LETTER





Wind Patterns Influence the Dispersal and Assembly of North American Soil Fungal Communities

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ABSTRACT

Wind is the primary dispersal mechanism of most fungal spores but is rarely considered in studies of fungal communities, limiting inference of assembly mechanisms and forecasting responses to climate change. We compiled wind-connectivity models—'windscapes'—to model potential dispersal of fungal spores at the continental scale and linked them with a molecular dataset of North American soil fungi. Our analyses demonstrate that prevailing windflow patterns exhibit a significantly stronger signal on fungal community structure than do geographic distances amongst sites. Notably, the signature of wind was detectable for mushrooms and fungi producing primarily wind-dispersed spores. Contrastingly, fungi primarily reliant on animal dispersal exhibited a strong signature of geographic distance but not wind-connectivity. Additionally, we show that directionally 'downwind' sites are more diverse than comparatively 'upwind' sites. Altogether, our findings suggest that future wind patterns will shape the adaptation potential of fungal communities dispersing into suitable climatic niches.

1 | Introduction

Dispersal of reproductive propagules is fundamental to the assembly of ecological communities (Levine 2001; Vellend 2010). While dispersal is known to influence microbial communities (Chaudhary et al. 2022; Peay et al. 2016) its relative importance in community assembly remains controversial and poorly characterised (Custer et al. 2024; Talbot et al. 2014). Some local and regional scale studies have directly estimated dispersal rates and barriers for microbial taxa (Abrego et al. 2018; Barbour and Martiny 2024; Peay et al. 2012), but whole community estimates of dispersal and its determinants remain lacking.

Fungi are dominant members of soil communities and play a significant role in biogeochemical cycles and plant responses

to climate change (Averill et al. 2022; Cavicchioli et al. 2019; Willing et al. 2024). Many fungi display high degrees of regional endemism, suggesting that despite their abundant microscopic propagules, dispersal limits their distribution (Abrego et al. 2024; Talbot et al. 2014). Understanding dispersal processes in fungal community assembly is also critical to projecting their influence on ecosystems in an era of global change. However, existing state-of-the-art species distribution models do not consider dispersal as a determinant of future fungal range sizes (Qin et al. 2023). Improving the accuracy of these projections is critical as many fungal taxa play consequential roles in the establishment and growth of plant seedlings (Smith and Read 2010). This is particularly important for plants attempting to track climatic niches and disperse into new habitats, such as in the boreal forest where mismatches

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between the range size of trees and fungal partners are now projected (Van Nuland et al. 2024). Consequentially, understanding fungal dispersal can inform mechanistic perspectives of ecosystem dynamics and ecosystem function under climatic change (Anderegg et al. 2020).

At relatively large scales (>1km), wind is the primary vector of fungal spore dispersal. The primacy of wind-dispersal is apparent throughout much of the fungal kingdom, as the majority of fungi have evolved highly specialised reproductive structures (e.g., mushrooms) to disperse wind-borne spores (Heitman et al. 2020; Wyatt et al. 2013). Fungal sporocarps range in shape and size, but the small size of spores, their staggering abundance (up to billions of spores per sporocarp) and the ability of sporocarps to alter convective currents to promote spore discharge make many spores amenable to long-distance wind transport (Chaudhary et al. 2022; Golan et al. 2023; Wyatt et al. 2013). Moreover, fungal fruiting phenology displays a strong synchronicity across temperate and boreal regions (Krah et al. 2023), a response thought to be tuned to optimise spore discharge during windier weather periods (Abrego et al. 2024). Consequentially, high spore load and diversity are regularly observed in high altitude sampling of dust and air (Abrego et al. 2024; Drautz-Moses et al. 2022; Kellogg and Griffin 2006; Maki et al. 2019). Importantly, not all fungi rely on wind for spore dispersal, and certain groups of fungi produce gasteroid-hypogeous (truffles) sporocarps that are reliant on small mycophagous mammals (Nuske et al. 2017; Vasutova et al. 2019) or invertebrates for dispersal (Lilleskov and Bruns 2005). Gasteroid-hypogeous fungi are thought to have a much narrower dispersal kernel than primarily wind-dispersed fungi (Chaudhary et al. 2022). Resultantly, for this subset of the fungal community, terrestrial geographic features that influence animal movement, rather than windflow, would represent a more biologically meaningful metric of dispersal difficulty (Borgmann-Winter et al. 2023).

