungal spore concentrations were sampled as part of long-term air quality monitoring schemes at seven sites in five countries across Europe and SW Asia, located in five different biogeographical regions (Fig. 2, Table 1). A 7-day volumetric spore sampler of the Hirst design (Hirst, 1952) was used at each site. Air monitoring and analysis were performed according to the methods described by the Spanish Aerobiology Network (Galán et al., 2007) and the Minimum Recommendations proposed by the European Aerobiology Society Working Group on Quality Control (Galán et al., 2014).

To compare the *Ganoderma* spore data from the study sites located in different climate and biogeographical zones, traditional spore season parameters were calculated, i.e., start, peak and end of season dates and the seasonal spore integral for each season and study site. To determine the timing of the spore season, the 90% method was used, which begins when 5% of the total spore sum was reached, and ends when the cumulative count reaches 95% of the total for that year (Nilsson and Nilsson and Persson, 1981). R software, version 3.6.3. (R Core Team, 2020) and *AeRobiology* R package (Rojo et al., 2019) were used to calculate the spore season dynamics.

2.2. Determination of potential inoculum sources

As *Ganoderma* are phytopathogens particularly of trees, the tree density was assessed quantitatively in a radius of 30 km from the spore trap. This distance was considered because most of the spores recorded by the Hirst-type trap originate from sources located up to 30 km away, as previously reported (e.g. Skjøth et al., 2016; Olsen et al., 2019). This has also been documented for *Ganoderma* spores (O'Connor et al.,

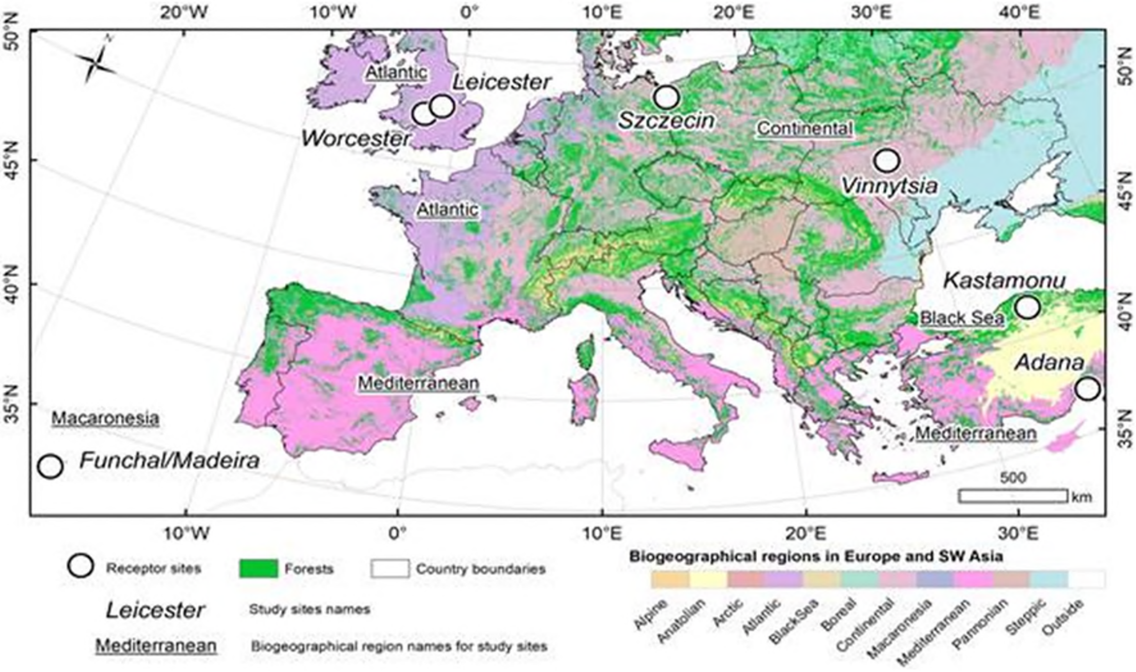


Fig. 2. Location of *Ganoderma* spore monitoring sites.

Table 1
Climate category of the study sites, based on the Köppen-Geiger climate classification (https://en.climate-data.org/), and the sites' respective sampling periods.

City/country	Annual mean temperature	Climate	Sum of annual precipitation	Dominant wind direction	Sampler height	Sampler location	Period of sampling
Worcester/United Kingdom	9.7 °C | 49.5 °F	temperate oceanic climate (Cfb)	647 mm | 25.5 in.	SW	25 m a.g.l.	52°11′N, 2°13′W	Jan 2006 - Dec 2010
Leicester/United Kingdom	9.7 °C | 49.4 °F	temperate oceanic climate (Cfb)	620 mm | 24.4 in.	SE	12 m a.g.l.	52°38′N, 1°05′W	Jan 2006 - Dec 2010
Szczecin/Poland	8.6 °C | 47.4 °F	temperate oceanic climate (Cfb)	542 mm | 21.3 in.	W, SW	21 m a.g.l.	53°26′N, 14°32′E	Jan 2006 - Dec 2010
Vinnytsia/Ukraine	7.6 °C | 45.7 °F.	humid continental climate (Dfb)	623 mm | 24.5 in.	W, SW	25 m a.g.l.	49°14′N, 28°29′E	Apr 2009 - Oct 2010
Kastamonu/Turkey	10.3 °C | 50.6 °F	temperate oceanic climate (Cfb)	508 mm | 20.0 in.	SW, NE	7 m a.g.l.	41°36′N, 33°76′E	Jan 2006 - Dec 2007
Adana/Turkey	19.3 °C | 66.8 °F	hot-summer Mediterranean climate (Csa)	673 mm | 26.5 in.	N, S	15 m a.g.l.	37°05′N, 35°36′E	Jan 2007 - Dec 2009
Funchal/Madeira, Portugal	18.8 °C | 65.8 °F	hot-summer Mediterranean climate (Csa)	587 mm | 23.1 in.	SW, N	10 m a.g.l.	32°39′N, 16°55′W	Jan 2006-Dec 2010

2014; Grinn-Gofroń et al., 2020). Since not only forest trees are affected but also small tree patches, the Tree Cover Density dataset (aggregated to 100 m resolution, Langanke et al., 2018) was used instead of the popular Land Cover Classification map to estimate the area covered by trees surrounding the study sites. The Food and Agriculture Organization map from the Global Forest Resources Assessment 2010 (FAO, 2013), with spatial resolution of ~250 m, was used for Vinnytsia because the Tree Cover Density dataset did not cover this area. Both datasets show the tree cover density using a 0–100% scale.

Tree cover was calculated using ArcMap 10.5 (ESRI). The datasets were initially assigned to a class based on the following classes of tree cover: <10%, 10–20%, 20–30%, 30–40%, 40–50%, 50–60%, 60–70%, 70–80%, 80–90%, 90–100%. Then, the area of each class was calculated and weighted according to the tree cover fraction, i.e., area covered by trees in 35% was multiplied by a factor $f = 0.35$ which resulted in a reasonable estimate of the area covered. Subsequently, the area covered by trees was intersected with buffer and sectors (as per Grinn-Gofroń et al., 2020) surrounding the study sites (total 96 sectors for each site). Finally, the total estimated area covered by trees was aggregated to these sectors showing the distribution of tree cover around each site.

We developed a new method to calculate local *Ganoderma* infection levels, which we have called the Pathogen Infection Level Index (PILI). Assuming that spores originating from a 30-km radius of the sampling site dominate the recorded concentrations, this index will show the relative pathogen abundance calculated per 1 km^2 area covered by potential host plants. The equation to calculate PILI is:

$$PILI = \frac{\sum_{i=1}^{SL} Spore\_conc}{A_H}$$

where *Spore_conc* is the daily airborne *Ganoderma* spore concentration, *SL* is the spore season length and A_H is the area covered by potential host plants – in this study within 30 km.

2.3. Meteorological data

Meteorological data were obtained from weather stations located in the vicinity of the air samplers at each study site (Table 2).

