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Environmental filtering affects soil fungal community composition more than dispersal limitation at regional scales

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ABSTRACT

The relative importance of dispersal limitation versus environmental filtering for community assembly has received much attention for macroorganisms. These processes have only recently been examined in microbial communities. Instead, microbial dispersal has mostly been measured as community composition change over space (i.e., distance decay). Here we directly examined fungal composition in airborne wind currents and soil fungal communities across a 40 000 km^2 regional landscape to determine if dispersal limitation or abiotic factors were structuring soil fungal communities. Over this landscape, neither airborne nor soil fungal communities exhibited compositional differences due to geographic distance. Airborne fungal communities shifted temporally while soil fungal communities were correlated with abiotic parameters. These patterns suggest that environmental filtering may have the largest influence on fungal regional community assembly in soils, especially for aerially dispersed fungal taxa. Furthermore, we found evidence that dispersal of fungal spores differs between fungal taxa and can be both a stochastic and deterministic process. The spatial range of soil fungal taxa was correlated with their average regional abundance across all sites, which may imply stochastic dispersal mechanisms. Nevertheless, spore volume was also negatively correlated with spatial range for some species. Smaller volume spores may be adapted to long-range dispersal, or establishment, suggesting that deterministic fungal traits may also influence fungal distributions. Fungal life-history traits may influence their distributions as well. Hypogeous fungal taxa exhibited high local abundance, but small spatial ranges, while epigeous fungal taxa had lower local abundance, but larger spatial ranges. This study is the first, to our knowledge, to directly sample air dispersal and soil fungal communities simultaneously across a regional landscape. We provide some of the first evidence that soil fungal communities are mostly assembled through environmental filtering and experience little dispersal limitation.

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Introduction

The processes controlling community assembly are a central focus of community ecology (Clements, 1912; Gleason, 1939; Hubbell, 2001; Leibold et al., 2004). A hierarchical framework of dispersal limitation, followed by species sorting through environmental and biotic filtering is the main progression controlling niche-driven community assembly (Leibold and McPeek, 2006). Conversely, neutral theory dictates that community assembly is a random process of dispersal, births and deaths, and genetic drift, stochastically regulated by the regional abundance of taxa (Bell, 2001; Hubbell, 2001). The relative importance of these processes in the community assembly of macroorganisms has received much attention (e.g., Funk et al., 2008; Leibold et al., 2010). However, how these filters affect microbial community assembly is largely unclear (Lekberg et al., 2007; Dumbrell et al., 2010a, b; Opik et al., 2010, 2013; Kivlin et al., 2011; Opik et al., 2013). In particular, the comparative influence of dispersal limitation versus environmental filtering is unknown for microorganisms. Determining community assembly rules is critical for microorganisms, as microbial taxa can alter ecosystem processes such as decomposition rates (Setala and McLean, 2004; Hattenschwiler et al., 2005) and aboveground productivity (Maherali and Klironomos, 2007).

Comparing dispersal limitation versus environmental filtering for microbial community assembly has been historically challenging due to two main obstacles: large population sizes and microscopic individual sizes. Because of these challenges, direct tests of the relative importance of dispersal limitation versus environmental filtering for microorganisms are rare (Bell, 2010; Langenheder and Szekely, 2011). Instead, studies commonly examine the relative importance of abiotic and biotic interactions for determining microbial community composition, often over small spatial scales (Lekberg et al., 2007; Dumbrell et al., 2010b) (but see Caruso et al., 2011, 2012 for tests of neutral community assembly). Any remaining differences in composition are then attributed to dispersal limitation measured as increasing dissimilarity in composition with geographic distance (i.e. distance decay). Recent work in microbial communities has demonstrated that distance decay patterns differ depending on spatial scale, which is analogous to communities of macroorganisms (Preston, 1960). For example, Martiny et al. (2011), showed that for ammonia oxidizing bacteria, dispersal limitation was most pronounced over centimeter scales, but not between continents. Contrastingly, Kivlin et al. (2011) demonstrated that for arbuscular mycorrhizal fungi, distance decay patterns were only noticeable between continents, but not within continents. Therefore, a general understanding of the effects of dispersal limitation in structuring microbial communities is lacking.