Despite the obvious role of wind for fungal dispersal, existing studies generally invoke dispersal processes by studying patterns of community dissimilarity across progressively increasing geographic distances (Talbot et al. 2014). In these distance-decay studies, geographic distance represents a simple proxy for the dispersal potential of fungal spores between different locations. However, a key limitation of this approach is the assumption of idealised dispersal surfaces in which dispersal barriers are either negligible or equally probabilistic across all directional vector fields. While this may be true at small spatial scales (< 1 km)(Amend et al. 2010; Bergemann et al. 2006), at larger spatial scales it is presently unknown how dispersal barriers influence fungal populations and communities. One potentially more direct way of assessing how dispersal links fungal communities is through measurements of wind connectivity across the Earth's surface, where windflow travel time can be thirty times more variable than measurements of geographic distances (Kling and Ackerly 2021). Landscape-scale dispersal barriers such as mountains and global drivers such as the rotation and curvature of the earth structure these windflow patterns. Because wind is the actual vector of most fungal spore movement (Chaudhary et al. 2022), windflow represents a mechanistic ecological process structuring communities, as opposed to geographic

distance, which is an indirect representation of many (community assembly) processes acting in concert.

In this study, we analyse windflow patterns as a proxy for aerial spore dispersal to investigate the role of dispersal in the assembly of soil fungal communities at landscape to continental scales. Unlike geographic distances, windflows linking a pair of sites can be separated into two distinct properties: wind 'connectivity,' a sum representing the total rate (speed) at which air moves between sites regardless of direction, and wind 'asymmetry,' a ratio capturing that wind strength can be stronger in one direction than another. We make two hypotheses, relating to each of these wind properties, H1 Windflow patterns are a stronger predictor of fungal community similarity than geographic distances, such that community similarity would be greater for sites with greater wind connectivity ((i.e., shorter windborne transit times), and H2) Relatively 'downwind' sites experience greater propagule rain and are thus more diverse than upwind communities. For both hypotheses, we additionally reasoned that the effect of wind would be evident exclusively for primarily wind dispersed fungi, whereas windflow would not exhibit a signature on the community structure of primarily animal dispersed fungi (e.g., Gasteroid-hypogeous sporocarps).

Identifying the role of wind in structuring the biogeography of fungal communities has proven challenging given that dispersal and establishment of fungal spores cannot be readily observed or tracked. To overcome this hurdle, we employ high resolution wind data coupled with time-integrated landscape connectivity algorithms to identify plausible fungal dispersal pathways or 'windscapes'. These 'windscapes' specifically model the dispersal of hypothetical particles (i.e., spores) using least cost path algorithms that estimate the mean number of hours it would take for an air parcel to diffuse from one location to another based on the full spatiotemporal enumeration of wind conditions across the landscape (Kling and Ackerly 2021). Our windscape models capture the 30-year time-integrated speed of wind diffusion between soil sampling sites as estimates of relative dispersal potential. We studied the impact of windscapes on soil fungal communities using molecular barcoding methods applied to a continental scale network of 108 sampling sites spanning tropical forests to temperate grasslands in North America (Qin et al. 2023).

2 | Methods

2.1 | Sampling Design

We combined data from two previously described continental scale soil fungal sequencing projects. Soil samples were derived from the Dimensions of Biodiversity of Ectomycorrhizal Fungi (DoB-Fun) network, including 63 sites distributed across North American forests dominated by mature *Pinaceae* overstory species, and the National Ecological Observatory Network (NEON), which includes 45 terrestrial sites distributed across all major eco-climatic zones in the United States. Combining these networks yielded soil samples from 108 sites. The soil sampling approach is broadly congruent in sites across both networks; conserved molecular sequencing methodologies allowed for harmonising these datasets. Notably, soils were generally taken

to similar sampling depths (~15 cm; however some NEON soil cores extended to 30 cm depending on soil properties) and sieved (2 mm) to remove roots. Soil cores for Dob-Fun were 7.6-cm diameter, whereas diameter varied for NEON samples, but generally ranged from 5 to 8 cm diameter. The soil sampling methods for NEON soil samples are described in NEON's standard operating procedures (National Ecological Observatory Network 2021). The sampling methods for DoB-Fun samples are described in (Steidinger et al. 2020; Talbot et al. 2014). See Supporting for additional details.