The relationship between weather and airborne spore concentrations was assessed for selected meteorological parameters: (1) dew point temperature (*dew*, °C), (2) daily mean air temperature (*tavg*, °C), (3) daily maximum air temperature (*tmax*, °C), (4) daily minimum air temperature (*tmin*, °C), (5) precipitation (*precip*, mm), (6) relative air humidity (*humidity*, %), (7) air pressure (*pressure*, hPa), (8) daily mean wind speed (*wind speed avg*, m s^{-1}), (9) daily maximum wind speed (*wind speed* max, m s^{-1}) and (10) wind direction (°). All meteorological parameters were recorded in hourly (or every third hour, depending on the site) resolution and daily mean values were used for the analysis. Hourly data for wind speed and direction were used to analyse the impact of local wind conditions on *Ganoderma* spore concentration. The data were obtained from the OGIMET database using *climate* R package (Czernecki et al., 2020).

Normality of distributions were tested with the Kolmogorov–Smirnov and Chi-square tests, then Spearman's rank association was used to examine the effects of the selected weather parameters on spore concentration. Kruskal-Wallis test with post-hoc pairwise Wilcoxon tests with Bonferroni correction were used to examine differences in daily *Ganoderma* concentrations between sites. The relationship between spore concentration and wind conditions was analysed in detail. By combining three variables, spore concentration, wind speed and wind direction, it was possible to partially explain the potential location of the local pathogen inoculum sources (Uria-Tellaetxe and Carslaw, 2014). Spore concentration [spore m^{-3}] was used in daily resolution but wind speed [m s^{-1}] and direction [°] were hourly resolution to maximize the potential of wind data, as per Grinn-Gofroń et al. (2020). Combining data in different time resolution was possible using R software 3.6.3. (R Core Team, 2020) and bivariate polar plots from the openair R package (Carslaw and Ropkins, 2012). The colour key scale for spore concentration in the polar plots was different for individual sites because of the variability in spore levels between sites.

To indicate transport pathways associated with high *Ganoderma* spore concentrations at study sites, the backward trajectories were computed by the Hybrid Single Particle Lagrangian Integrated Trajectory model (HYSPLIT) (Rolph et al., 2017; Stein et al., 2015). A vertical velocity model (obtained from meteorological data) was used for trajectory calculations. Global Data Assimilation System (GDAS) meteorological data of 1° × 1° spatial resolution were used as this dataset, being

Table 2
Meteorological stations' location, and their distance to the spore trap.

Spore sampling station	Meteorological station	Distance between spore monitoring and meteorological station (km)	Longitude of meteorological station (°)	Latitude of meteorological station (°)
Worcester	Pershore	13.9	−2.03	52.15
Leicester	Church Lawford	32.2	−1.33	52.37
Szczecin	Szczecin	6.8	14.62	53.40
Vinnytsia	Vinnytsia	9.2	28.60	49.23
Kastamonu	Kastamonu	6.3	33.77	41.37
Adana	Adana	12.5	35.42	37.00
Funchal/Madeira	Funchal	14.2	−16.77	32.68

available for all the examined years. One trajectory starting height of 500 m above ground surface was chosen because the influence of the surface is minimized at this altitude. The trajectories were calculated every two hours up to 72 h back in time for days with the highest *Ganoderma* spore concentration at particular sites. Two threshold values were used to indicate days with high and extremely high spore concentration (90th and 98th percentile of daily spore concentration at particular sites, respectively). Back-trajectories calculated for all days with spore concentration exceeding thresholds were subjected to cluster analysis. As a result, four dominant directions associated with the elevated *Ganoderma* spore concentrations were determined. In the case of 98th percentile counts recorded at Kastamonu, Vinnytsia and Funchal/Madeira, only two dominant directions were indicated due to the low number of days with such high values. The method of Sirois and Bottenheim (1995) was used to obtain a site-specific, angle-based distance matrix taking into account distances between each pair of trajectories, as also used in Bogawski et al. (2019). This method is specifically designed to create trajectory direction-dependent clusters. R software 3.6.3. (R Core Team, 2020) and openair R package (Carslaw and Ropkins, 2012) were used to perform all calculations. The results from the cluster analysis were plotted on a map formatted using ArcMap (ESRI) software.

2.4. Random forest models

2.4.1. Models development and validation

A random forest model (Breiman, 2001) was built to predict fungal spore concentration for each study site. Seven meteorological parameters (except for wind direction) from the same day as fungal spores values were used as independent variables. For each site, the accuracy of the model was obtained using the following steps:

1. Data were split into a training set (75%) and a testing set (25%).
2. The training set was split using 10-fold cross-validation (Kuhn and Johnson, 2013) into ten groups of approx. equal size (folds).
3. Random forest model was built on nine folds and tested on the remaining fold. Each time three metrics were calculated: RMSE (*root mean squared error*), and R^2 (*coefficient of determination*) and SMAPE (*symmetric mean absolute percentage error*). This was repeated ten times.
4. The final model was applied to the testing set, and R^2, RMSE and SMAPE were calculated.

The three accuracy metrics were selected to show different aspects of the models' quality. RMSE is the square root of the average of squared errors, where the lower value indicates better model accuracy. This metric is on the same scale as the data being measured, and therefore depends indirectly on the variability of the fungal spore concentrations at each site. R^2 and SMAPE, on the other hand, can be used to compare models between sites. R^2 is the coefficient of determination providing the goodness-of-fit between predicted and observed values and ranges from 0 to 1, where larger values indicate better model accuracy. SMAPE (Makridakis, 1993) also measures the models' quality in relative terms. It focuses on the differences between predicted and observed values. Lower values of SMAPE indicate better model accuracy. Models were created and validated using random forest (Liaw and Wiener, 2002), parsnip (Kuhn and Vaughan, 2019a), rsample (Kuhn et al., 2019) and yardstick (Kuhn and Vaughan, 2019b) R packages.

2.4.2. Models interpretation

The general effect of independent variables on the models was determined using permutation testing (mean decrease in accuracy) (Breiman, 2001; Liaw and Wiener, 2002). For each model, the three most important variables were selected. The relationship between each pair of the most important variables and the model predictions was presented using the prediction interaction plot (Paluszynska et al., 2019). This type of plot randomly shuffles other variables values (except the two selected), and subsequently creates a prediction. The plot shows both variables on an *x*- and *y*-axis, while the colour represents prediction value. It facilitates the understanding of how different variables' values impact model predictions.

3. Results

3.1. Spore seasons across Europe and SW Asia

The shortest spore season was recorded in Kastamonu (109 days) and Vinnytsia (125 days) whereas the longest (282 days) was in Funchal/Madeira. The *Ganoderma* spore season started earliest in southern Europe and SW Asia, i.e., in Funchal/Madeira (February), then in Adana (March). The *Ganoderma* spore season started in May in Worcester, Leicester and Vinnytsia, and started latest in in Szczecin and Kastamonu, in June. The difference in spore season start dates between Funchal/Madeira and Kastamonu was 103 days (on average, 25 February in Funchal/Madeira and 7 June in Kastamonu). A 70-day difference was recorded when comparing Funchal/Madeira and Kastamonu spore season end dates (on average, 2 December and 23 September, respectively) (Fig. 3, Table S1).

Spore concentrations differ significantly between sites ($p < 0.001$) with the exception of the three sites with the highest concentration (Leicester-Worcester: p ~ 1, Szczecin-Worcester: p ~ 1, Szczecin-Leicester: $p = 0.68$). Overall, daily mean spore concentrations were the highest in Szczecin, Worcester and Leicester (peak values: 522 spore m^{-3} in 2007, 376 spore m^{-3} in 2006 and 372 spore m^{-3} in 2008 for these three cities, respectively). Substantially lower peak values were recorded in southern Europe and SW Asia (e.g. Adana: 21 spores m^{-3} in 2009, Kastamonu: 23 spores m^{-3} in 2006, Funchal/Madeira: 35 spores m^{-3} in 2008). A similar pattern was found in daily median spore concentration, i.e., the highest values were seen in Szczecin, Worcester and Leicester reaching 73, 62 and 52 spores m^{-3} of air, respectively (Fig. 4, Table S1).

