Airborne DNA metabarcoding reveals that fungi follow predictable spatial and seasonal dynamics at the global scale

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Summary

Fungi are among the most diverse and ecologically important kingdoms of life, yet they are difficult to survey comprehensively. Consequently, the distributional ranges of fungi remain largely unknown, as do the ecological mechanisms that shape their distributions. To provide an integrated view of the spatial and seasonal dynamics of fungi across taxa and substrates, we implemented a standardised global aerial sampling of fungal spores in 47 sampling locations distributed across six continents, each location collecting two 24-hour samples per week for one to two years. The vast majority of OTUs were detected only within one climatic zone, and the spatio-temporal patterns of species richness and community composition were mostly explained by annual mean air temperature. Tropical regions hosted the highest fungal diversity with the exception of lichenized, ericoid mycorrhizal, and ectomycorrhizal fungi, which reach their peak diversity in temperate regions. All fungal guilds showed consistent and predictable patterns, with sporulation activity being shorter and more pronounced towards higher latitudes. Regarding spore size, we found asexual spore size decreasing but sexual spore size increasing with increasing distance from the Equator. The sensitivity in climatic responses was associated with phylogenetic relatedness, suggesting that large-scale distributions of some fungal groups are partially constrained by their ancestral niche. There was a strong phylogenetic signal in seasonal sensitivity, suggesting that some groups of fungi have retained their ancestral trait of sporulating only for a short period. Overall, our results show that the hyperdiverse kingdom of fungi follows globally highly predictable spatial and temporal dynamics, with seasonality in both species richness and community composition increasing with latitude. Our study reports patterns resembling those described for other major groups of organisms, thus making a major contribution to the long-standing debate on whether organisms with microbial lifestyles follow the global biodiversity paradigms known for macro-organisms.

Main

Global biodiversity of micro-organisms and the factors determining their distribution and activity remain poorly known despite their great ecological and economic importance in various ecosystems[1–3]. Recently developed technologies and analytical methods provide groundbreaking opportunities for the improved sampling of biodiversity and for unravelling how biodiversity is structured at large spatial and temporal scales[4–6]. These novel methods thus provide the opportunity to uncover previously unmapped biodiversity patterns of microbial communities and to discover the ecological processes that shape their diversity at global scale.

Fungi are among the most diverse and ecologically important living organisms. They mediate crucial processes in terrestrial ecosystems as decomposers of dead tissues (saprotrophs), mutualistic partners (ectomycorrhizal, ericoid, endophytic, and lichenized fungi), and pathogens of almost all terrestrial multicellular organisms. In spite of its importance, fungal diversity remains poorly explored[7]. Ca. 156,000 species of fungi have been scientifically described and recognized as valid to date[8] yet estimates of global species richness vary from 0.5 to 10 million[9,10]. Consequently, the global spatial and temporal distributions of fungi remain largely unknown. Recently developed DNA-based survey methods have greatly improved our knowledge of large-scale patterns of fungal diversity[11–15]. Soil sampling has been particularly popular, driven by an interest in the important functions of soil fungi as plant symbionts and nutrient cyclers[12,14,16,17]. Yet, it remains to be seen whether patterns in soil-borne fungi reflect patterns in other fungal taxa or indeed in general biodiversity[18]. In fact, studies targeting different fungal groups have produced disparate results. Tedersoo et al.[12] found that while overall fungal diversity in soil increases toward the Equator, this pattern does not apply to ectomycorrhizal fungi, which are most diverse in boreal and temperate regions. However, a meta-analysis of metabarcoding data from soil and root-associated fungi reported that total fungal diversity is higher at higher latitudes[15]. As further disparities, the diversity of leaf-associated aquatic fungi has been found to peak at mid latitudes[19], whereas the diversity of terrestrial leaf endophytes increases in tropical regions[20].

Local studies conducted in arctic and temperate environments have shown that fungal activity presents pronounced seasonal variation[21–25], whereas a study conducted in the tropics showed no such variation[26], suggesting that seasonality may be latitude-dependent. However, most large-scale surveys of fungi have included limited temporal replication of the same locations, leaving a major knowledge gap about their global seasonal dynamics. The few larger-scale studies that involve temporal replication include meta-analyses on heterogeneous datasets[27,28] or historic records of fruiting-body occurrences[29]. The general conclusion drawn from these studies is that the composition and biomass of fungal communities follow the phenology of their hosts and seasonal changes in precipitation and temperature. Hence, the lack of controlling for effects of local seasonal variation may have also confounded some conclusions on the global spatial patterning of fungal diversity.

A recent methodological breakthrough for the survey of fungi consists of sampling fungal spores (and other airborne particles, which may include fungal structures such as hyphae and soredia) from the air, followed by DNA sequencing and sequence-based species identification[30]. Air sampling has revealed higher diversity and stronger ecological signals in community composition than soil sampling[31]. Recently, the feasibility of air sampling to investigate global patterns of fungal diversity was demonstrated[32]. Since this method captures airborne fungal spores, it depicts reproduction and dispersal at high temporal resolution. Here, we report on the application of air sampling for fungal spores in a new initiative called the Global Spore Sampling Project (GSSP)[33]. The GSSP involves 47 sampling locations distributed across all continents except Antarctica, each location collecting two 24-hour samples per week over one year or more (Fig. 1AB). Although the European temperate region is

overrepresented in the data, the sampling locations also include arctic, temperate, and tropical areas from other regions (Fig. 1A). As described in detail in Ovaskainen et al.[33], we targeted DNA sequencing to a part of the nuclear ribosomal internal transcribed spacer (ITS) region, which is the universal molecular barcode for fungi[34]. However, we note that for some fungal taxa other markers are better suited, such as the nuclear SSU rRNA gene fragment for arbuscular mycorrhiza [35]. We applied a DNA spike-in to generate quantitative estimates of change in the amount of DNA[32]. To convert sequence data into species data, we denoised the sequence data to form amplicon sequence variants (ASVs)[36], applied probabilistic taxonomic placement using Protax[37,38], and used constrained dynamic clustering to group these ASVs into species-level operational taxonomic units (OTUs)[39]. These OTUs were then classified into previously known vs. unknown taxa (see Ovaskainen et al.[33] for details) at all taxonomic levels from phylum to species. To link spatio-temporal patterns in species composition to the ecological drivers behind them, we complement here the fungal species data derived from DNA analyses with environmental and trait data (Fig. 1C). Trait data was compiled using guild and spore size data from several sources (see *Methods*) and environmental data includes time- and site-specific climatic data from the Copernicus Climate Change Service (C3S) Climate Data Store[40].

The fully standardized sampling of fungi at unprecedented spatial and temporal scales enabled an integrated analysis of the ecological drivers behind the spatial and seasonal patterns of global fungal diversity. To achieve this, we first examined how fungal communities differ among the major bioclimatic zones and how much climatic variables explain such differences. We expected to find a clear differentiation in the community composition among the main bioclimatic zones, although we expected the spatial differentiation of airborne spores to be less pronounced than previously reported in soil-based studies[12,15], as microscopic propagules can be expected to mix more readily in air (although the samples were collected close to the ground, and often within habitats with limited air flow compared to open areas). Second, we examined how global seasonal patterns of airborne fungi vary with latitude and weather conditions. We expected higher levels of seasonality in species richness and amount of fungal DNA towards higher latitudes, where resources are available for shorter periods of time, and where local weather conditions may have a stronger effect on reproductive phenology[29]. Finally, we examined whether the ecological drivers shaping the composition of fungal communities translate into predictable variation in species-level traits. To this end, we asked whether species' responses to climatic and seasonal factors are phylogenetically and functionally structured. As relevant traits, we considered fungal guild[12,41] and spore size[42,43]. We expected to find higher seasonality in host-dependent guilds (pathogenic and symbiotic fungi) than in free-living guilds (saprotrophs), but that spatial patterns of seasonality should be consistent across guilds. We expected to find predictable seasonal variation in spore size, reflecting taxonomic turnover throughout seasons. Finally, because earlier research has found phylogenetic niche conservatism reflected in the large-scale biogeography of soil fungi[44], we expected to find a phylogenetic signal on the responses of air-fungal communities to the environmental factors that influence their large-scale distributions.