Here we explicitly focus on the relative role of dispersal limitation and environmental filtering in soil fungal community assembly, as these taxa provide critical ecosystem functions such as carbon (Hattenschwiler et al., 2005) and nutrient cycling (Maherali and Klironomos, 2007). The main dispersal vector of soil fungi is via airborne wind currents (Ingold, 1965; Warner et al., 1987; Brown and Hovmoeller, 2002). Chemical analyses of airborne particles indicate that fungal membranes comprise the majority of the organic matter fraction (Womiloju et al., 2003). In a study of airborne fungal composition in central Germany, Frohlich-Nowoisky et al. (2009) found that airborne fungal diversity was equivalent to that found in soils and varied seasonally. Inputs of fungal diaspora may mostly vary over weeks or months, as Fierer et al. (2008) observed little daily temporal turnover in fungal composition in air samples. Despite the advances of these recent studies, the relative importance of dispersal limitation in soil fungal community assembly is unknown because these studies only focused on airborne fungal communities at single locations and did not correlate airborne composition to potential soil sources or sinks.

Airborne fungal spore dispersal is mainly considered to be an unlimited, stochastic process influenced by local abundance of fungal populations (Baas-Becking, 1934; Finlay, 2002; Martiny et al., 2006). Indeed, current models of fungal dispersal treat propagules as dust particles (Womack et al., 2010; Wilkinson et al., 2012) and rarely consider life history or trait differences among fungal taxa. However, fungal spore traits and niches have the potential to affect dispersal (Levetin, 1990; Griffin, 2004; Ulevicius et al., 2004; Roper et al., 2008, 2010). Many fungal species have spores that are produced aboveground (i.e. epigeous) and optimized for aerodynamic airborne dispersal (Roper et al., 2008, 2010), while other taxa produce spores belowground (i.e. hypogeous) that are dispersed mainly by rodents (Mangan and Adler, 2000). Fungal spores may also be adapted to survive airborne dispersal by resisting desiccation (Levetin, 1990; Griffin, 2004) and UV radiation (Ulevicius et al., 2004). Moreover, fungal fruit bodies can form under abiotic conditions that are ideal for dispersal and subsequent establishment; for example immediately following rainstorms (Kauserud et al., 2011). These morphological and phenological characteristics suggest that airborne fungal dispersal may be driven by fungal traits or life history rather than stochastic chance.

In contrast to dispersal, the effects of environmental filtering are well known for soil fungal taxa. Soil fungal communities and physiology shift with soil moisture (Hawkes et al., 2011), temperature (Allison and Treseder, 2008; Bradford et al., 2008), and nitrogen concentrations (Allison et al., 2007). All of these abiotic conditions are altered by global change (IPCC, 2007). Predicting the response of soil fungal communities to these environmental shifts is not straightforward. If dispersal limitation influences soil fungal community assembly more than environmental filtering, fungal taxa adapted to a specific moisture or temperature regime may not be able to disperse to new, suitable, habitats. Therefore, the relative importance of dispersal limitation and environmental filtering on fungal taxa can also lend insight into future soil fungal community assembly.

Here we aim to test the relative importance of dispersal limitation versus environmental filtering for assemblages of soil fungal communities in southern California. We focus on directly sampling the airborne dispersal vector of fungi, as this mode is likely to dominate over long ranges. Southern California is an ideal area for understanding the relative importance of these mechanisms. Wind patterns are distinct and

well characterized throughout the year (Conil and Hall, 2006). Throughout the majority of the year, wind currents are predominantly from the northwest to the southeast (Conil and Hall, 2006). However, during the winter months, dry desert conditions cause Santa Ana winds, which blow from the northeast to the southwest. Because winds are seasonally distinct in this region, they are potentially carrying fungal spores from a range of sources over the course of a year.

If fungal taxa are dispersal limited, we predicted that soil and airborne fungal communities would be spatially autocorrelated such that sites closer together would be more similar while sites farther apart would be more distinct. If fungal dispersal is influenced predominately through neutral processes, we hypothesized that the most abundant taxa would also be most widespread in soils, as assembly would be a stochastic process. Alternatively, if fungal dispersal is influenced by fungal traits, we expected fungal taxa with smaller spore sizes and aboveground fruiting life history to have larger distributions. Finally, if environmental filtering is occurring in our soil communities, we predicted that soil fungal communities would correlate with the abiotic parameters of soil moisture, soil pH and/or soil carbon and nutrient concentrations.

To test these predictions, we characterized spatial and temporal patterns in the richness and community composition of airborne fungi from five locations sampled continuously from 2009 to 2011. We compared airborne community composition to wind direction and atmospheric conditions, and to nearby soil fungal communities. Furthermore, we examined how spatial and abiotic soil parameters affected fungal community composition belowground in these sites plus sixteen additional sites. Because fungal spore traits and life history are suspected to influence dispersal rates (Roper et al., 2008, 2010), we also contrasted spore size and growth habit with the abundance and range of each fungal taxon.