3.2. Source of fungal spores

The largest areas covered by trees within 30 km radius from the sampling locations was found at Kastamonu (1138.39 km^2) and Szczecin (787.64 km^2) whilst Funchal/Madeira, Worcester and Leicester had the lowest tree cover density. The trees irregularly surrounded the study sites; the largest area covered by trees was located 0–5 km (Leicester), 15–20 km (Funchal/Madeira and Adana), 20–25 km (Worcester, Vinnytsia and Szczecin) and 25–30 km (Kastamonu) from the sampling sites (Table 3, Fig. 5). Combining potential sources of fungi with recorded spore counts, we showed that the PILI value was highest at the UK sites, reaching 84.18 spore/km^2 in Leicester. Markedly lower values

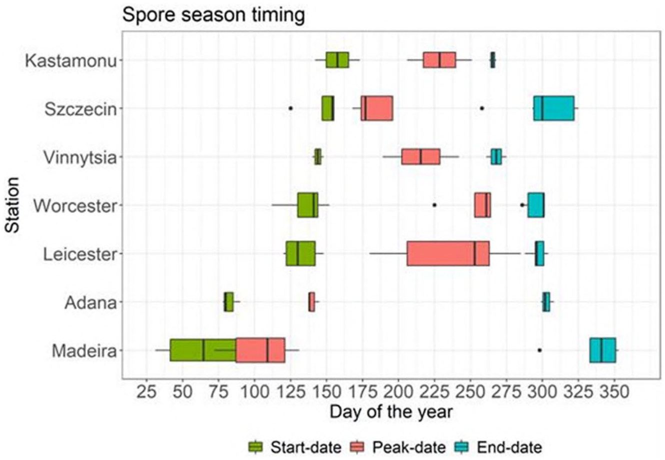


Fig. 3. *Ganoderma* spore season occurrence variability in study sites.

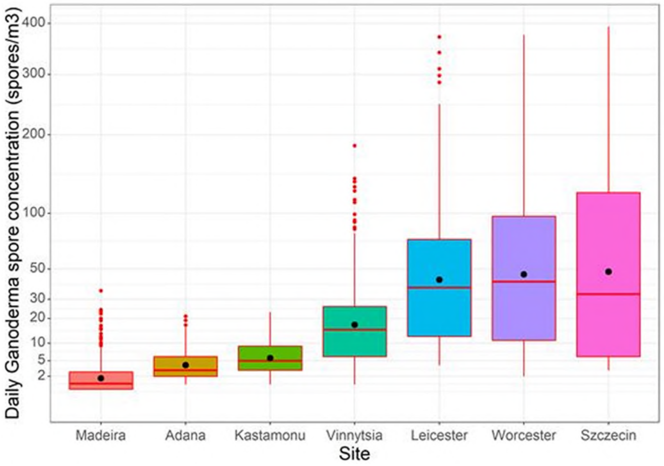


Fig. 4. Comparison of daily mean *Ganoderma* spore concentrations at the study sites. Boxes show first and third quartiles, bold line is median, black points are mean values and red points are extreme values (above 90th percentile).

were observed in the remaining sites with the minimum of 1.61 and 0.64 spore/km^2 in Funchal/Madeira and Kastamonu, respectively (Table 4).

3.3. Relationship between spore occurrence, weather and potential sources of fungal spores

The only study site which did not have statistically significant relationships between weather variables and *Ganoderma* levels was Funchal/Madeira. In the remaining sites, all thermal variables significantly correlated with spore concentrations, especially in the three most northern sites, with the strongest relationship being observed at Worcester, $r = 0.77$, $p < 0.001$ (Table 5). The correlation coefficient between thermal variables and spore concentration increased along with increasing latitudes and, excluding Funchal/Madeira, with increasing longitudes too (Fig. S1). Although the relationship between spore concentration and wind speed was relatively weak, a clear geographical trend towards increasing correlation along increasing longitudes was nonetheless observed (after excluding Funchal/Madeira) (Fig. S2).

Despite the relatively low correlation between daily values of spore concentrations and wind speed, wind conditions were important when data were clustered seasonally. The highest concentrations were recorded in summer and autumn and were associated with high wind speed, especially for Szczecin. In this site, winds with at least 8 m s^{-1} and 6 m s^{-1} caused extremely high *Ganoderma* spore concentrations in summer and autumn, respectively (Fig. 6). Extremely high wind speed (>10 m s^{-1} and even 60 m s^{-1}) in Funchal/Madeira were associated with the highest daily *Ganoderma* spore concentrations locally. Also in Kastamonu and Vinnytsia (only spring and summer), moderate wind speeds (>4 m s^{-1}) were required to reach the highest spore concentrations in particular seasons at these sites. In Worcester, Leicester (spring to autumn), Vinnytsia (autumn) and Adana (all seasons), markedly lower wind speed was enough to record season-specific high spore concentrations (<2 m s^{-1}) (Fig. 6). Season-specific high spore counts were recorded regardless of the wind direction (Adana, Worcester, Vinnytsia in autumn), but for the remaining sites wind direction was important (several dominant directions: Szczecin, SW, S, SE, N, NW; Kastamonu NW, N, NE, E; Funchal/Madeira NW, N, NE; Leicester NE, E, SE; Vinnytsia in spring and summer W, NW, N, NE).

We clustered back trajectories associated with the highest (above 90th and 98th percentile) daily *Ganoderma* spore concentrations to investigate possibilities of long-distance transport of *Ganoderma* spores when the concentrations are high (Fig. 7). Two UK cities located close to each other (ca. 100 km) showed a similar pattern of back-trajectories when comparing those calculated for the 90th percentile threshold. However, 60% of back-trajectories associated with extremely high (>98th percentile) spore concentrations in Leicester originated from the eastern direction compared to 38.8% in Worcester. The primary source of *Ganoderma* spores in Szczecin was located to the East of the city (ca. 45% of trajectories), however, when considering the extreme spore concentrations, the Western direction became equally important. In Vinnytsia, it was clear that the high spore concentrations occurred when the air masses came from the North-East. It was even more pronounced when considering the extremely high concentrations (66.7% of back trajectories were associated with the North-East direction). In Kastamonu and Adana, the highest concentrations were related primarily to back-trajectories from the North and South-West, respectively. The most interesting phenomenon was observed in Funchal/Madeira. When considering concentrations >90th percentile threshold, up to 75% of trajectories came from the sea, and only 25% might originate from the continent (Spain, Portugal). However, if only the concentrations >98th percentile are considered, at least 33% of back-trajectories (but probably more) originate from the continent (Iberian Peninsula) (Fig. 7).

3.4. Random Forest model

Three meteorological parameters, i.e., dew point temperature, daily maximum air temperature and daily minimum air temperature had the most substantial impact on the models; this can be seen on the variable importance plots (Fig. 9). The relationship between two of these three variables and the random forest model predictions are presented using the prediction interaction plot (Fig. 8). For example, the second from the bottom left plot shows the relationship between dew point temperature and maximum air temperature in the Adana model results. It can be seen that the highest values of *Ganoderma* daily mean spore concentrations in the air were predicted to occur when dew point temperature was above 8 °C and maximum air temperature was above 28 °C.

In most cases, the plots indicated threshold value(s) above which the predicted spore concentration was relatively high (Fig. 8). For example, the first threshold can be seen for a dew point temperature of 7 °C and the second threshold can be seen for a dew point temperature of 8 °C in Szczecin. Another example is Kastamonu, with a visible threshold

Table 3
Estimated area covered by trees [km^2, %] in the area surrounding the study sites.

Monitoring station	Buffer zones for monitoring stations											
	0–5 km	%	5–10 km	%	10–15 km	%	15–20 km	%	20–25 km	%	25–30 km	%
Worcester	5.8	7.2	17.4	10.9	37.2	15.5	41.1	12.9	65.3	16.3	75.8	15.8
Leicester	7.7	9.6	10.5	6.6	18.9	7.9	22.1	6.9	23.9	6.0	36.7	7.6
Szczecin	16.8	21.0	49.4	30.9	102.3	42.6	182.3	57.0	233.0	58.3	203.9	42.5
Vinnytsia[a]	15.7	19.6	42.6	26.6	59.2	24.7	101.7	31.8	140.1	35.0	122.0	25.4
Kastamonu	28.9	36.1	72.5	45.3	140.6	58.6	224.8	70.2	280.8	70.2	390.9	81.4
Adana	6.7	8.4	28.6	17.9	37.9	15.8	72.2	22.6	86.0	21.5	95.6	19.9
Funchal/Madeira	3.0	3.7	16.3	10.2	36.4	15.2	49.5	15.5	21.7	5.4	20.5	4.3

[a] These values were produced using different tree cover density datasets.