Results

Climatic effects on spatial distributions

Our samples of airborne fungi include all major taxonomic groups (Fig. 2A). However, some fungal groups are overrepresented, and others underrepresented as compared to previously reported patterns among soil fungi (Fig. 2B). The air samples are particularly rich in plant pathogens, general saprotrophs, and wood saprotrophs, while other common groups such as ectomycorrhizal and lichenized fungi are relatively poorly represented.

Among the 27,954 species-level OTUs detected in this study, only 3.5% were observed in all three climatic zones (Fig. 2C). As expected, sampling locations in the polar-continental zone shared the fewest species with sampling locations in the tropical-subtropical zone. However, most order-level taxa were present in all three climatic zones (Fig. 2C). Such an increase in taxonomic overlap among regions with increasing taxonomic rank is also reflected by the stability of the proportions of species belonging to different phyla, with the proportion of *Ascomycota* species being 55%-59% and the proportion of *Basidiomycota* species being 38%-43% within each of the three climatic zones.

Among the ten most prevalent genera in our data (Table 1), seven belonged to the phylum *Ascomycota* (out of which four to the order of *Pleosporales*) and three to *Basidiomycota* (out of which two to the order *Tremellales*). Overall, the three most prevalent genera were the ascomycetes *Cladosporium*, *Ascochyta,* and *Alternaria*. Genera that were in the list of the ten most prevalent genera in all three climatic zones were the ascomycetes *Cladosporium, Ascochyta, Alternaria,* and *Aureobasidium,* and the basidiomycetes *Cryptococcus.*

Species composition of local fungal communities was most strongly affected by the mean annual air temperature (MAT) of the site, which when used as the sole environmental predictor explained 78% of the deviance in the ordination space (Fig. 2D). By comparison, mean annual precipitation (MAP) at the site explained 42% and the mean aridity index (MAI) 25%, while mean annual wind speed (MAW) – which could have added to the mixing of spores to the atmosphere – did not explain much deviance (22%). We then compared the relative importance of differences in MAT (selecting for species with similar environmental preferences) and differences in space (likely reflecting the potential for dispersal between two sites, as well as other environmental conditions not considered in the analyses). As spatial and environmental distances were correlated, we disentangled the effects of these two by partitioning variance in community dissimilarity. We found the direct contribution of spatial distance to be 13%, the direct contribution of climatic distance (derived from MAT) to be 7%, and their shared contribution to be 21%. When repeating the analyses with climatic distances derived from MAP (or MAI), the direct contribution of spatial distance was 29% (27%), the direct contribution of climatic distance 2% (0%), and their shared contribution to be 6% (7%). Hence MAT, rather than MAP or MAI, turned out to be a key driver in determining the large-scale distributions of air-borne fungi.

Latitudinal effects on seasonal patterns and weather responses

Within the airborne spore communities, both OTU diversity and DNA amount increased towards the Equator (Fig. 3AB). This result was robust with respect to seasonality, as tropical-subtropical sites hosted greater diversity of fungal species and greater amounts of DNA than temperate and polar-continental sites at all times of the year (Fig. 3AB). In terms of temporal patterns, seasonal variation in both DNA amount and species richness increased as expected with distance from the Equator, being the highest in the Arctic (Fig. 3AB). During the winter at the polar-continental sites, few air samples had detectable levels of fungal DNA, and the amount of DNA and the number of species showed a sharp peak during the growing season (Fig. 3AB). In samples from temperate sites, fungal DNA was found throughout the year, but its amount increased markedly from spring to autumn, with the lowest values in winter. In tropical-subtropical sites, the fungal DNA amount was high throughout the year. The composition of the fungal community followed the same pattern: in the polar-continental sites, there was more turnover in species composition from spring to autumn than there was in the tropical regions during a comparable period (Fig. 3C). However, a comparison of linear mixed models fitted to the data on DNA amount and species richness (see *Supporting Information*) showed that while the effect of seasonality generally increased with latitude, the exact timing and amplitude of seasonal variation also had a site-specific component. Thus, while we found that the phenology of fungal spore

production is largely consistent within each latitudinal zone, the site-specific component suggests that local factors also play a role in controlling the timing of sporulation. Regarding the effects of weather, we found that both the amount of DNA and the observed species richness were generally higher for warm and windy sampling days (see *Supporting Information*). While most trophic guilds followed the same pattern as overall species richness, endophytes and lichenized species showed higher richness on days with little precipitation. These results were consistent across all latitudes in the sense that, for all but one response variable, the best supported model was that of constant weather effects (model W1, see *Methods*).

Phylogenetic and functional structure

The proportion of fungal occurrences for which we had at least family-level information about asexual (respectively, sexual) spore volume varied between 72%-74% (respectively, 68%-70%) among the three climatic zones. However, species-level information was more frequent in the polar-continental and temperate zones (7-8% for asexual and 12%-13% for sexual spores) than in the tropical zone (8% for asexual and 5% for sexual spores). Assuming that the detected species were in the asexual stage, spores were the largest in the tropical-subtropical zone, whereas assuming the spores were in the sexual stage, spores were the largest in the temperate and polar-continental zones (Fig. 3). In temperate and polar-continental zones the spore sizes showed marked seasonality, the mean asexual spore size peaking in the autumn whereas the mean sexual spore size peaking in the spring (Fig 3). This difference between asexual and sexual spores prevailed across all species and within *Basidiomycota*, but not within *Ascomycota* (*Supporting Information*).

Following the main patterns found for the total fungal species richness, all fungal guilds exhibited strong seasonality in species richness in the polar-continental and temperate zones (*Supporting Information*). Most guilds were more abundant in the tropics even during the peak season, with the exceptions of ericoid mycorrhizal, ectomycorrhizal, and lichenized fungi, which were most abundant in the temperate region (*Supporting Information*). To determine how phylogenetic relatedness of fungal species affects global distribution and sporulation patterns, we performed an HMSC analysis[45] where we used as a proxy for the phylogenetic tree a taxonomy of the OTUs at the levels of kingdom, phylum, class, order, family, genus, and species[33]. Even if this model included only the MAT and seasonality as predictors, it reached a high explanatory power (averaged over the species, mean AUC=0.90, mean Tjur's R^2=0.16). This analysis revealed variation in the strength of the phylogenetic signal among how species responded to focal environmental predictors. Among the species-level responses to environmental conditions, climatic sensitivity showed a moderate phylogenetic signal (Pagel's lambda=0.28; p=4E-12), as illustrated by groups of highly related species that showed high or low climatic sensitivity (the red and blue bands in Fig. 4A in the climatic sensitivity column), e.g. the orders *Agaricales* and *Helotiales* beinglittle influenced by climate (Fig. 4B). In contrast, the optimal MAT of the site at which the probability of species occurrence is predicted to be maximized did not show any phylogenetic signal (Pagel's lambda=-0.01; p=0.81). Thus, some species within the same group preferred colder temperatures, whereas other species preferred warmer temperatures (Fig. 4). When we measured the seasonal sensitivity of the species by the proportion of variation in species occurrence explained by latitude-dependent seasonality, we observed a strong phylogenetic signal (Pagel's lambda=0.39; p=2E-16). In particular, species within the orders *Polyporales* and *Erysiphales* showed pronounced seasonal dynamics, whereas the orders *Agaricales*, *Tremellales,* and *Chaetothyriales* showed low sensitivity to seasonality (Fig. 4C). Regarding the timing of the seasonal peak, we did not observe any phylogenetic signal (Pagel's lambda=-0.04; p=0.80). However, this lack of a signal may be partially explained by the fact that few species showed sufficient seasonality for the time of the optimal season to be defined (Fig. 4A).