Materials and methods

Sample collection

Our study was conducted in coastal southern California between 34.61° N, 120.23° W; 34.15° N, 116.46° W; and 33.46° N, 117.04° W, approximately a 40 000 km^2 area (hereafter referred to as regional scale) (Fig 1). To capture potential spatial and seasonal shifts in airborne fungal communities, we sampled air from eddy covariance towers located at 33.73° N, 117.7° W; 33.74° N, 117.69° W; 33.81° N, 116.78° W; 33.61° N, 116.45° W; and 33.60° N, 116.46° W, approximately a 3 000 km^2 area (hereafter referred to as landscape scale), from Nov. of 2009 to Mar. of 2011. These towers continuously sample air at a rate of 640 l hr^{-1} through two 0.45 μm nylon filters placed roughly 7 m aboveground. Filters were exchanged every 2–3 months, or as needed when airflow was obstructed. While air sampling duration varied over the course of the study, fungal composition on the filters did not vary based on sampling interval ($r^2 = 0.04$, $P = 0.33$). Thus, we assumed that sampling duration did not affect our results. Wind direction, relative humidity, total rainfall and air temperature was also recorded at each of our towers every 30 min for the duration of the study.

We collected soils in Mar., Jul., and Nov. of 2010 from the five sites with eddy covariance towers as well as 16 additional sites throughout southern California (Fig 1). At each site, five 2.5 × 10 cm soil cores were taken over a 0.01 km^2 area and homogenized. While this sampling scheme did not allow us to exhaustively sample the entire 0.01 km^2 area, we attempted to homogenize our samples over a large area to avoid effects due to the microenvironment. However, because fungal communities are very spatially heterogeneous (Baldrian et al., 2012), we may not have detected all of the fungal community with our sampling protocol.

Soil biogeochemistry

A subsample of soil was processed to determine soil pH with a 1:1 ratio (w/v) of soil to diH_2O. Another subsample was acidified and then combusted to determine total soil carbon, nitrogen and the C:N ratio. We determined soil moisture gravimetrically and soil ammonium, nitrate, and inorganic phosphate concentrations via resin extraction and colorimetric assays (Robertson et al., 1999). We also examined fungal biomass belowground by extracting fungal hyphae in a 1.5 M solution of sodium hexametaphosphate and then visually inspecting at 200x via the gridline intersect method (Brundrett and Kendrick, 1990). All measurements were conducted in triplicate and pooled for each site at each sampling time.

DNA extraction

Airborne fungal DNA was extracted in duplicate from ½ of a 0.45 μm nylon filter from each tower at each sampling time using a Lysing E kit (MP Biomedicals) followed by a subsequent extraction with a MoBio Power Soil extraction kit (MoBio; Carlsbad, CA). In addition, DNA was extracted in duplicate from approximately 0.25 g of soil from each site at each sampling time using the MoBio Power Soil extraction kit. All duplicate DNA extractions were pooled and DNA concentrations were standardized to 10 ng μl^{-1} before PCR.

PCR amplification and sample preparation

DNA was amplified with conserved, barcoded fungal primers in the 18S region. The forward primer consisted of the 454 adapter B, a 2-bp linker sequence (AG) and the fungal-specific 18S primer, 817f (5′-TTAGCATGGAATAATRRAATAGGA-3′). The reverse primer consisted of 454 adapter A, a 12-bp barcode, a 2-bp linker sequence (AC), and the 18S primer 1196r (5′-TCTGGACCTGGTGAGTTTCC-3′) (Rousk et al., 2010). These primers were chosen as they flank a conserved region of the 18S gene that differs between fungal families, but is similar enough to be aligned in multiple sequence alignments. This 18S region is often considered to be more conserved than the ITS or 28S ribosomal region, which may lower our diversity estimates and make our findings most generalizable at the family level of resolution. However, diversity estimates of our study are on par with those recovered in a meta-analysis of 10 other fungal studies that used high-throughput sequencing of