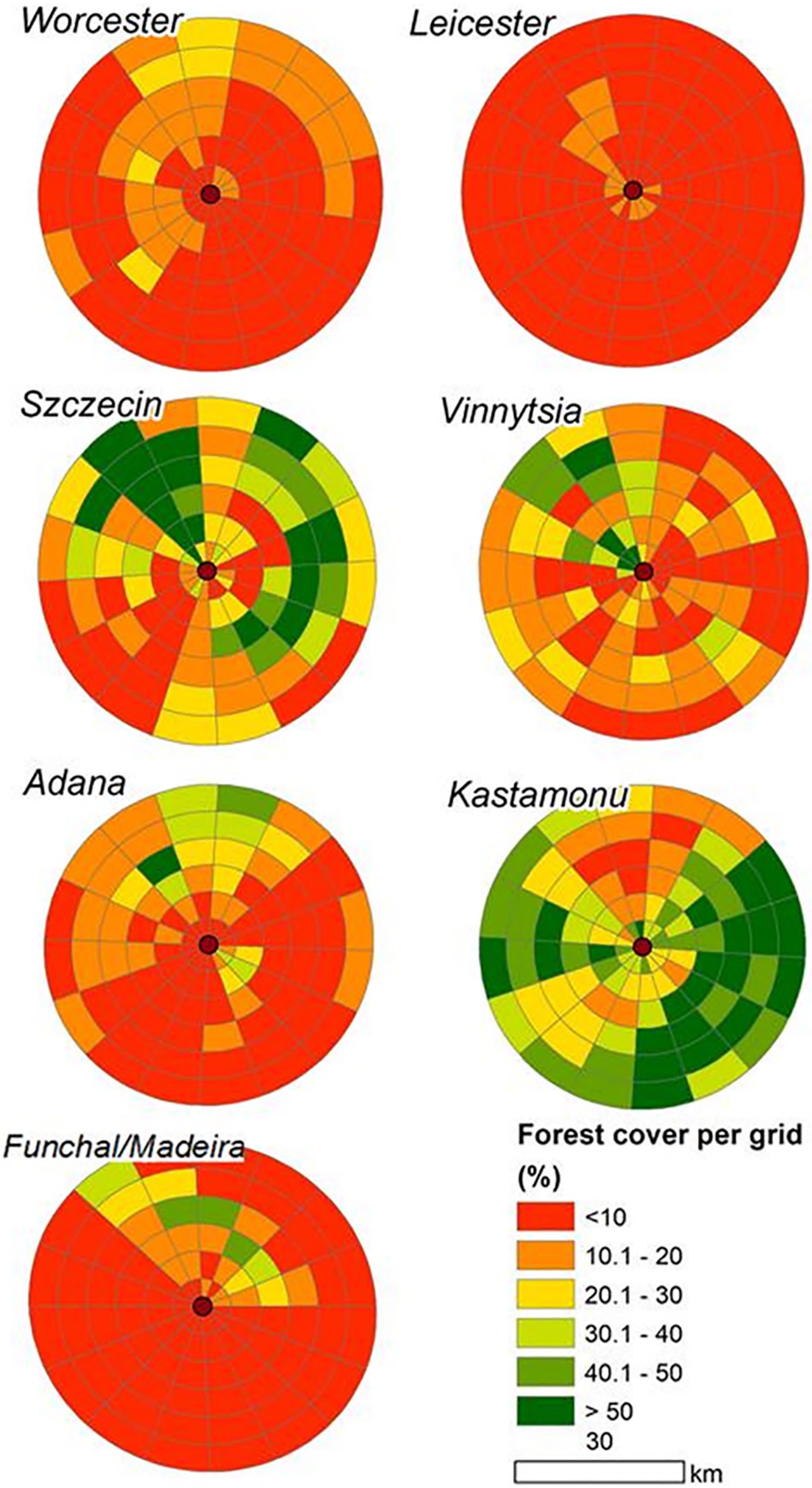


Fig. 5. Forest density in a 30 km radius of study sites.

of 10 °C of daily minimum air temperature. There are some interesting exceptions to this rule (Fig. 8). Firstly, the relationship of daily maximum and minimum air temperature in Adana with the highest predicted concentration values were observed when the minimum air temperature values were between 15 °C and 20 °C. Secondly, plots for Funchal/Madeira were mostly showcasing random noise: the meteorological

Table 4
Pathogen Infection Level Index (PILI) showing the relative abundance of airborne *Ganoderma* spores calculated per 1 km of area covered by potential hosts (in descending order of values).

Sampling site	Pathogen Infection Level Index (PILI)
Leicester	84.18
Worcester	65.04
Szczecin	20.24
Vinnytsia	6.19
Adana	3.34
Funchal/Madeira	1.61
Kastamonu	0.64

variables were unable to predict the *Ganoderma* spore concentrations there.

Finally, a random forest model of daily mean concentrations of airborne *Ganoderma* spores was created for each study site (Table 6).

The Worcester model showed the highest value of R^2 of 0.71. Medium values of R^2 (0.44–0.55) were found for Kastamonu, Leicester and Adana. Worcester and Leicester are located approx. 100 km apart and their daily concentrations of *Ganoderma* spores were similar (Spearman's rank correlation of $r = 0.761$, $p < 0.001$; for non-zero days); the differences in the models' performance expressed by R^2 are probably due to a few unusually high values in Leicester (it is more difficult to predict less frequently occurring values). Kastamonu had two years of observations and Adana three years of observations, therefore, if their models were based on a longer period of time, they could potentially yield in results similar to the Worcester model. The Szczecin model had the value of R^2 of 0.36. The Vinnytsia model had the value of R^2 of 0.21, which is probably due to the very short measurement period. The last model, for Funchal/Madeira, had the value of R^2 of 0.01, where, apparently, daily mean concentrations of *Ganoderma* spores cannot be explained using the examined here meteorological data. Importantly, models seemed to be stable (not overfitted) as their performances for training and test sets were similar (Fig. 10).

4. Discussion

Airborne *Ganoderma* spore concentrations were recorded in five different biogeographical regions representing four climate types in Europe and SW Asia. The highest airborne concentrations in Europe were found to the North (Latitudes > 45°N) whilst there were low levels in the South of Europe and the studied part of Asia. This may result from the higher humidity levels in the northern part of the study area; previous studies have shown a positive relationship between high humidity and *Ganoderma* spore concentrations in the air (Kasprzyk et al., 2011; Sadyś et al., 2014). Similarly to our findings, Haard and Kramer (1970) reported that increasing temperature, relative humidity or both lead to increased spore release of *Ganoderma*. Airborne spores of *Ganoderma* have been documented to positively correlate with maximum, minimum and mean temperatures (Hasnain, 1993; Li and Kendrick, 1995). Regarding relative humidity, spore concentrations are known to also correlate with it positively (Li and Kendrick, 1995), even though such a relationship with precipitation has been proven negative (Hasnain, 1993). Overall, *Ganoderma* produces a vast amount of spores per fruiting body, e.g. *G. applanatum* can release 30 billion basidiospores day^{-1} over 6 months (Buller, 1922); also, the genus seems to consist of quite tolerant sporophores (distinctive among basidiomycetes) that seem to be able not only to just survive under very dry conditions, but also to continue liberating their spores in spite of drought (Ingold, 1971). The above show the expansive and infesting potential of *Ganoderma*, as well as its dependence on specific meteorological and climatic regimes.

In this study, thermal variables were most important in explaining daily *Ganoderma* concentrations, however, the correlations with temperature decreased with decreasing latitudes. The spore sampling sites markedly differed in terms of tree density in the surrounding areas and therefore the density of potential host plants for the fungi. Interestingly, Kastamonu was the site with the largest forest area but the spore concentrations were significantly lower than in Worcester and Leicester – sites with small areas covered by forests. One possible explanation could be that trees in the UK are much more heavily infected with *Ganoderma* species than the other study sites. This confirms the Forest Commission in England report, which indicated *Ganoderma* to be an important pathogen (McKay, 2011). We propose a new measure, the "Pathogen Infection Level Index (PILI)" which combines spore concentrations and the area covered by potential pathogen hosts. The interpretation is that the higher the PILI value, the higher the level of infection. It should be emphasized that PILI values for Leicester are ~80 times larger than for the sites in Southern Europe.