2.2 | Sequence Analysis and Bioinformatic Methods

Analysis and bioinformatic methods to harmonise these molecular datasets have been previously described (Qin et al. 2023). Briefly, fungal DNA was extracted from each soil core, and the ITS1 locus of the internal transcribed spacer (ITS) region was amplified using the ITS1F–ITS2 primer pair (Smith and Peay 2014; Talbot et al. 2014). All NEON samples and a majority of DoB-Fun Samples were sequenced on the Illumina MiSeq platform (2×250 bp), while the remaining DoB-Fun samples were sequenced using 454 pyrosequencing technology. We assigned taxonomy to OTUs clustered at 97% sequence similarity using established methods(Tedersoo et al. 2022). See Supporting for additional details.

Taxa were assigned sporocarp morphologies based on taxonomic genus level matches with the Fungal Traits database (v.1.2) (Põlme et al. 2020). We characterised fungal sporocarps based on their presumed dispersal modes. Taxa characterised as Agaricoid in their sporocarp morphology were presumed to be primarily wind dispersed whereas those characterised as Gasteroid-hypogeous were presumed to be primarily animal or insect dispersed due to their belowground fruiting bodies. The ectomycorrhizal genus Rhizopogon was manually reassigned to Gasteroid-hypogeous fruiting body form based on expert knowledge. Ascomycetous fungi were presumed to be wind dispersed, however, some Ascomycetes produce 'gasteroid' or 'gasteroidhypogeous' sporocarps, and those taxa (n = 120 out of 15,065) were removed from the Ascomycete category (as they were included in the Gasteroid-hypogeous category). The fruiting body assignment of taxa were confirmed using literature searches. In total, 28,265 OTU's were detected. In our dataset, Agaricoid Fungi were represented by 3515 OTUs, Gasteroid-hypogeous (n = 215 OTUs) and Ascomycete fungi (n = 14,945 OTUs). At the site level, a mean of 27.0% of sequences were assigned to Agaricoid fungi (SD = 0.13), Ascomycota (mean = 19.9%, SD = 0.098), and Gasteroid-Hypogeous (mean = 1.0%, SD = 0.015).

2.3 | Vegetation Data

To obtain plant community data for each site, we extracted plant vegetation data from 'distributed' NEON plots for each study site. For these plots, the diameter and identity of all plants greater than 5cm was recorded in each distributed plot. Diameter at breast height (DBH) for each plant species was averaged across all distributed plots within each site. Similarly, for each DoB-Fun site, vegetation was surveyed at five subplots. For the DoB-Fun sites, each sub-plot consisted of a 5 m radius (at the plot center, and the plot corners) within which all plants with a DBH of at least 10 cm were recorded, identified, and measured for DBH. Taxonomic names were harmonised across datasets and taxa were agglomerated at the level of plant genus, with the proportional composition weighted by stem DBH. Dissimilarity matrices amongst were calculated using Bray-Curtis distances.

2.4 | Soil and Climate Data

Elemental analysis of soil carbon, nitrogen, and soil pH (1:1 soil water slurries) was obtained for both DoB-Fun and NEON sites. Briefly, the soil carbon and nitrogen elemental analysis protocol and soil pH for DoB-Fun sites followed (Talbot et al. 2014). Soil metadata, such as soil carbon, nitrogen, and soil pH, was extracted from NEON data products (https://www.neons cience.org/data-collection/soils). Climatological data for all sites (1970–2000) was sourced from World-Clim v. 2.1 (Fick and Hijmans 2017).

2.5 | Wind Flow Analysis

We used the windscape R package (Kling 2024) in conjunction with the Climate Forecast System Reanalysis (CFSR) dataset (Saha et al. 2014). The CFSR dataset spans three decades (1980-2009) of hourly global wind data timesteps in every location, and can be used to estimate wind connectivity amongst sampling sites. The CFSR represents a gridded dataset with resolution of ~35 km at a 10 m height above the land surface, and has been increasingly employed to study the role of wind in the assembly of insect communities (Epele et al. 2021) and genetic diversity of plant populations (Kling and Ackerly 2021). The most efficient 'wind route' between each of the sampling site pairs was estimated using a least cost path (LCP) algorithm, where the 'cost' of travel is estimated as the mean number of hours required for wind to diffuse from one location to another based on the spatiotemporal distribution of wind conditions across the landscape (Kling and Ackerly 2020). Windflow patterns represent the time it takes for an air parcel to diffuse from one location to another, averaged over the spatial and temporal heterogeneity in wind speed and direction. Moreover, because windflow patterns represent the composite of the speed and directionality of wind movement they can be decomposed into constituent components. For each site-pair, the two flow values are used to calculate windflow asymmetry (i.e., the ratio of outbound to inbound windflow). Wind connectivity is calculated as the mean of the windflows in each of the two directions. We calculated windflow for each of the site pairs in both directions across the full soil sampling network. See Supplement for additional analytical detail.