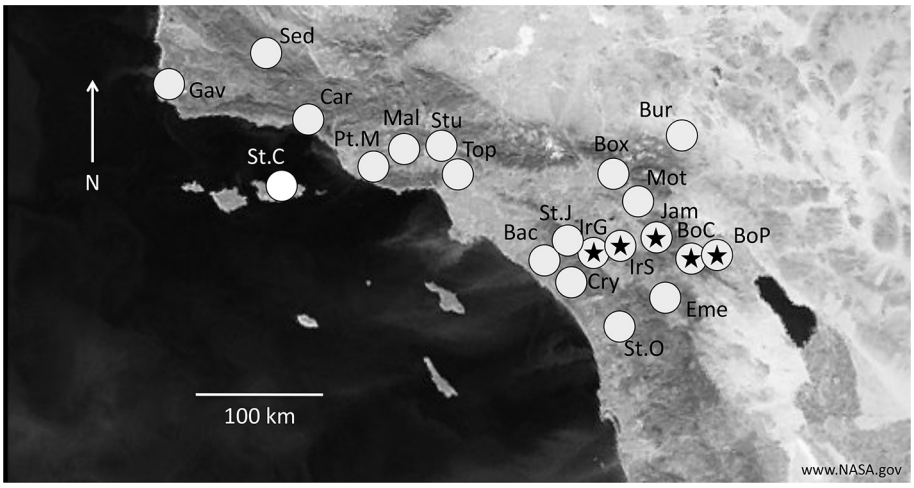

Fig 1 – Map of sample locations. White circles indicate soil sampling sites and black stars indicate air sampling sites. Site names are abbreviated to the first three letters. Full site characteristics are available in Supplementary Table 3.

the ITS region (Meisner et al., 2014). Each reaction was performed in triplicate and contained: 2 μl of ~10 ng DNA template, 1 μl of BSA, 0.75 μl each primer, and 22.5 μl of Platinum PCR Supermix (Invitrogen, Carlsbad, CA). The reaction ran for 30 cycles of 94 °C for 45 s, 52 °C for 30 s and 72 °C for 90 s with a hot start at 94 °C for 10 min and final extension step at 72 °C for 10 min. Triplicate PCR products were combined and purified using a MoBio UltraClean-htp PCR Clean-up kit to remove primer dimers and quantitated via fluorescence with a Qubit fluorometer. Samples were then pooled in equal amounts into one sample for 454 pyrosequencing and concentrated using a Purelink PCR Purification Kit (Invitrogen, Carlsbad, CA). The pooled sample was sent to the Environmental Genomics Core Facility at the University of South Carolina for pyrosequencing via a 454 Life Science Genome Sequencer FLX Roche machine.

Processing of pyrosequencing data

We obtained ~400 000 sequences from half a plate of a pyrosequencing run. Sequences were quality checked using the default settings in the Mothur pipeline (Schloss et al., 2009). Sequences were denoised using the Denoiser algorithm (Reeder and Knight, 2010). Then sequences were filtered if they had a quality score lower than 25, contained fewer than 150 bases, had ambiguous bases in the barcode region or contained anomalous homopolymers. This excluded ~10 % of the run. The 12 b bar code was used to assign sequences to samples. Sequences were clustered into operational taxonomic units (OTUs) at the 97 % cutoff using the furthest neighbor approach based on alignments created with MUSCLE v. 3.8 (Edgar, 2004). Sequences that were singletons in the entire dataset were removed, as these sequences were assumed to largely consist of sequencing errors (Dickie, 2010). All samples were then rarefied to 1 000 sequences to avoid bias in sampling effort between sites. Sequences were assigned a taxonomic identity by using the BLASTn algorithm on one representative sequence per OTU against the NCBI database with an expect value of 1 e^{-6}. With this criterion, we were able to classify 87 % of OTUs to genus. We calculated the relative abundance of each fungal taxon as the proportion of sequences within the 1 000 sequence rarefied subset at each site. Inferring taxon abundance from sequence abundance may not reflect the absolute number of individuals of every taxon at each site, due to differences in ribosomal copy numbers between species (Amend et al., 2010). Nevertheless, we used these data only to compare the relative abundance of individual taxa to themselves across sites, not to other taxa, which should result in equal bias in all samples. All analyses were performed in both the Mothur and Qiime (Caporaso et al., 2010) pipelines with no significant difference in results. Therefore, we present data from the Mothur pipeline analysis. All sequences were deposited in the GenBank sequence read archive with the accession number SRA046762.1. One representative sequence from each OTU sampled in soils in Jul., 2010 was used to create a maximum likelihood phylogeny with SATe (Liu et al., 2009) (Fig S1).