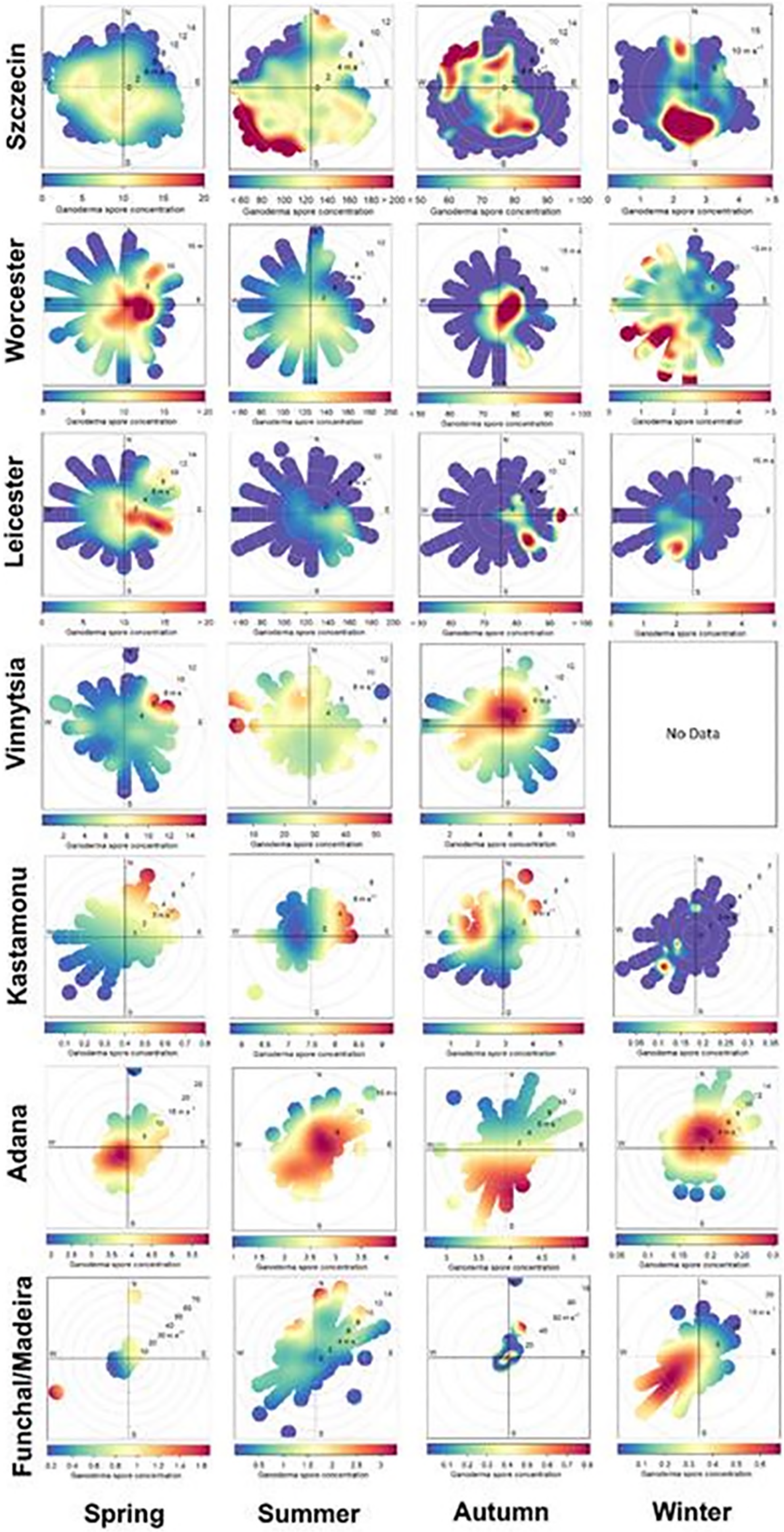
Combining spore concentrations with potential sources of fungi (location and size of the area covered by trees in this case), local wind conditions and back trajectories can be used to indicate primary spore source areas (Fernández-Rodríguez et al., 2015; Grinn-Gofroń et al., 2020). For example, north directions are interesting in Szczecin because elevated spore concentrations were recorded in three different seasons during North winds (Fig. 6). Specifically, in summer, autumn and winter *Ganoderma* spores were delivered from North North East (wind speed > 8 $m\ s^{-1}$), North (2 ms^{-1}) and North North West (~5 $m\ s^{-1}$), respectively. This suggests that sources of emission for *Ganoderma* spores recorded in Szczecin were located to the north to the city. The furthest putative source was located NNE of Szczecin and contributed spores in

Table 5
Spearman correlation coefficients between daily mean *Ganoderma* spore concentrations in the air and local meteorological parameters.

Meteorological parameters	Worcester		Leicester		Szczecin		Vinnytsia		Kastamonu		Kastamonu		Funchal/Madeira	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p
tavg	**0.77**	**<0.001**	**0.63**	**<0.001**	**0.56**	**<0.001**	**0.38**	**<0.001**	**0.39**	**<0.001**	**0.39**	**<0.001**	0.01	0.867
tmax	**0.77**	**<0.001**	**0.59**	**<0.001**	**0.52**	**<0.001**	**0.36**	**<0.001**	**0.34**	**<0.001**	**0.34**	**<0.001**	0	0.959
tmin	**0.77**	**<0.001**	**0.42**	**<0.001**	**0.54**	**<0.001**	**0.41**	**<0.001**	**0.4**	**<0.001**	**0.4**	**<0.001**	0.02	0.716
dew	**0.75**	**<0.001**	**0.62**	**<0.001**	**0.59**	**<0.001**	**0.45**	**<0.001**	**0.32**	**<0.001**	**0.32**	**<0.001**	0.01	0.894
humidity	**−0.15**	**<0.001**	**−0.13**	**<0.001**	**−0.22**	**<0.001**	0.09	0.133	**−0.27**	**<0.001**	**−0.27**	**<0.001**	−0.03	0.434
wind speed avg	**−0.28**	**<0.001**	**−0.24**	**<0.001**	**−0.09**	**0.001**	**−0.12**	**0.047**	**0.16**	**0.01**	**0.16**	**0.01**	−0.04	0.401
wind speed max	**−0.24**	**<0.001**	**−0.17**	**<0.001**	**−0.06**	**0.041**	−0.05	0.434	**0.2**	**0.001**	**0.2**	**0.001**	−0.05	0.208
precip	**−0.13**	**<0.001**	**−0.12**	**<0.001**	−0.04	0.207	−0.01	0.869	−0.05	0.413	−0.05	0.413	0.03	0.542

Significant correlations ($p < 0.05$) are shown in bold.

Fig. 6. Daily *Ganoderma* spore concentrations (spores m^{-3}) in different wind conditions and seasons for all the sites (2006–2010). The radial scale shows wind speed ($m\ s^{-1}$), which increases radially outwards from the middle of the plot (scale in right upper corner). Main wind directions are displayed (N, E, S, W) and can be read in degrees (°), when N direction = 0° and S direction = 180°.


Szczecin
Worcester
Leicester
Vinnytsia
Kastamonu
Adana
Funchal/Madeira
Spring
Summer
Autumn
Winter
No Data
Ganoderma spore concentration