2.6 | Statistical Methods

We used two primary statistical approaches to model the role of wind in structuring distinct components of fungal communities. First, we employed generalised dissimilarity modelling (GDM) to isolate the role of wind connectivity in fungal community structure (H1). Second, we used a partial Mantel analysis to identify if 'downwind' fungal communities are relatively more diverse (H2). These analyses were replicated independently for different components of the dataset to focus on different spore dispersal modalities.

In its original conceptualization, it was suggested that GDM could be used to identify dispersal impedance across the landscape (Ferrier et al. 2007), but it has rarely been implemented in this fashion. Prior to incorporation in GDM, wind connectivity measurements were log-transformed to identify fine- and largescale variance amongst relatively distant communities. Initially, we incorporated the full range of climatological predictors derived from Bioclim (n = 19), as well as soil chemical data (bulk soil carbon and nitrogen concentrations), soil pH and plant community dissimilarity. We calculated distances between sites, using Haversine 'great circle' geographic distances to account for the curvature of the earth and incuded them in the GDM to account for spatial autocorrelation in the sampling networks. We used backwards model selection procedures to identify a parsimonious set of statistically significant predictors remaining in the final model assessed via permutation test (Mokany et al. 2022). We additionally repeated this step-wise modelling procedure for various subsets of the fungal community (i.e., Agaricoid, Gasteroid-hypogeous, and Ascomycetous fungi). Because windflow and geographic distances were in the majority of the final model constructions, we generated additional models incorporating either geographic distances or windflow into additional GDM models (alongside additional environmental predictors), thus protecting against statistical collinearities amongst windflow and geographic distances. Additional detail on the GDM approach and implementation can be found in the Supporting Information—S1.

To interrogate the role of directional windflow asymmetries (i.e., the ratio of outbound to inbound wind flow), amongst sitepairs in influencing fungal diversity, we utilised a modified Mantel test implemented in *windscape* package (Kling 2024). This specific test differs from traditional Mantel tests' in that it can accommodate different upper and lower matrix 'triangles', which in this case, are reciprocally symmetrical (Kling and Ackerly 2021). Because environmental gradients are known to influence fungal richness patterns, we additionally incorporated ratios of MAT and MAP amongst site-pairs, along with a plant community dissimilarity matrix. We used matrix permutation (n = 1000) whereby the rows and columns are randomly reordered to derive a null distribution, against which a model *p*-value representing the test of the overall hypothesis is calculated.

3 | Results

This dataset represents one of the most comprehensive for North American soil fungi, spanning very cold Alaskan tundra to tropical Puerto Rican soils (Figure 1; Qin et al. 2023). The majority of the fungal taxa were in the phyla Basidiomycota, Ascomycota, and Mortierellomycota (Table S1). Soil fungal communities exhibited significant community differentiation across geographic regions and habitat types within North America.

As expected, windflow times and great circle geographic distances were highly correlated ($R^2 = 0.63$; Figure S1). Other environmental predictors exhibited strong, albeit weaker, spatial co-variation with wind connectivity (Figure S1). We studied the factors influencing fungal community structure at the continental scale using partial correlations in GDM. We found that a large proportion of community variation is due to differences in mean annual temperature, soil pH and plant community composition (Figure 2; Table S2). In support of our hypothesis (H1), when both windflow and geographic distance variables were included, windflow connectivity was a significant predictor of fungal community dissimilarity (p = 0.01), whereas geographic distances were not (Figure 2; Table S2). Interrogation of the GDM response splines (i.e., their shape and height) finds that wind connectivity influences fungal community structure across the full range of spatial scales in this study, whereas the effect of geographic distance showed signs of saturation at larger spatial scales (i.e., was asymptotic; Figure 2; Ferrier et al. 2007). Altogether, this model (including both geographic distances and windflow connectivity) explained 50.8% of fungal community variation, a proportion of deviance consistent with previous studies investigating fungal communities at continental scales (van der Linde et al. 2018; Steidinger et al. 2020). Due to the inherent collinearity of geographic distances and windflow patterns, we also computed separate models with model terms as above, but incorporating either geographic distances or windflow connectivity (Tables S3 and S4). Comparison of these separate models, and their associated coefficients, further suggests that windflow is a stronger predictor of fungal composition than geographic distance; overall deviance explained for the windflow only model is higher, that is, 50.0% versus 47.6% (for geographic distances) (Tables S3 and S4).