Discussion

Our results show that fungi follow predictable latitudinal diversity gradients that resemble other major groups of organisms[46]. This finding represents a major contribution to the long-standing debate over whether organisms with microbial lifestyles follow the global biodiversity paradigms known for macro-organisms[47,48]. Our results are consistent with an increasing body of literature showing that, like macroorganisms, microbial communities are spatially structured at large scales[49,50,12]. Interestingly, only a small minority of all species-level OTUs detected in our study were observed in all three climatic zones. These widespread species were Ascomycota genera that have previously been found to be highly common in soil[51] and in air[13]. However, the vast majority of OTUs were detected only within one climatic zone, and the spatio-temporal patterns of species richness and community composition were highly constrained by climatic conditions. Although previous large-scale studies of soil fungi have found clear effects of the climate on community composition[12,15], the fact that in our data MAT explains most of the variation in the distributions of fungi is striking, especially given that our data are based on the dispersal stage of airborne spores. Likewise, previous studies on soil fungal communities have found that biomes, as defined based on MAT and MAP, explain a major part of their global distributions[12].

A major novelty in our data is the high level of temporal replication, enabling a first global analysis of climatic effects on the phenology of fungal reproduction. Seasonality in the amount of DNA and the species richness of air-borne fungi increased with increasing distance from the Equator. Therefore, seasonality was the highest in arctic climates. Less trivially, we found that seasonal turnover in community composition increased with increasing distance from the Equator, even if tropical regions also show high seasonality (e.g., rainy versus dry periods). In line with this finding, a long-term study of airborne fungi in the tropics revealed no seasonality[26]. In addition to the seasonal effects, our study also highlights the importance of the short-term local weather conditions on the diversity or sporulation phenology of airborne fungi. The results showed that airborne fungal species richness peaks during warm and windy sampling days. This result coincides with previous observations that temperature influences the fungal reproductive phenology[29] and that spore release peaks when the wind speeds are high[52].

Comparison of trophic guilds showed that not only the overall species richness, but also most guilds, were most abundant in the tropics, with the notable exceptions of lichenized, ericoid mycorrhizal, and ectomycorrhizal species. This result is in line with the patterns found for soil fungi by Tedersoo et al.[12], who also found a general increase towards the tropics, except ectomycorrhizal fungi which were most diverse in boreal and temperate regions. While the higher diversity of these fungal groups at higher latitudes could be related to greater knowledge gaps of their diversity in the tropics, this result could also reflect the distribution and diversity of their host species[53]. To minimize the possibility of such an artefact, we borrowed information among taxonomic levels for the functional classifications, making a compromise between minimizing bias (by only including not only the minority of OTUs reliably classified to species but also genus- or family-level classifications) and minimizing the noise of false classifications (by not borrowing information from ranks higher than family). In terms of seasonality, many earlier studies have reported longer sporulation and reproductive seasons in warmer regions for specific parts of the world and for particular groups of fungi[29,54]. Our results generalize these earlier findings to the global distribution of the entire fungal kingdom: all fungal guilds showed consistent and predictable patterns, with sporulation activity being shorter and more pronounced towards higher latitudes. Regarding spore size, we found asexual spore size decreasing but sexual spore size increasing with increasing distance from the Equator. During the main reproductive season in the temperate and polar-continental zones, we further found asexual spore size to increase but sexual

spore size to decrease during the season. The latter result, which is consistent with the earlier finding of Kauserud et al.[55], is partially generated by ascomycetes having on average larger sexual spores[56] and earlier sporulation phenology than basidiomycetes[30]. To our knowledge, our study is the first to report opposing spatial and temporal patterns between sexual and asexual spores, suggesting contrasting evolutionary forces behind the size of these two types of dispersal propagules. This result may also relate to the opposing environmental triggers of sexual and asexual spore production, with sexual reproduction occurring especially under unfavourable environmental conditions, such as at the end of the growing season[57,58].

In terms of the processes that structure ecological communities, we may distinguish between the ultimate evolutionary processes that give rise to species and determine their traits, and the proximate contemporary ecological processes that shape the assembly of communities[59,60]. Our data on global aerial communities shed light on both aspects. In terms of evolutionary processes, fungi exhibited a strong niche conservatism regarding sensitivity to dispersal seasonality, and moderate conservatism for sensitivity to climatic conditions. These results suggest that fungi have continuously adapted to climatic conditions, rather than being stuck in their ancestral climatic niches. This interpretation is supported by the fact that while most species showed climatically restricted distributions, the majority of genera and the vast majority of orders were detected in all three climatic zones. The high phylogenetic signal in dispersal seasonality was driven by certain taxonomic groups. In particular, *Polyporales* showed a high level of seasonality for almost all species. Our findings suggest that *Polyporales* have been especially adapted to seasonal climates, as their morphological and physiological traits support high spore production for a brief portion of the fruiting season. Among the ecological selection processes, we showed that environmental drivers, in particular MAT, play a major structuring role on fungal communities at large scales.

While substrate-specific sampling will mainly reveal the DNA of mycelia locally present in the focal substrates, aerial DNA will provide an integrated view of the airborne propagules from all substrates. As evidence, all trophic guilds supported by the guild database we used were represented in the data. However, some functional groups were better represented than others, highlighting the importance of surveying different complementary substrates to gain a complete view of fungal diversity. Importantly, the proportional representation of fungal taxa in the air is clearly affected by their dispersal strategy In particular, plant pathogens, saprotrophs, and wood saprotrophs were very abundant in our data (Fig. 2B). In contrast, ectomycorrhizal fungi, not all of which produce conspicuous and abundant above-ground reproductive bodies, contributed only a small fraction of airborne spores globally (Fig. 2B). This points to other dispersal means, e.g., via mycophagous animals, as being important for this functional group. Alternatively, the relative scarcity of airborne spores from ectomycorrhizal fungi may be due to the trade-off between spore size and number[43]. As many ectomycorrhizal fungi develop large spores, they are expected to produce fewer spores, which in turn would appear less frequently in airborne data. Note that typically, both large and small spores are unicellular and contain a single nucleus.

Our results demonstrate that the sampling of airborne DNA can provide a synthetic, cumulative view of global fungal diversity across individual substrates. This integrated view provides a huge step forward in the understanding of the distributions and dynamics of the whole fungal kingdom, which has lagged behind research in other major organism groups, partially due to the methodological difficulties in surveying fungi comprehensively. Overall, our results reveal highly predictable patterns of spatial and seasonal variation in airborne fungi and suggest that the drivers of microbial community assembly are largely similar to those determining the assembly of macro-organisms. Our results highlight the role of temperature as an underlying driver of fungal dynamics, with fungal diversity

increasing with warmer climates and sporulation activity increasing with warmer days. This finding suggests that global climate change with generally warming climates will have a major role in restructuring fungal communities.

Table 1. Most common genera found in the GSSP data. The table shows the prevalence (%) of each genus, computed as the fraction of samples in which it was detected, as well as the ranking of the genus in terms of its prevalence. The prevalences and rankings are shown for all samples, as well as separately for the samples from each of the three climatic zones. Genera that rank in the top ten are highlighted, and only genera that ranked in the top ten in at least one of the climatic zones are included.