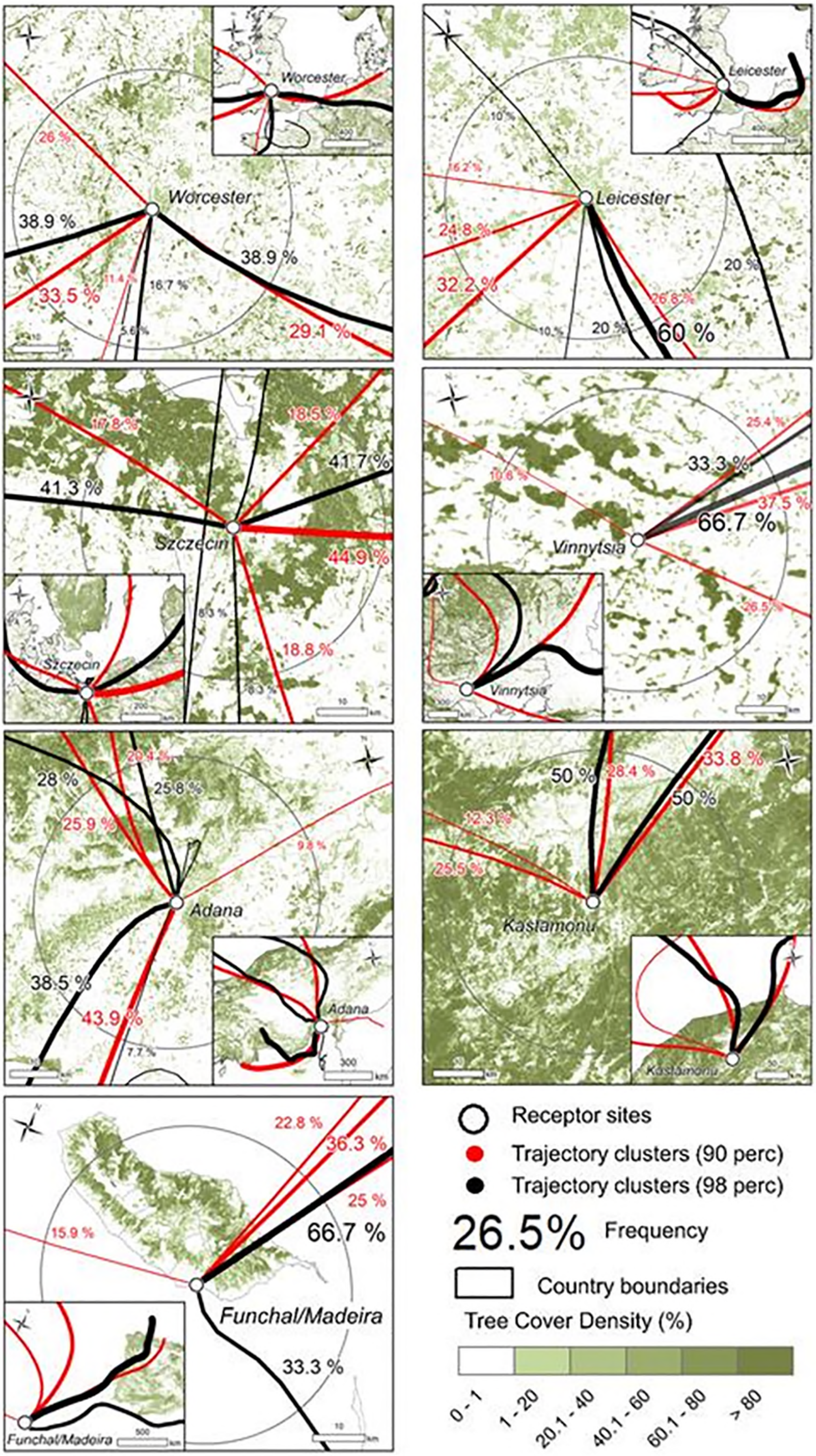


Fig. 7. Clusters of back trajectories associated with high spore concentration at study sites (90th and 98th percentile).

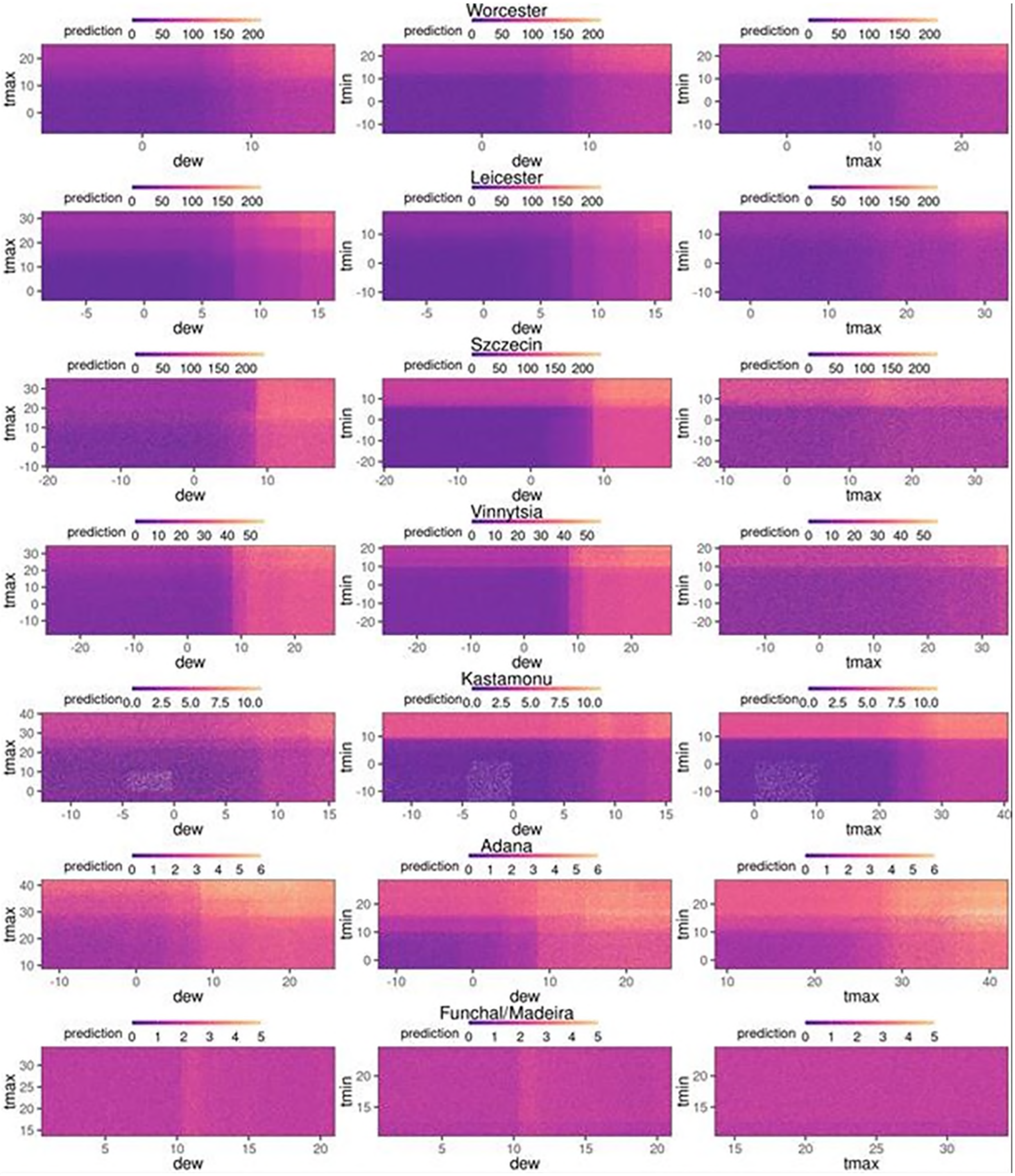


Fig. 8. Variable interactions between values of dew point temperature (dew), daily maximum temperature (tmax), and daily minimum temperature (tmin) for each of the random forest models.

summer, whereas in the autumn sources were located closer to the study site, although not in the immediate vicinity. A similar phenomenon was observed in Vinnytsia – spores recorded in autumn originated from a close proximity source, whilst in spring and summer the potential sources were found further away, however, they were responsible for higher spore concentrations. The high number of potential sources of fungi (areas with trees) close to sites such as Szczecin and Vinnytsia can complicate the production of reliable predictive models of *Ganoderma* spore concentration. In contrast, Worcester, Adana and Leicester, required lower wind speed to achieve higher concentrations of *Ganoderma* spores in all seasons, which may be explained by the close location of potential fungal sources. However, aerial photographs of Worcester (Google Maps 2019) show that local trees are scattered and there are only two small patches of forests located to the East of the study site. It is possible that *Ganoderma* spores trapped in Worcester may have originated from *Ganoderma* fruiting bodies living on local scattered trees during the summer, however, the two forest patches in the East (distance 3–5 km) may contribute to the autumn pool of *Ganoderma* spores recorded in