We additionally studied separate subsets of fungal community structure to test for differences in the influence of wind amongst separate sporocarp morphologies. Windflow connectivity along with soil and climatic variables were significant predictors of Ascomycetous fungal communities (p=0.017), whereas geographic distances were not (Table S5). Separate models including either windflow or geographic distances further indicate that windflow is a stronger predictor 16.2%, than geographic distances 12.9% (Tables S6 and S7). For Agaricoid fungi, geographic distances and other soil and climatological variables were statistically significant in the GDM; however, wind connectivity was not significant (p = 0.17; Figure 3; Table S8). Model comparison with either windflow or geographic distances was equivocal for Agaricoid fungi, with windflow and geographic distances representing near equivalent proportions of model deviance (windflow: 17.1%, geographic distances: 17.2%; Tables S9 and S10). In contrast, the influence of geographic distances was particularly pronounced for Gasteroid-hypogeous communities (Table S11), and windflow distances were excluded during model selection due to a lack of model deviance explained (Figure 3). We repeated additional modelling procedures including either windflow or geographic distances, which recapitulate the significance of geographic distances, but not windflow patterns, in influencing Gasteroid-hypogeous fungal communities (Tables S11 and S12).

We utilised a modified partial Mantel test to accommodate directionally asymmetric windflow data. In support of our hypothesis (H2), relatively downwind sites were significantly more diverse when examined across all fungal taxa (Observed



FIGURE1 | Location of sampling sites across North America. The contours indicate the windflow connectivity model coloured by outbound wind travel hours for one arbitrarily selected site (marked in yellow). The connectivity model encompasses spatiotemporal variability in wind direction and speed across the continent, demonstrating that from the focal site, hypothetical dispersal is much faster to the East Coast, than to comparatively closer sites on the West Coast.

richness, r=0.2, p=0.008, Figure 4). Focusing on subsets of fungal taxa, Agaricoid communities in comparatively downwind sites were significantly more diverse (Observed diversity; r=0.26; p=0.002; Figure 5). We observed a similarly positive relationship for Ascomycete fungal diversity and windflow asymmetry (Observed richness; r=0.17, p=0.03; Figure 5). In contrast, and as hypothesised, we observed no significant richness trend for Gasteroid-hypogeous fungi (r=0.06; p=0.5; Figure 5).

4 | Discussion

By studying historic windflow patterns, the physical process responsible for the movement of most fungal spores, we provide a novel advance in understanding the potential significance of wind dispersal in shaping the assembly of fungal communities. Overall, we find that North American soil fungal communities strongly connected by wind-based transit are more compositionally similar to each other. This finding complements theoretical expectations on the biophysical movement of spores by demonstrating that windflow patterns could meaningfully influence dispersal at a scale that shapes biogeographic patterns observed in a number of fungal ecology studies (Golan and Pringle 2017). By focusing on the wind-based dispersal processes that generate these patterns, our results provide a mechanistic advance over the traditional, but indirect estimates of dispersal limitation inferred from geographic distances (Allen et al. 1989; Chaudhary et al. 2022; Talbot et al. 2014). The degree to which fungal community assembly is affected by dispersal has important implications for a number of ecological questions, such as the management and spread of invasive species and fungal pathogens (Delgado-Baquerizo et al. 2020), or the potential for fungi to track changing environments. Although our results are inherently correlative, they complement long-standing observations of spore dispersal via atmospheric transport and signal that wind-based dispersal processes play an important and underappreciated role in shaping established soil fungal communities.

Several lines of evidence converge to support our core conclusion that windflow patterns influence the dispersal and assembly of soil fungal communities at the continental scale. Because windflow and geographic distance are highly correlated, we employed multiple approaches to infer the influence of windflow in structuring fungal communities. First, we disentangled the influence of windflow and geographic distances on fungal community structure using partial correlations derived from a GDM modelling framework, finding that windflow correlates significantly with fungal community composition after



FIGURE 2 | Major ecological determinants of fungal community structure across North America assessed using Generalised Dissimilarity Modelling (GDM). Each panel represents I-splines (partial regression fits) for variables associated with fungal β -diversity. The maximum height reached by each curve represents the total amount of compositional turnover associated across each predictor variable; the shape of each spline indicates how the instantaneous rate of compositional turnover varies predictor variable. Although Geographic Distances are not a significant model predictor after model selection, they are presented for graphical comparison only. Grey ribbons indicate bootstrapped uncertainty estimates of ±1 SD. (a) Mean Annual Temperature (b) Geographic Distances (km) (c) Soil pH (d) Wind Connectivity Distance (e) Plant Community Dissimilarity (f) Splines are z-scaled for comparative purposes, colours represent individual predictor variables (a-e), but uncertainty bounds are not included for visualisation. Model output represents 50.8% deviance (Table S2).