Climatic zone			**All**		**Polar-continental**		**Temperate**		**Tropical-subtropical**	
Phylum	**Order**	**Genus**	**%**	**Rank**	**%**	**Rank**	**%**	**Rank**	**%**	**Rank**
Ascomycota	*Capnodiales*	*Cladosporium*	53	1	36	1	60	1	68	1
Ascomycota	*Pleosporales*	*Ascochyta*	40	2	19	3	50	2	52	2
Ascomycota	*Pleosporales*	*Alternaria*	34	3	18	4	43	3	40	4
Basidiomycota	*Tremellales*	*Cryptococcus*	33	4	22	2	39	4	38	6
Ascomycota	*Dothideales*	*Aureobasidium*	28	5	12	10	38	5	35	9
Basidiomycota	*Polyporales*	*Trametes*	28	6	12	11	35	6	38	5
Ascomycota	*Pleosporales*	*Phaeosphaeria*	25	7	15	7	32	8	27	13
Ascomycota	*Pleosporales*	*Phoma*	22	8	09	28	26	13	36	7
Basidiomycota	*Tremellales*	*Dioszegia*	22	9	16	6	32	7	15	48
Ascomycota	*Chaetothyriales*	*Capronia*	22	10	13	8	29	9	24	18
Basidiomycota	*Cantharellales*	*Sistotrema*	21	11	16	5	25	14	19	29
Ascomycota	*Helotiales*	*pseudogenus*	19	16	13	9	28	12	13	65
Basidiomycota	*Filobasidiales*	*Filobasidium*	19	17	11	16	29	10	14	59
Ascomycota	*Pleosporales*	*Periconia*	20	14	07	49	18	32	41	3
Basidiomycota	*Polyporales*	*Phlebia*	20	12	10	21	21	20	36	8
Ascomycota	*Capnodiales*	*Pseudocercospora*	14	25	04	121	12	74	33	10

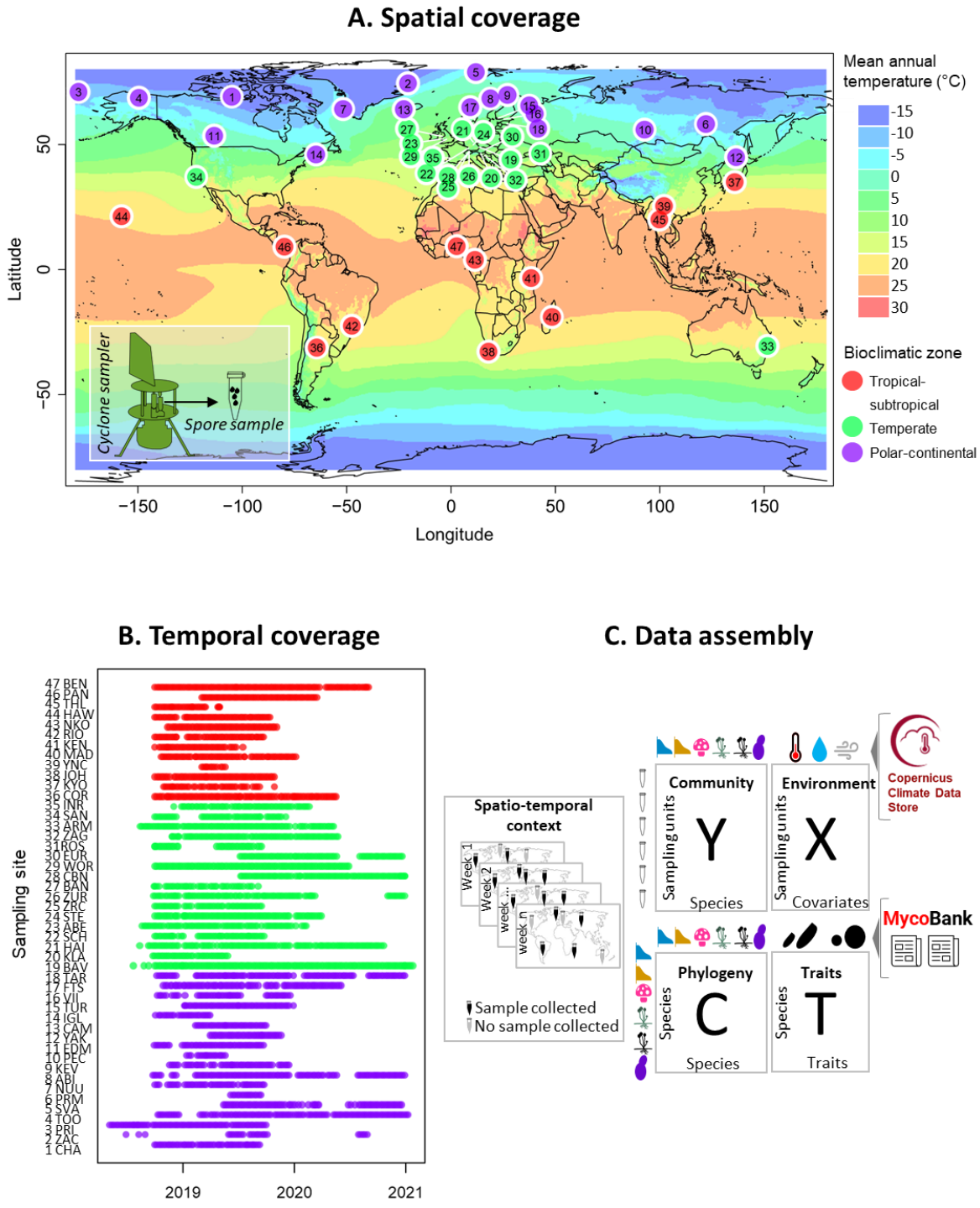


Figure 1. Global Spore Sampling Project (GSSP) study design and data. (A) The sampling sites include locations in the tropical-subtropical (red), temperate (green), and polar-continental (blue) climatic zones, shown here superimposed on a map of the mean annual air temperature (MAT). Airborne fungal samples were collected by a cyclone sampler, each sample consisting of fungal spores filtered from 24 m^3 of air during the 24hr sampling period. (B) The study design included weekly samples over one to two years, with some variation among sites due to logistical constraints. (C) The data generation pipeline produced data matrices that were used for the ecological analyses: the spatial and temporal coordinates of the samples, species occurrence data (Y), climatic and weather data (X), fungal guild and spore size data (T), and taxonomic affiliations as a proxy for phylogenetic relationships (C).