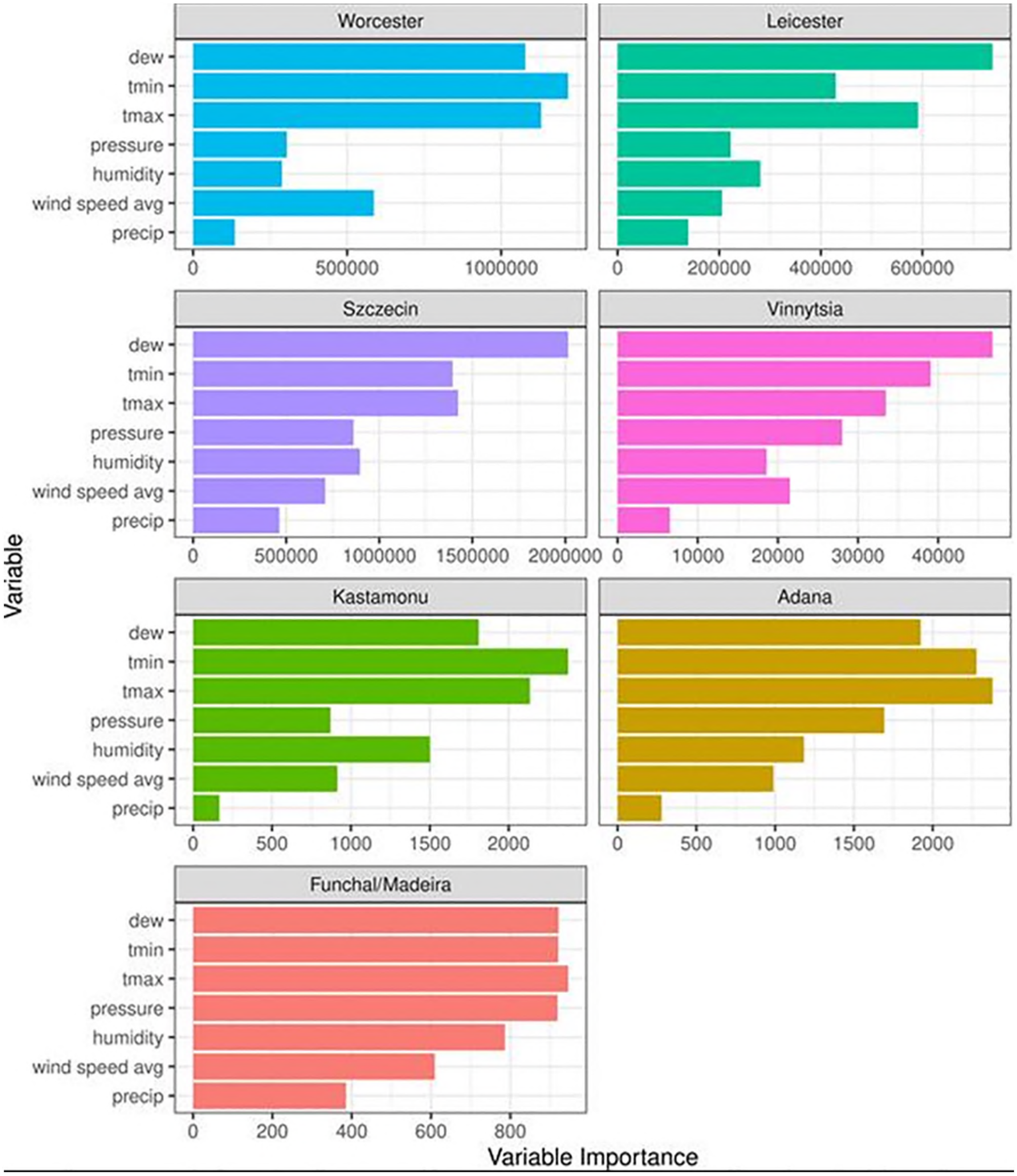


Fig. 9. Variable importance for each site model.

Worcester. This interpretation is consistent with typical use of bivariate polar plots for assessing the sources of anthropogenic air pollutants (Grange et al., 2016; Uria-Tellaetxe and Carslaw, 2014; Carslaw and Beevers, 2013).

Mean daily airborne *Ganoderma* spore concentrations appear to have a closer relationship with meteorological factors than *Alternaria* and *Cladosporium* spore concentrations. In a previous study using four of the study sites from this study (Leicester, Worcester, Szczecin and Vinnytsia, Grinn-Gofroń et al., 2019), symmetric mean absolute percentage error (SMAPE) was used to describe how well the regression models fit the *Alternaria* and *Cladosporium* airborne spore data. The lower the value of SMAPE, the better the model. The SMAPE values for Leicester were 0.73 for *Alternaria* and 0.54 for *Cladosporium,* compared to 0.30 for *Ganoderma* in this study. Values for Worcester were 0.75 and 0.53 for *Alternaria* and *Cladosporium,* respectively, and 0.22 for *Ganoderma.* For Szczecin SMAPE values were 0.69 and 0.60 for *Alternaria* and *Cladosporium,* respectively and 0.39 for *Ganoderma.* Finally, Vinnytsia had values of 0.6 and 0.56 for *Alternaria* and *Cladosporium*, respectively, and 0.48 for *Ganoderma,* even though there were only two years of *Ganoderma* daily mean concentrations compared to five years for *Alternaria* and *Cladosporium*. The random forest models for *Alternaria* and *Cladosporium* (Grinn-Gofroń et al., 2019), and *Ganoderma* (the current study) were developed based on local meteorological data. The lower SMAPE values in this study indicate that *Ganoderma* spores are more dependent on local atmospheric conditions than *Alternaria* and *Cladosporium,* which may indicate that local *Ganoderma* sources are more important for the recorded spore concentration than for *Alternaria* or *Cladosporium*. A local source for the *Ganoderma* spores is suggested in several polar plots (Worcester, Leicester, Adana, Vinnytsia in autumn). Based on our present findings, maximum spore concentrations were observed during very low wind speed conditions. During such mild winds, there is typically limited horizontal atmospheric transport, which

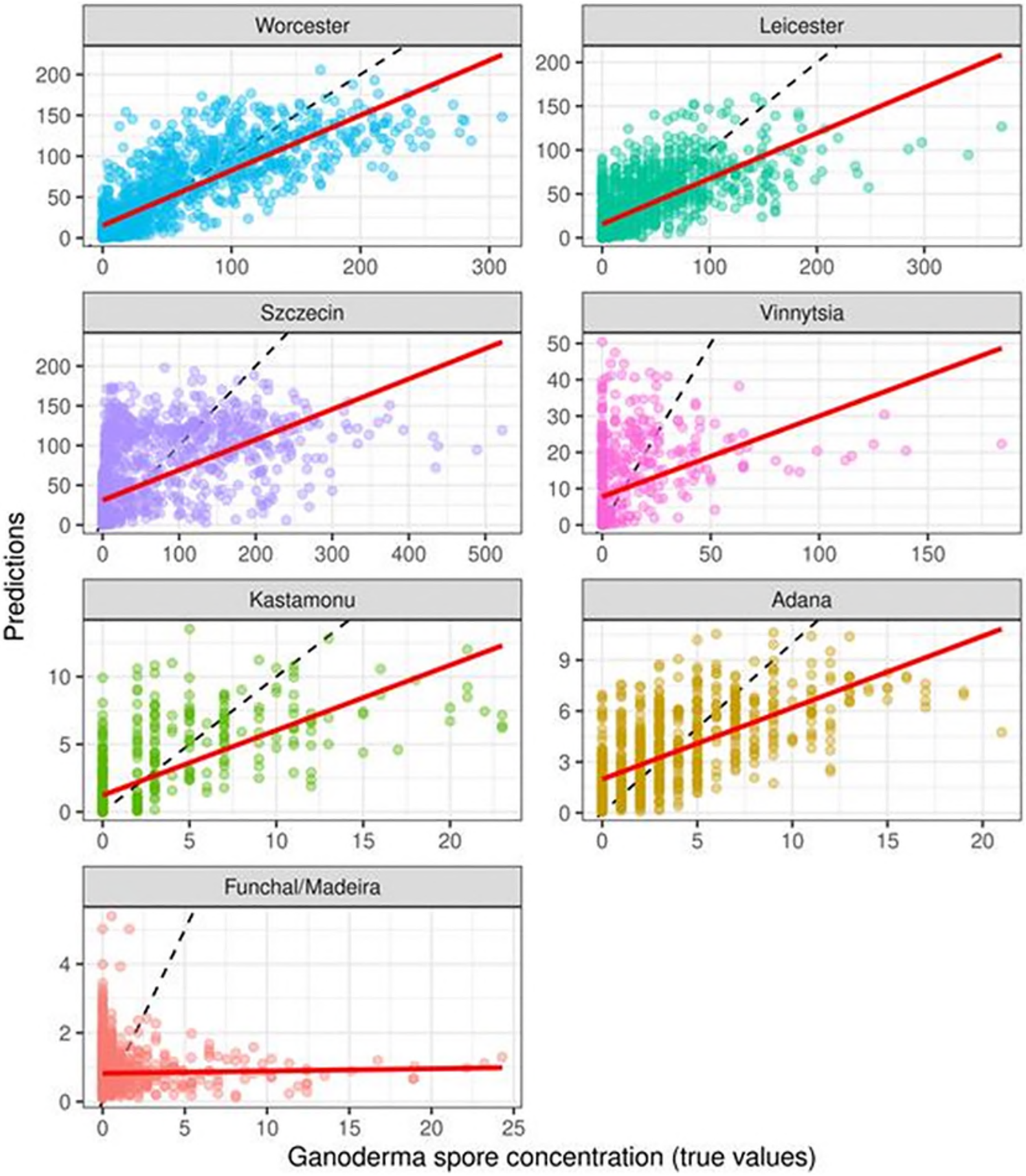


Fig. 10. Comparison of the models' predictions and true values in the testing set for each site. Linear regression lines are shown in red, while the dashed lines represent diagonals. The dashed lines represent diagonals and the red colour is used for the linear regression lines.