controlling for distance and environment. This conclusion was further strengthened by our finding that fungi primarily dependent on animal-mediated dispersal exhibit a strong signature of geographic distance, but not windflow connectivity. Secondly, we find that fungal communities in relatively downwind landscape positions are more diverse; this was especially true for primarily wind-dispersed fungal community subsets (Agaricoid and Ascomycetous fungi), but not for truffle-forming fungi. Although the relative importance of wind is a moderate predictor of fungal community composition relative to soil chemical and abiotic variables, dispersal processes represent an understudied component of fungal community assembly relative to abiotic filtering. For example, observations of a West to East gradient of fungal diversity in North America remain unexplored, but could be in some way linked to prevailing windflow patterns (Mikryukov et al. 2023). Cumulatively, our findings contribute towards a growing understanding that continental-scale windflow patterns and dispersal processes more broadly influence the biogeography of soil inhabiting fungi.

For many macro-organisms, variation in dispersal modes is known to influence range sizes and community assembly dynamics (Jønsson et al. 2016). Our results expand this paradigm by documenting how distinct fungal sporocarp morphologies and primary dispersal strategies differentially influence continental-scale distributional patterns of soil fungi. We detected notable differences in the role of wind connectivity amongst taxa with distinct life-history strategies (i.e., spore discharge methods). This complements recent studies identifying eco-regions amongst ectomycorrhizal fungi as influenced by sporocarp morphologies (Delhaye et al. 2024). In the present study, communities of Ascomycetous fungi, the majority of which have evolved explosive discharge mechanisms to expel wind-dispersed sexual spores (Fritz et al. 2013; Yafetto et al. 2008), were more strongly influenced by wind connectivity than geographic distances. We can only speculate as to why the statistical significance of wind flow patterns was not stronger for Agaricoid fungi, which are thought to be primarily wind dispersed. Certain ungulates and insects are known to consume macroscopic and fleshy Agaricoid sporocarps and incidentally disperse their spores (Borgmann-Winter et al. 2023; Vasutova et al. 2019). While the magnitude of animal vs. spore dispersal is not known for most taxa, it is plausible that even mild zoochorous dispersal for Agaricoid fungi could serve to weaken a signature of wind-based dispersal. However, comparison of model splines, an indicator of the effect size of each predictor variable (Mokany et al. 2022) suggests that the role of wind flow on Agaricoid fungal communities was comparable to that of Ascomycetous fungi, and in both cases, directional wind flow was a significant predictor of alpha diversity patterns. These patterns contrast strongly with those observed for Gasteroid-hypogeous fungal communities. Geographic distances exerted a remarkably strong effect on the community structure of Gasteroid-hypogeous communities, with no detectable signature of wind, a result consistent with their reliance on animal dispersal of specialised spores and



FIGURE 3 | Ecological determinants of community structure in North America fungi with different dispersal modes. Each panel shows GDM splines for significant predictors of fungal β -diversity. Models were run independently for Agaricoid (n=3515 OTUs), Gasteroid-hypogeous-hypogeous (n=215 OTUs) sporocarps, or Ascomycete fungi (n=14,945 OTUs). (a) Mean Annual Temperature (b) Geographic Distances (km) (c) Soil pH (d) Wind Flow Distances (Wind Connectivity) (e) Plant Community Dissimilarity. The height and shape of the splines denote the relative importance and rate of compositional change in the community for each predictor, respectively. Grey ribbons indicate bootstrapped uncertainty estimates of ±1SD.

belowground spore-bearing structures. Gasteroid-hypogeous fungi are dominant members of soil spore banks, which may be an advantageous ecological strategy after disturbances (Glassman et al. 2015), particularly if these fungi are relatively more dispersal limited than wind-dispersed taxa and cannot rapidly colonise new sites (Bruns et al. 2009; Jones et al. 2003). Overall, given the contrasting findings amongst fruiting-body types and their general alignment with the understanding of spore dispersal, we have further confidence that our statistical approach (GDM) is sufficiently sensitive to disaggregate the role of wind connectivity and geographic distances in influencing fungal community structure.