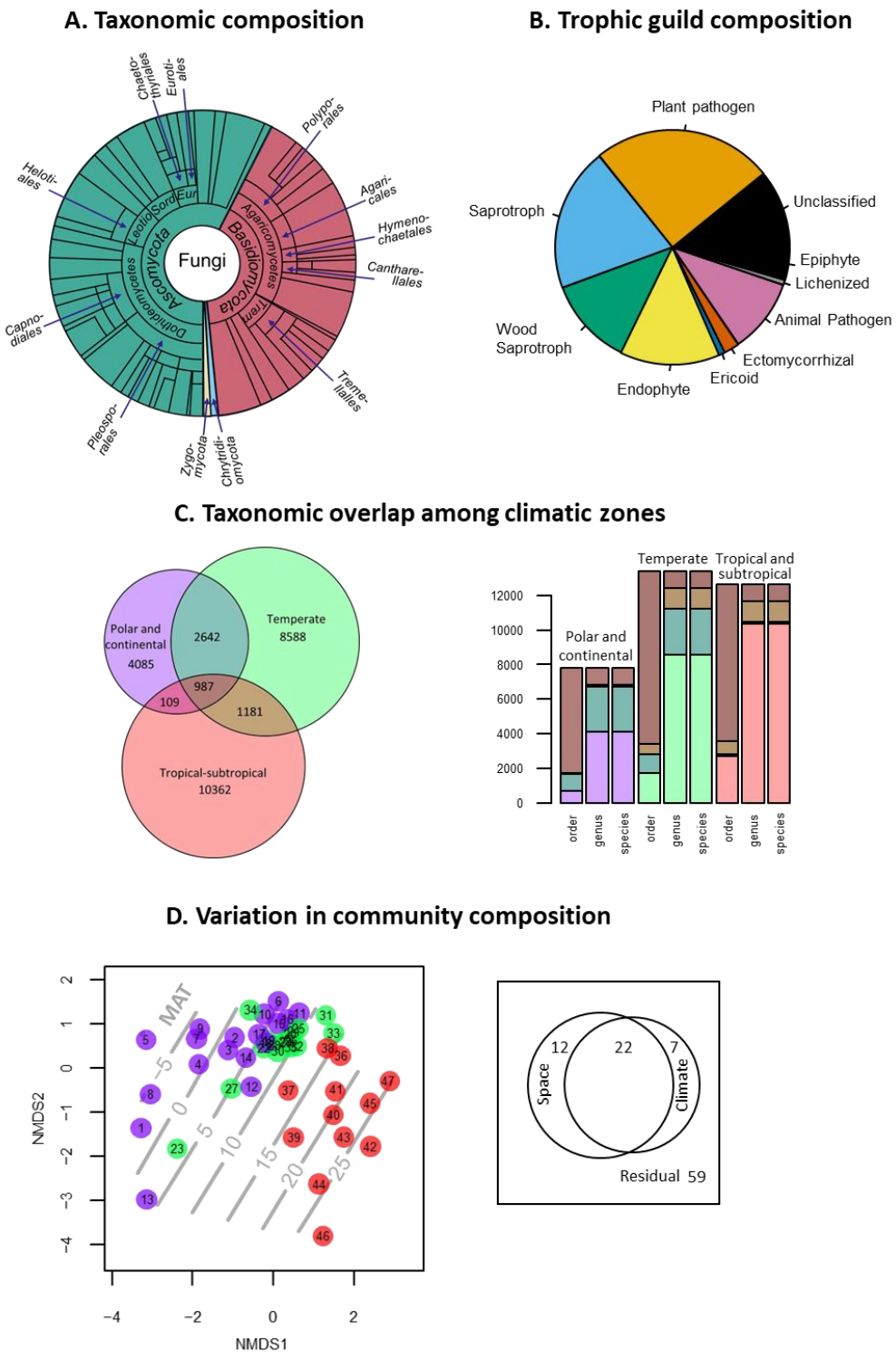
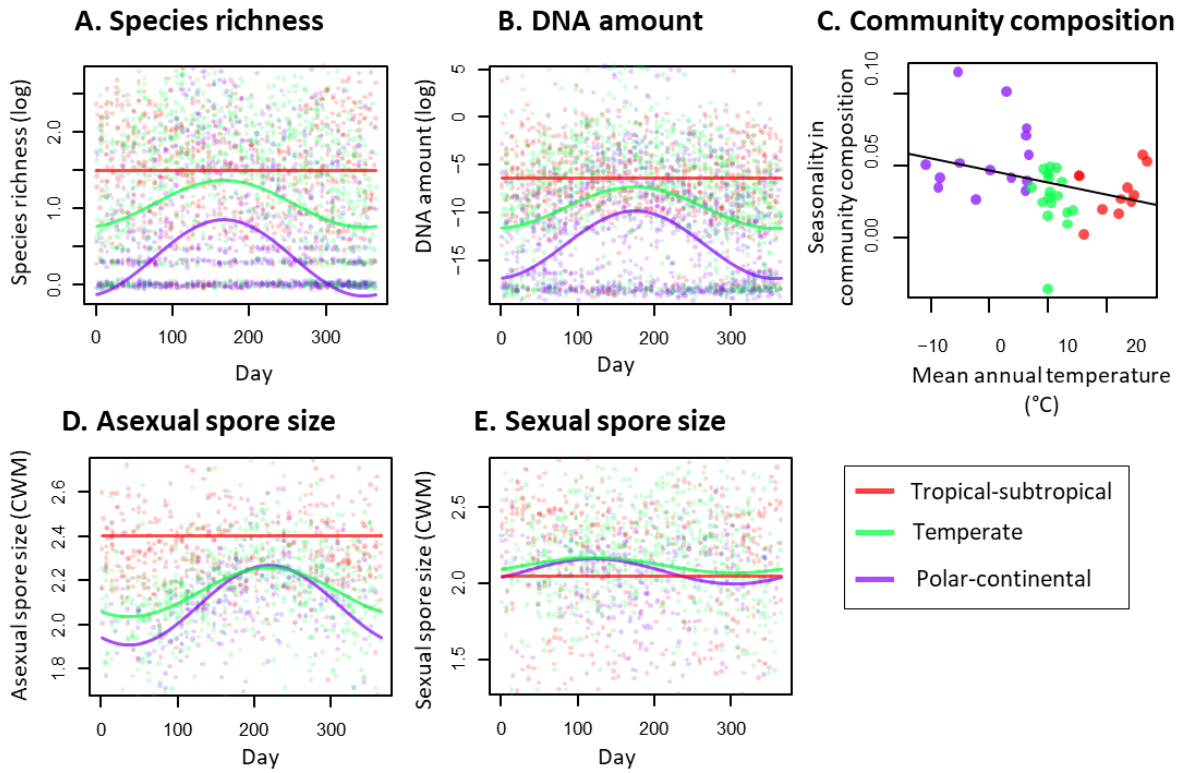


Figure 2. Taxonomic, trophic, and spatial variation in airborne fungal diversity. (A) Taxonomic and (B) trophic guild composition of the data as weighted by prevalence, i.e., the number of samples from which the taxon was found. Taxonomic composition is shown for the levels of phylum, class, and order. Trophic guild composition is shown based on Aguilar-Trigueros et al.[56]. (C) The Venn diagram shows the number of OTUs that were distinct or shared among the three major climatic zones included in our study. Note that shown are raw numbers that do not control for the somewhat smaller sampling effort in the tropical-subtropical zone (Fig. 1B). The bar chart shows the number of OTUs that belonged to a genus or order that was either distinct or shared among the three climatic zones. Note that the species-level bars replicate the patterns shown in the Venn diagram. (D) Variation in the composition of the fungal community among sites illustrated in the NMDS ordination space, with contour lines representing the MAT (°C) of the site. The circles partition the variation in community dissimilarity into distinct and shared effects of spatial and climatic distance.



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519 **Figure 3. Seasonal variation in airborne fungal diversity.** The lines in the panels for species richness (A), DNA amount (B),
520 and community weighted mean of asexual (D), and sexual (E) spore size show the predictions of the best supported linear
521 mixed models (see *Methods*) for tropical-subtropical (red), temperate (green), and polar-continental (blue) climatic zones.
522 Note that the predictions are shown for the Northern Hemisphere, whereas for the Southern Hemisphere the seasonal
523 patterns would be mirror images. For community composition (C), seasonality for each site is defined as the difference in
524 the Jaccard index between samples taken in the same season versus samples taken in different seasons (see *Methods*). The
525 dots in (ABDE) that show the raw data have been slightly jittered to reveal overlap. The line in (C) shows that seasonality in
526 community composition was higher at colder sites (linear regression, p=0.04).