further supports that local sources and local meteorology together can determine spore concentrations at those locations. Furthermore, differences in *Ganoderma* spore concentrations between adjacent urban and rural areas (~ 40 km apart) and between urban and suburban sites (~5 km apart) confirm the local source nature of *Ganoderma* spores (Oliveira et al., 2010; Grinn-Gofroń et al., 2015). Therefore, we recommend that local *Ganoderma* spore concentration models need to be developed, and emphasize the importance of local studies on airborne *Ganoderma* spores to assess the risk of pathogen transmission. Nevertheless, although local sources are clearly important, in some cases the extremely high spore concentrations recorded at each site could have resulted from additional spores being transported from remote pathogen sources, as suggested in this study by the back-trajectory results for Funchal/Madeira and Leicester sites. The random forest models generated for Funchal/Madeira showed no predictive power, and there was no significant correlations between spore concentration and meteorological variables. This may suggest that the spores can be transported from outside the Madeira Island, although it is noted that the *Ganoderma* counts from the Madeira site are the lowest of all sites in this study, and lack of significance may be due to a lack of power due to low numbers. Comparing Leicester and Worcester, two sites geographically close to each other, the dominant directions of back-

Table 6
Average performance of the models for the training and testing sets based on calculated values of root mean square error (RMSE), coefficient of determination (R^2), and *symmetric mean absolute percentage error (SMAPE).*

Receptor site	Training sets			Testing sets		
	RMSE	R^2	SMAPE	RMSE	R^2	SMAPE
Worcester	35	0.67	0.23	33	0.71	0.21
Leicester	31	0.51	0.30	32	0.51	0.30
Szczecin	61	0.36	0.39	66	0.36	0.39
Vinnytsia	17	0.28	0.48	17	0.21	0.48
Kastamonu	3	0.49	0.36	2.7	0.55	0.33
Adana	2.8	0.42	0.30	2.7	0.44	0.29
Funchal/Madeira	2.3	0.01	0.74	2.1	0.01	0.74

trajectories associated with extremely high *Ganoderma* spore count were different. This suggests that, despite the close location, *Ganoderma* spores recorded in Leicester and Worcester likely have different sources, and this was most obvious during the extremely high spore concentration episodes.

Our results support observations by Sadyś et al. (2014), which state that *Ganoderma* spores may be transported over long distances (due to their substantially lower volumes when compared to well-flying *Alternaria* spores and *Betula* pollen) to distant and uninfected areas. This scale includes transport of bioparticles tens to thousands of meters above the surface of the Earth and this transport interacts with a suite of abiotic factors e.g. wind, rainfall, and UV light (Schmale and Ross, 2015). In the present study, we showed that *Ganoderma* spores are transported >900 km from the Iberian Peninsula to Madeira and, possibly also to Leicester from central Europe (> 300 km). At such distances, transport models can predict the movement of plant pathogens in the atmosphere, however, that does not mean the spores will be viable. Several studies have shown the radioprotective properties of *Ganoderma* spores against UV radiation. Some *Ganoderma* species possess peptidoglycans and polysaccharides capable of enhancing the cell repair process after gamma irradiation treatment in various cancer cells and animal models (Suárez-Arroyo et al., 2017). Such protective effects induced by UV radiation may ensure a higher viability of *Ganoderma* spores during long-distance transport, and as such, probably higher infection rates during deposition process on exposed hosts.

The study site in Funchal/Madeira is a unique case. Our data suggests that most of the sources of the *Ganoderma* spores were likely to be located on Madeira island, but at least 33% of the highest values could be attributed to long distance transport from the Iberian Peninsula (trajectories that come directly from the sea, Fig. 7). Several factors support this statement. The distance between Madeira archipelago and the closest mainland territory in Europe is about 1000 km, and between the archipelago and the closest point of the Western African coast approx. 600 km. The prevalent wind directions observed during the high *Ganoderma* spore concentrations in Madeira were coming from the north and northwest directions. The air masses blowing from the southwest originated over the Atlantic Ocean and should be free from any biological material (Urbano et al., 2011). The air masses arriving from the southeast, although they originated along the African continent, would not have contributed significantly towards the airborne spore concentrations in Madeira due to the lack of suitable pathogen host sources. Whilst 33% of the high *Ganoderma* values could be attributable to transport from the Iberian Peninsula, it must be emphasized that the highest concentrations (>98th percentile threshold; black lines in Fig. 7) should be considered as originating from the continent (Portugal, Spain). Compared to the other study sites, lower *Ganoderma* levels were detected in the atmosphere of Funchal/Madeira, which may be explained by the coastal proximity of the city and its insular position. Airborne particle concentrations tend to be lower in coastal stations compared to mainland sites due to the proximity of the sea (Belmonte et al., 2008), which may be due to less land mass for growth and development of fungi, and the sea preventing resuspension of particles (Sousa et al., 2015).

5. Conclusions

This is the first comprehensive study of airborne *Ganoderma* spores and thus *Ganoderma* pathogen abundance in Europe and SW Asia. We found significant differences in *Ganoderma* spore concentrations and season timing between four different climates and five biogeographical regions, and showed that the concentrations increased with increasing latitudes (up to 55°N). Airborne *Ganoderma* concentrations were positively associated with thermal variables at all sites apart from Madeira Island, although the correlations were lower in southern compared to northern parts of the study area. Significant correlations with local meteorological variables and high spore concentrations recorded at low wind speed indicated a local source of airborne *Ganoderma* spores, therefore we developed random forest models predicting spore concentration based on local meteorological data. In cases when predicted values substantially differed from observed spore concentrations, spore transport from remote source areas was hypothesized to be the cause. Back-trajectories calculated for days with high spore counts revealed the possibility of long-distance transport, as in the case from the Iberian Peninsula to Madeira Island (at least 33% of the concentrations >98th percentile). These long-distance spore transport incidents in Madeira are further supported by the lower performance of the random forest model there and the complete lack of significant relationships of spore concentrations with local meteorology.

It should be emphasized that, in sites with a substantial contribution of long distance transported spores, relying only on local meteorological data is insufficient to develop high-performance models predicting spore concentrations, even if sophisticated and robust methods as random forests are used for analysis. Therefore, before developing models predicting local spore concentrations, the likely origin of the spores should be investigated. If the origin of the spores is determined to be local, *Ganoderma* spore concentrations will significantly contribute as an additional bio-indicator of pathogen abundance and, thus, complement existing bio-indicators of local tree-health. We propose a new Pathogen Infection Level Index (PILI), which shows the relative pathogen abundance per 1 km^2 of area covered by host plants in a 30 km area of the sampling site. This index is a combination of spore concentration and pathogen hosts density and revealed that forests in the UK are much more infected with *Ganoderma* pathogens than the other study sites.

CRediT authorship contribution statement

AGG: Conceptualization, methodology, data curation, writing original draft, reviewing and approving final draft; PB, JN: methodology, writing original draft, reviewing and approving final draft; BB: Conceptualization, writing original draft, reviewing and approving final draft; CAS, VR, TC: provision of data, data curation, reviewing and approving final draft; IC, MS, CHP: provision of data, data curation, writing original draft, reviewing and approving final draft; CTH: reviewing and approving final draft; AD: writing original draft, reviewing and approving final draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary information

Supplementary information to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.148509.

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