Soil is the most diverse habitat on earth (Anthony et al. 2023), and the processes mediating coexistence for soil fungi remains an open area of research (Vályi et al. 2016). While many studies have focused on edaphic, atmospheric (i.e., deposition) factors and biotic interactions (van der Linde et al. 2018; Peay et al. 2016; Talbot et al. 2014; Tipton et al. 2019), direct evidence linking dispersal processes with fungal diversity patterns have remained elusive, particularly at the community scale. Our results provide support for the idea of directional dispersal in moderating fungal community diversity. In support of our second hypothesis, both Agaricoid and Ascomycetous fungi were significantly more diverse in relatively 'downwind' sites, whereas no such directional influence of wind was detected for Gasteroid-hypogeous communities. Although other latent abiotic gradients could possibly influence the richness patterns described here, we accounted for trends in vegetation structure and gross environmental variables such as precipitation and temperature in our models. Overall, these findings contribute to a broader recognition of dispersal barriers influencing population structure and biodiversity patterns. For example, manipulative studies in riverine ecosystems similarly demonstrate that directional (downstream) dispersal of propagules can overwhelm local interactions (e.g., biotic filtering),



FIGURE 4 | The influence of directional windflow patterns on fungal alpha diversity. Richness ratios between site-pairs are positively correlated with windflow asymmetry ratios (partial-Mantel test; r = 0.20, p = 0.008), indicating that relatively 'downwind' landscape positions are more diverse. Note that one outlier was removed for plotting purposes but retained in statistical tests. Perfectly 'symmetrical' ratios would have a log-value of zero. Trend line represents outcome of partial Mantel tests. Density plots are coloured by density of points.



FIGURE 5 | Fungi primarily reliant on wind-dispersed are significantly more diverse in relatively 'downwind' landscape positions (Ascomycete and Agaricoid fungi). No such trend was observed for Gasteroid-Hypogeous fungi. Density plots are coloured by density of points. Perfectly 'symmetrical' ratios would have a log-value of zero. Red trend-lines represent the results of the partial-Mantel test.

with relatively downriver river islands accumulating greater plant diversity (Levine 2001). Similarly, directional windflow patterns generate a gradient of insect diversity in montane lake ecosystems (Epele et al. 2021). At finer spatial scales, directional dispersal patterns similarly influence the population structure and allele diversity of fungal populations. For example, a study that integrated landscape topography (i.e., connectivity) amongst forest stands found evidence of gene flow amongst *Matsutake* fungi which could not be explained by geographic distances alone (Amend et al. 2010). Similarly, the significance of wind asymmetries has also been shown to influence the allele diversity of globally distributed, wind pollinated, tree populations (Kling and Ackerly 2021). Many processes are known to influence fungal diversity, and because our results are based on partial correlations, they should be experimentally confirmed to corroborate the findings presented here.

Our analysis provides a unique dispersal-centric lens into the future response of fungal communities to climate change. Similar to other studies (Abrego et al. 2024; van der Linde et al. 2018; Steidinger et al. 2020) we identify mean annual temperature as a primary determinant of fungal community composition. As a result, projected increases in temperature can be expected to exhibit profound impacts on fungal communities (Qin et al. 2023; Willing et al. 2024). The adaptation potential of fungi requires dispersal to track suitable niches, however estimating dispersal barriers confronting fungi remains challenging. Resultantly, our findings are particularly significant as climate change is predicted to result in a global 'stilling' of wind patterns (Deng et al. 2022). Taken in the context of global stilling and altered windflow patterns, our results suggest that similar to plant communities (Kling and Ackerly 2020), the ability of fungal taxa to track climatic niches in the future may be compromised in certain locations. Complicating this picture, many meridional windflow patterns blow South-to-North in temperate North America, making it possible that fungi occupying this latitudinal band may be more readily able to disperse into suitable habitats. Altogether, our results suggest that complex interactions amongst climate change and windflow patterns will influence the ability of fungi to disperse into suitable climatic niches.

Amongst community assembly processes, ecological selection is the best studied and presumed to be the most important for microbial communities, including soil fungi (Peay et al. 2016). However, the significance of dispersal in shaping fungal communities is poorly understood in established fungal communities, in part because it is typically measured in developing or experimental communities at relatively small spatial and temporal resolution (Dickie et al. 2012; Peay et al. 2012). The fact that we were able to identify the effect of multi-decadal historic windflow patterns on established, contemporary fungal communities suggests that dispersal processes play an important and lasting role in structuring fungal communities. This insight is aligned with the emerging view of priority effects as a major factor shaping ecological communities in general and fungal communities specifically (Debray et al. 2022; Fukami 2015; Fukami et al. 2010). Although we cannot determine the arrival order of different taxa or their relative longevity in the studied soil cores, because many soil fungi sampled here are known to produce large and long-lived genets (years to decades), the signal of wind in our dataset does not appear to be exclusively an artefact of detecting ephemeral and transient taxa (or inert spores). Further study on the dispersal and establishment of fungal spores is necessary to understand this possibility. We may additionally make cautious insights into rates of fungal dispersal using metacommunity theory. High levels of dispersal are theorised to homogenise communities (Mouquet and Loreau 2003; Vellend 2010); resultantly, the relatively high degree of fungal community differentiation detected here suggests that windflow patterns mediate relatively rare dispersal events that still exhibit a detectable influence on fungal community structure (Drautz-Moses et al. 2022).