527

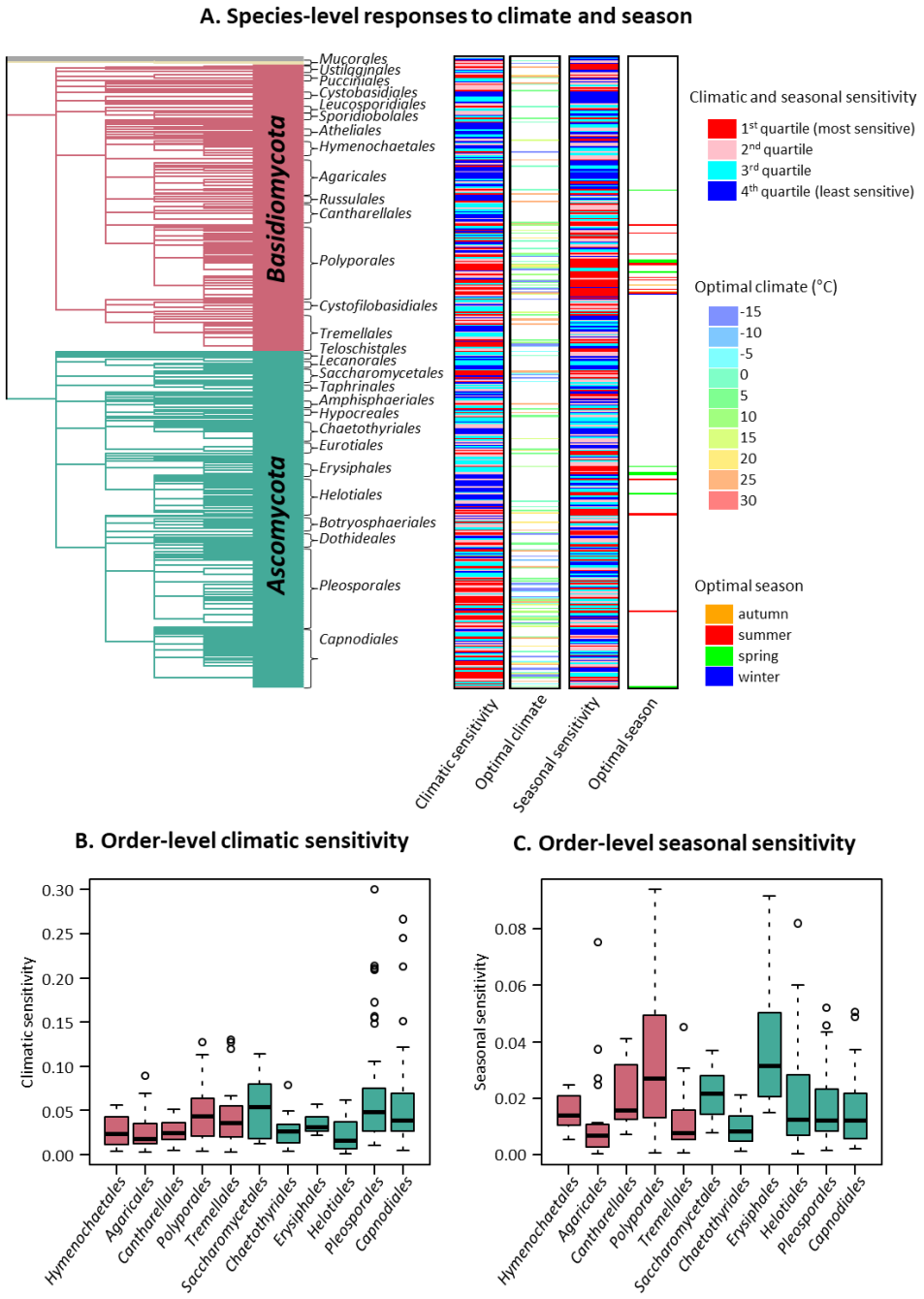

Figure 4. Phylogenetic signal in climatic and seasonal variation. The results are based on a joint species distribution model (JSDM) fitted to data on the most common 485 species in our data. The columns in (A) quantify variation in climatic sensitivity, optimal climate, seasonality sensitivity, and optimal season among species. For climatic and seasonal sensitivity, the colours show proportion of variance explained by the second-order polynomial of the MAT of the site (for *climatic sensitivity*) and by the periodic functions of sin(2π*d*/365) and cos(2π*d*/365), where *d* is the day of the year (for *seasonal sensitivity*), coded as blue, cyan, pink, and red for the four quantiles, from lowest to highest. For *optimal climate*, we show the MAT at which the second-order polynomial of the MAT was maximized (i.e., the point at which a further increase in MAT will turn from an estimated increase to an estimated decrease in species occurrence) in the colour scale of the world map in Fig. 1A. Similarly, for the *optimal season*, we show the day of the year at which the estimated occurrence of the species will peak, with colours coded as blue for winter (December-February in the Northern hemisphere; for the Southern hemisphere we assumed a six-month difference in seasonality) green for spring (March-May), red for summer (June-August), and orange for autumn (September-November). For cases in which the climatic sensitivity was too low to determine optimal climate and for which seasonal sensitivity was too low to determine, optimal seasons are shown in white. The boxplots in (BC) show the distributions of climatic and seasonal sensitivities for those orders that were represented in these analyses by at least 10 species. For the list of taxa included in the analysis, see *Supporting Information.*

Methods

Study design, DNA extraction, sequencing, and bioinformatics

For full details on study design and sample collection, DNA extraction and sequencing, bioinformatic processing, as well as technical data validation, see Ovaskainen et al[33]. Here we summarize these steps.

The study design consists of 47 sampling sites, each equipped with a cyclone sampler (Burkard Cyclone Sampler for Field Operation, Burkard Manufacturing Co Ltd; http://burkard.co.uk/product/cyclone-sampler-for-field-operation). The sampling sites were selected to represent local natural environments, where intensive, continuous sampling was possible. The cyclone samplers collected particles >1µm in size from the air directly into a sterile Eppendorf vial, with average air throughput of 23.8 m^3 during each 24-hour sampling period. Prior to the start of our global sampling, a field test was performed to evaluate the quantity of fungal DNA collected over different time frames. We also included field blanks handled with and without gloves, in which the sampler was not activated, and the Eppendorf vials were removed after one minute and sealed. As a result of the field tests, we selected a 24-hour sampling period and instructed the participants to handle the samples with gloves and to clean the cyclone parts monthly.

We amplified the ITS2 region using the polymerase chain reaction (PCR) for 20 cycles with fusion primers ITS_S2F[61], ITS3, and ITS4[62] tailed with Illumina adapters, and sequenced them on Illumina MiSeq. In the MiSeq runs, we included two sets of negative control samples, introduced at the DNA extraction step and at the PCR step, respectively. Of the 99 total negative control samples, 89% (88 samples) did not yield any reads of fungal origin. The remaining 9 negative control samples included a few fungal reads (relative to the study samples) of relatively common OTUs, suggesting infrequent cross-contamination. To test the robustness of the results with respect to such cross-contamination, we repeated three of the main analyses (variation in overall species richness, variation in guild-specific specific species richness, and joint species distribution modelling) with data that we purposely contaminated with the observed level of cross-contamination. To do so, we added to the OTU reads of each field sample the OTU reads of a randomly selected negative control sample. We replicated the cross-contamination simulation for ten independent replicates, with results being almost identical to results obtained to the original data (see *Supporting Information*). To quantify the amount of fungal DNA, we applied a spike-in approach, and we converted the ratio of the non-spike vs. spike-sequences into semi-quantitative estimates of DNA amount[32]. Demultiplexed paired-end reads were trimmed, denoised, and chimera checked using Cutadapt version 4.2[63], DADA2 version 1.18.0[64], and VSEARCH version 2.22.1[65]. As reference database, we used Sanger sequences from the UNITE v9 database[66] supplemented with the synthetic spike sequences. Sequences representing non-spike amplicon sequence variants (ASV [36]) were aligned between the ITS3 and ITS4 primer sites. Discarding sequences that did not match the full length of the model, or which had a bit score less than 50 resulted in a 65,912 ASVs x 2,768 samples matrix of read abundance.

Due to the unsuitability of using ITS-based ASVs as proxies for species[67], we developed a taxonomically-guided clustering approach to form species-level OTUs. We performed a probabilistic taxonomic placement of the ASVs with Protax-fungi[38] with a 90% probability threshold. Additionally, sequences whose best match to UNITE Sanger sequences was to a kingdom other than Fungi were annotated as potential non-fungi. We applied constrained clustering by first forming cluster cores by the ASVs which had been assigned to taxa by Protax-fungi. We then matched the unassigned ASVs to

the closest cluster core using optimized sequence similarity thresholds. Finally, remaining unclustered ASVs were clustered using de novo single-linkage clustering. These de novo clusters were assigned to placeholder taxonomic names of the form “pseudo{rank}_{number}”. The final result of this process was a 27,954 species-level OTUs x 2,768 samples read abundance matrix, along with taxonomic annotations at each rank from phylum to species, including pseudotaxon placeholders.

The mean sequencing depth (total number of fungal and spike sequences) among the samples was 86,845 sequences per sample. Based on rarefaction analyses presented in Ovaskainen et al.[33], we discarded samples that did not contain at least 10,000 sequencing reads, representing 1.8% of the samples. To avoid losing some OTUs detected in the most diverse samples, we controlled for variation in sequencing depth by statistical means rather than using rarefied values[68].

Extraction of weather and climate data

Weather variables were extracted from the “ERA5 hourly data on single levels dataset”[40] available at the Copernicus Climate Data Store (https://cds.climate.copernicus.eu/cdsapp#!/home). To download the weather variables, we used the R-package ecmwfr[69]. We downloaded hourly data on 1) "2m_temperature”, i.e., instantaneous temperature (k) at 2 metres height (henceforth called temperature), 2) "total_precipitation", i.e., precipitation (m) accumulated over one hour period (called henceforth precipitation), 3) "10m_v_component_of_wind", i.e., horizontal speed (m/s) of air moving towards the north at a height of ten metres, and 4) "10m_u_component_of_wind", i.e., horizontal speed (m/s) of air moving towards the east at a height of ten metres. The latter two variables were combined to compute the wind speed by applying the formula $\sqrt{v^2 + u^2}$). All four variables were downloaded for the latitude range from -80 to 80 and longitude range from -180 to 180, for the period from 07th May 2018 to 2nd February 2021, which extended well past our study period. We then averaged the hourly data to daily data and extracted the data for the sampling locations of our study. We downloaded the climatic data using the same tools but using the sis-biodiversity-era5-global dataset. As climatic variables, we included the 40-year averages (1979-2018) of “annual_mean_temperature", "annual_precipitation", "wind_speed", and "aridity".

Extraction of spore size and trophic guild data

We extracted the spore size and trophic guild data from the data assembled by Aguilar-Trigueros et al[56]. The spore size data originates from species-level taxonomic descriptions in Mycobank[70] (containing spore dimension data for >36 000 species) and includes for every fungal species the sizes of the spores produced in both the sexual and asexual cycles. The trophic guild data consists of a compilation of recordings of fungal functions across major databases (see Aguilar-Trigueros et al[56] for a detailed list of the compiled databases).

Connecting the spore volume data to molecularly identified species is not straightforward, as some of the taxa were identified only to a higher taxonomic level than species, and because the spore volume databases are not complete. For those OTUs that were identified to the species level and for which a spore volume estimate was available, we used the species-level estimate. When a species-level estimate was not available, we used the genus-level estimate, computed as the average over the species belonging to the focal genus. When a genus-level estimate was not available, we used the family-level estimate, computed as the average over the genera belonging to the focal family. If a family-level estimate was not available, we considered the spore volume for the focal species as missing data. We computed the community-weighted mean of log-transformed spore volume for each sample as the average log-transformed spore volume over the species that were present in the sample. When doing so, we distinguished between spores produced during asexual (i.e., asexual

spores) and sexual cycles (i.e., sexual spores), thus resulting in community-weighted mean sizes of asexual and of sexual spores. We note that this analysis is based on the molecular classifications of the ITS2 sequences rather than e.g., direct microscopy of the sampled spores, and hence we cannot distinguish whether the spores in the samples were asexual or sexual. Hence, these variables should be interpreted as the mean size of the asexual or sexual spores of those species that were present in the sample.

When assigning the trophic guild data, we included only the most common trophic guilds and grouped some of them (Table 2). We first matched those OTUs that were identified to the species level and which matched a species in Aguilar-Trigueros et al[56] database. In the cases where an OTU was only identified to the genus level or the species-level identification was not available in the database, we assigned from the database all trophic guilds categories of the species belonging to the focal genus. Likewise, when the OTU was only identified to the family level, we assigned from the database all trophic guilds categories of the species belonging to the focal family. As result, some OTUs were assigned to more than one trophic guild, and hence the classifications should be considered as potential guilds to which the OTU may belong to, often based on information borrowed from its relatives.

Table 2. The numbers of OTUs classified into trophic guilds used in this study. Note that each OTU may be classified to more than one trophic guild and hence the sum of #OTUs over the trophic guilds exceeds the total number of OTUs detected in our study.

Trophic guild	#OTUs
Plant pathogen	12539
Saprotroph (including dung saprotroph)	10380
Wood saprotroph	4856
Endophyte	7480
Ericoid mycorrhizal	610
Ectomycorrhizal	1698
Animal pathogen (including human pathogens).	4109
Lichenized	494
Epiphyte	1316

Multivariate analyses addressing how variation in community composition depends on climatic conditions and geographic distance

We conducted multivariate analyses at the site, rather than at the sample level. For each site, we measured the abundance of each taxon by its prevalence, i.e., the proportion of samples where it was present. We then computed the site-to-site community distance matrix using either the Bray dissimilarity index (using the *vegdist* function of the R-package vegan[71]), or alternatively the unifrac distance (using the *UniFrac* function of the R-package phyloseq[72]) that accounted for the taxonomic relatedness among the taxa. As candidate environmental variables used to explain community dissimilarity, we used mean annual air temperature (MAT), mean annual precipitation (MAP), mean annual aridity (MAI), and mean annual wind speed (MAW), all averaged over the 40-year period from 1979 to 2018. The reason for including only a small number of site-specific variables in the analysis is that, while the study is global in scope, it includes only 47 sites. The data thus hold limited information to statistically disentangle the effects of many spatially-varying covariates. Instead, the main strength of the study lies in its high temporal replication, which allowed us to identify effects of the spatiotemporal covariates, such as seasonality.

We visualized the community distance matrices with nonmetric multidimensional scaling (using the metaMDS function of the R-package vegan) and illustrated the effect of each candidate environmental variable on the ordination space (using the *ordisurf* function of the R-package vegan). To partition the variation in community dissimilarity explained by spatial distance and by each candidate environmental variable, we used linear models where community dissimilarity was explained by either geographic distance, environmental distance, or both geographic and environmental distances. We computed the proportions of variance explained by space alone, by environment alone, and shared effect following Whittaker[73].

Univariate analyses addressing how variations in DNA amount, species richness, spore size, and trophic guild composition depend on climate, season, and weather

We fitted a series of mixed linear models for each of the following response variables: log(DNA amount), log(species richness+1), CWM log(sexual spore size), CWM log(asexual spore size), and log(number of species classified to each trophic guild+1). For analyses concerning spore sizes, we included only samples that contained at least ten species to reduce noise in the response variables. In addition to conducting the analyses for CWM computed for all species, we also repeated the spore size analyses with restricting the analyses for basidiomycetes only and for ascomycetes only. These additional analyses were motivated by the question of whether the results were consistent among these two major groups.

As described in more detail below, we considered four models (models CS1 through CS4) of climatic and seasonal variation. In addition to the best-supported model of climatic and seasonal variation, we considered four models (models W1 through W4) of weather variation, each of which further consisted of 64 variants according to which weather variables they included. We describe these model variants verbally below and illustrate them conceptually in the *Supporting Information*. We performed model selection among these model variants with AIC and used the explanatory powers of the models to assess the proportion of the total variation they explain.

Influence of climatic and seasonal variation. To evaluate the effects of climatic and seasonal variation, we considered the following four nested models, described in order of increasing complexity.

- *Model CS1: Null model.* The null model does not include any ecological predictors as fixed effects but includes log(sequencing depth) for the species richness model. To account for the study design with multiple samples from the same locations, the null model includes the site as a random intercept.
- *Model CS2: Climate-dependence.* In this model, we assumed the response variable to vary systematically with the MAT of the site. Thus, we extended model CS1 by including a fixed effect of MAT and its square.
- *Model CS3: Climate-dependence and latitude-dependent seasonality.* In this model, we assumed that the response variable additionally shows seasonal variation that systematically depends on latitude. We thus extended Model CS2 by including as fixed effects the interaction between latitude and seasonality. We modelled "seasonality" with the periodic functions $sin\left(2\frac{\pi d}{365}\right)$ and $cos\left(2\frac{\pi d}{365}\right)$, where d is the Julian day of the year. As latitude is positive for the Northern and negative for the Southern Hemisphere, we note that the interaction between seasonality and latitude assumes opposite patterns of seasonality in the two hemispheres. It is thus appropriate to account for the six-month difference in seasonality between the two hemispheres.
- *Model CS4: Climate-dependence and site-specific seasonality.* Model CS4 extends Model CS3 by including the random effect of the site not only in the intercept, but also as random slopes related

to latitude, seasonality, and their interaction. This model thus assumes that each site may show a deviation from the systematic latitude-dependent variation in seasonality, generated by some site-specific effects not included in the model.