While multiple lines of evidence point to an effect of windmediated dispersal on fungal community structure, our conclusions are not without certain limitations. Identifying dispersal processes at the continental scale is highly challenging, in part due to high collinearity between windflow and geographic distances. Inference about the role of windflow in this study is inherently based on partial correlations. At smaller spatial scales, both windflow and geographic distances appear similarly predictive of community dissimilarity. In contrast, geographic distances saturate at intermediate to larger spatial scales, whereas the significance of windflow remains largely unsaturated at larger spatial scales (Figures 2 and 3). Indeed, our ability to resolve the significance of wind flow patterns in fungal dispersal may be greater at relatively larger spatial scales (10s-1000's of km). Although it is important to interpret our correlative results with caution, the possibility of spore dispersal via long-distance atmospheric

transport patterns is well established (Golan and Pringle 2017). Moreover, many studies document regionally endemic fungal communities (Abrego et al. 2024; Chaudhary et al. 2022; Drautz-Moses et al. 2022), suggesting that prevailing windflow patterns could transport distinct fungal assemblages, a result in line with the observations documented here. Notably, Abrego et al. (2024) also demonstrate that aerial spore communities are primarily determined by mean annual temperature, which is consistent with our broader GDM-derived findings. However, other studies of aerial fungal communities demonstrate a decoupling between fungal community structure and global environmental conditions (Tipton et al. 2019). While animals are known to orient their movement based on prevailing landscape characteristics (Chapman et al. 2011), and it is possible that animal dispersal of gasteroid-hypogeous fungi could be somehow confounded with prevailing windflow processes, this seems biologically implausible given the small size of these animals and their somewhat sub-terranean lifestyles. Finally, this study is based on amplicon sequencing of fungal DNA; therefore, it is unknown if the fungi detected here are metabolically active.

The majority of soil-inhabiting fungi rely on wind to disperse their spores. By coupling time-integrated windflow patterns with molecular profiling of fungal community structure, our results support a generalised understanding of windflow influencing the assembly and biogeography of soil fungal communities. Because our analysis supports dispersal processes as exhibiting a sizable influence on the composition and richness of established soil fungal communities, we suggest that windscapes could be used in future analyses of fungal biogeography. For example, if windscapes represent a mathematically tractable representation of fungal dispersal, it may allow for the development of improved forecasting of fungal species distributions (Kivlin et al. 2021). Given the primacy of soil fungi in terrestrial biogeochemical cycles and their vulnerability to climate change, understanding barriers to their dispersal is critical for predicting the future functioning of terrestrial ecosystems.

Author Contributions

Peter T. Pellitier, Clara Qin, Kai Zhu, and Kabir G. Peay jointly conceived of the manuscript. Peter T. Pellitier wrote the manuscript with contributions from all co-authors. Matthew M. Kling, Clara Qin, and Kai Zhu contributed analytical tools.

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Conflicts of Interest

Michael E. Van Nuland and Clara Qin are members of the Society for the Protection of Underground Networks (SPUN), an organisation that conducts scientific research on belowground network-forming fungi in support of environmental conservation efforts.

Data Availability Statement

The data that support the findings of this study include openly available data from the National Ecological Observatory Network at https:// doi.org/10.48443/ybrs-zv89, RELEASE-2021 (DP1.10086.001), and can be downloaded using Qin et al. 2021, *Ecosphere*. The data from the Dimensions of Ectomycorrhizal Biodiversity project is available from the NCBI Sequence Read Archive via accession number PRJNA950128. Windflow data is available from https://climatedataguide.ucar.edu/ climate-data/climate-forecast-system-reanalysis-cfsr. Code required to complete this study relied upon functions built into established packages in the statistical program R.

Peer Review

The peer review history for this article is available at https://www.webof science.com/api/gateway/wos/peer-review/10.1111/ele.70130.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.