Influence of weather variation. The aim of these analyses was to assess how the prevailing weather conditions influence the four response variables. As weather-related covariates, we used temperature, precipitation, and wind speed. We added these covariates as additional predictors to CS4, the most complex climatic model. As weather variables (especially temperature) follow seasonal patterns that depend on latitude, using them as such would confound their effects with the effects of the climatic and seasonal predictors. For this reason, we included the covariates as the difference between the actual values and the values expected based on latitude and season; henceforth, we call them temperature, precipitation, and wind-speed anomalies. We calculated these anomalies as the differences between the daily observed values and the predictions of site-specific seasonality models (i.e., Model CS4) fitted to each weather covariate. For example, the temperature anomaly for a given day and site describes how much warmer (positive anomaly) or colder (negative anomaly) that site was compared to what would be expected for that site and that season. Furthermore, we note that the weather covariates may influence variation in fungal communities either through their effect on detection (e.g., prevailing wind conditions during sampling) or through their influence on production of fruiting bodies and sporulation (e.g., temperature and humidity conditions over the past week). As the timescales at which climatic conditions influence spore production are generally unknown and can vary among species, we computed the weather predictors in three alternative ways, averaging them over a period of either one day, one week, or one month before the sampling. We considered the full set of candidate models in which each weather covariate was either excluded or included at the time scale of day, week, or month. As there are three weather covariates, and each of them has four options, the number of candidate models is 64, encompassing the null model where no weather covariates were included. Concerning how we assumed the weather to influence the response variables, we considered the following four nested models, each of which included as baseline the best supported model of climate and seasonality.

- *Model W1: Constant weather effects.* Model W1 includes in the fixed effects the main effects of weather covariates.
- *Model W2: Weather effects depend on the site.* Model W2 extends Model W1 by including in the fixed effects also the interactions between climatic variables (MAT and its square) and weather covariates, as well as site and weather covariates, thus allowing temperature anomaly to have a site-specific effect that possibly varies systematically with climate.
- *Model W3: Weather effects depend on the site and on latitude-dependent seasonality.* Model W3 extends Model W2 by including in the fixed effects also the interactions between latitude-dependent seasonality (the interaction between latitude and periodic functions of the day of the year) and weather covariates, thus allowing, e.g., temperature anomaly to have a positive effect in spring but negative effect in autumn.
- *Model W4: Weather effects depend on the site and on site−dependent seasonality climate.* Model W4 extends Model W3 by including in the random effects the effect of the site, and the slopes related to interaction between seasonality and the weather covariates. This model thus assumes that the effects of the weather covariates show site-specific variation in both their mean effect and in their seasonality.

Univariate analyses addressing how seasonality in community composition depends on climate

To characterize how seasonality in community composition depended on climate, we computed for each site an index of seasonality in community composition, and then fitted a linear model where we

regressed this index against the MAT of the site. To describe seasonality in community composition, we examined how much more similar pairs of samples were in terms of their community composition if they were sampled from the same season compared to if they were sampled from different seasons. We considered a pair of samples to belong to the same season if they were taken at most one month apart, whereas we considered them to belong to a different season if they were taken three months (plus or minus half-a-month) from each other. As a measure of community similarity, we used the Jaccard similarity index, which we averaged over those pairs of samples that contained at least five species. We then used an index of seasonality in community composition calculated as the average Jaccard similarity index for pairs of samples that were taken in the same season, minus the average Jaccard similarity index for pairs of samples that were taken in a different season. We accounted for the Jaccard similarity index for pairs of samples that were taken in the same season to control for possible variation in the baseline turnover and thus to extract the sole effect of seasonality.

Joint species distribution modelling of phylogenetic signal in climatic and seasonal variation

To examine for phylogenetic signals in climatic and seasonal variation, we analysed the data with Hierarchical Modelling of Species Communities (HMSC)[74,45]. HMSC is a joint species distribution model[75] which includes a hierarchical layer modelling how species environmental covariates relate to their traits and/or phylogenetic relationships[76]. We restricted these analyses to the 485 species that occurred in the data at least 50 times and therefore had sufficient data to estimate climatic and seasonal responses. As the response variable, we used the presence-absence of species at the level of the sample, which we modelled through the Bernoulli distribution and probit-link function. To measure climatic responses, we included as fixed effects the second-order polynomial of the MAT of the site. To measure seasonal responses, we also included as fixed effects the interaction between latitude and seasonality that we modelled with the periodic functions $\sin(2\pi d/365)$ and $\cos(2\pi d/365)$, where d is the Julian day of the year. To control for variation in sequencing depth (i.e., the number of sequences obtained for each sample), we also included the log-transformed sequencing depth as fixed effect. To control for repeated samples from the same sites, we included the site as a random effect. To examine how the species responses to the predictors related to their phylogenetic relationships, we included in the HMSC model a taxonomic tree, where we assumed equal branch lengths at the levels of phylum, class, order, family, genus, and species.

We fitted the model with the R-package Hmsc[77] assuming the default prior distributions[45]. We sampled the posterior distribution with four Markov Chain Monte Carlo (MCMC) chains, each of which was run for 37,500 iterations, of which the first 12,500 were removed as burn-in. The chains were thinned by 100 to yield 250 posterior samples per chain and so 1000 posterior samples in total. We examined the convergence of MCMC by the potential scale reduction factors[78] of the model parameters. We examined the explanatory power of the model through species-specific AUC[79] and Tjur's R^2 metric[80] values, which provide complementary insights of predictive performance[81].

To quantify the phylogenetic signals of climatic and seasonal variation, we extracted our output variables for each species from the fitted HMSC models: *climatic sensitivity, optimal climate, seasonal sensitivity,* and *optimal season*. We measured *climatic sensitivity* by the proportion of variance explained by the second-order polynomial of the MAT of the site. Similarly, we measured *seasonal sensitivity* by the proportion of variance explained by the periodic functions $\sin(2\pi d/365)$ and $\cos(2\pi d/365)$. We multiplied the proportions of variance that the predictors explained out of the explained variation by the proportion of variation that the model explained, the latter measured by the species-specific Tjur's R^2 values. We measured *optimal climate* as the MAT at which the second-order polynomial of the MAT was maximized, truncated to values within the observed range of MATs. As it is meaningful to estimate the optimal climate only for species that show climatic variation, we

included in the analyses of optimal climate only those species for which climatic sensitivity was at least 5%. Similarly, we measured the *optimal season* by the day of the year on which the estimated linear combination of the periodic functions sin(2πd/365) and cos(2πd/365) peaked and included in the analyses of optimal season only those species for which seasonal sensitivity was at least 5%. We then fitted phylogenetic regression models for each of these four response variables. We fitted the models with the R-package nlme[82] using the *gls* function, no covariates, and the *corPagel* correlation structure. We quantified the strength of the phylogenetic signal by the estimated lambda parameter, and we estimated its statistical significance by the p-value of the comparison (performed by the *anova* function) between models that included vs. did not include the *corPagel* correlation structure.

Data availability and reproducibility of results

The data and the R-pipeline that can be used to reproduce the results of this paper are available at Zenodo. Abrego et al. Data and scripts for: Airborne DNA metabarcoding reveals that fungi follow predictable spatial and seasonal dynamics at the global scale. https://doi.org/10.5281/zenodo.10896659 (2024).

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