Statistics

Alpha and Gamma diversity were determined for each individual sample and for the entire dataset by rarefying all samples to 1000 sequences. Alpha diversity was calculated as the rarefied number of taxa that occurred at each location at each time point. Gamma diversity was calculated as the average rarefied total number of taxa in all air or soil samples at each sampling date. In addition, we calculated the standard error of gamma diversity between sampling dates to understand how species richness varied throughout our study. Differences in community composition, represented as the Bray–Curtis dissimilarity metric of the relative abundance of each taxon, were examined for both airborne and soil samples for the categorical variables of site, and month using nonmetric multidimensional scaling in PcORD followed by multiple regression permutation procedures (MRPP) (McCune and Mefford, 2006). We examined these same parameters based on a presence–absence community composition dissimilarity

matrix without any statistically significant differences in the results (data not shown). To examine the relative influence of spatial, temporal, abiotic and biotic factors on airborne fungal composition, we calculated partial regressions between the continuous variables of latitude, longitude, sample duration, vegetation community, wind direction, relative humidity, total rainfall, air temperature, and the Bray–Curtis dissimilarity metric of airborne community composition with a perMANOVA using the Adonis function in the Vegan package of R (Oksanen et al., 2009; R Development Core Team., 2009). Similarly, perMANOVA was used to determine the relative importance of spatial, abiotic and biotic factors structuring soil fungal composition by calculating partial regressions between the continuous variables of latitude, longitude, elevation, mean annual precipitation, soil moisture, total soil C, total soil N, soil C:N, soil NH_4^+, soil NO_3^-, soil PO_4^{3-}, soil pH and vegetation community and the Bray–Curtis dissimilarity metric of soil fungal community composition. While some soil chemistry variables are correlated with each other, perMANOVA is robust to these correlations. Furthermore, to avoid this bias, all partial regressions were run in a leave-one-out fashion to include only those variables that explained the largest portion of variation in community composition. Mantel tests were used to assess correlations between Havensine geographic distances between study locations and Hellinger transformed Euclidian community similarity for all soil and air samples in R (R Development Core Team., 2009). However, the use of latitude and longitude only may hinder our ability to determine dispersal limitation at multiple scales (i.e. Borcard et al., 2004). Because samples were collected across three time points, we used time as a covariate in all analyses. Time never significantly interacted with any other variables.

Spatial range and abundance

For each soil fungal OTU sampled in Jul. 2010, we determined the spatial range and relative abundance at each sampling site. Spatial range was simplified as the longest geographic distance between two sites that contained a focal OTU. We then performed logarithmic regression in R between abundance and spatial range for OTUs found only in soil, in both soil and air, and only in air (R Development Core Team., 2009).

Trait analysis

For the Jul. 2010 sampling date, we also collected the average spore volume and growth habit (i.e., aboveground/epigeous versus belowground/hypogeous) for each soil OTU genus from MycoBank (Crous et al., 2004). We obtained spore sizes for each genus from MycoBank instead of using our collected spores, as it is difficult to identify spores from environmental samples to genus. We calculated an index of dispersal ability for each OTU as

$$\text{Dispersal ability} = \frac{\text{Farthest distance between sites}}{\text{Mean abundance across sites}}$$

Thus, a higher dispersal ability for a taxon indicates that individuals of that taxon can disperse farther, on average. We assessed if spore traits were linked with dispersal ability by running phylogenetic independent contrasts in the AOT module of Phylocom on the SATe maximum likelihood phylogeny that was transformed to be ultrametric (Webb et al., 2008). We also used AOT to confirm contrasts in dispersal ability between epigeous and hypogeous fungi.

Results

Diversity

At each sampling point, the alpha diversity of airborne fungal communities was not significantly different from that of soil fungal communities (average air OTU richness = 162 ± 12, soil OTU richness = 152 ± 4, $P = 0.35$). Gamma diversity of airborne fungal taxa, however, was higher than soil fungi (2 799 ± 1 airborne taxa, 1923 ± 41 soil taxa), suggesting that airborne fungal assemblages varied more between samples than soil fungal communities.

Airborne composition

Airborne fungal communities generally clustered by sampling date with marginally significantly different fungal communities occurring overall between sampling months ($T = -1.34$, $A = 0.02$, $P = 0.09$) (Fig 2). Airborne fungal communities did not differ spatially (data not shown, $T = 0.35$, $A = -0.003$, $P = 0.61$). There was also no significant spatial autocorrelation between geographic distance of sampling locations and Euclidean distance between communities ($r = 0.01$, $P = 0.36$) (Fig 3A), so the hypothesis that fungal communities are dispersal limited at the landscape scale was not confirmed. The perMANOVA indicated that airborne fungal communities did not vary significantly with space, abiotic or biotic variables or sampling duration (Table S1).

In total, approximately 33 % of airborne fungal taxa also co-occurred in soils sampled in our study (Fig S2). However, the compositions of airborne and soil fungal communities were

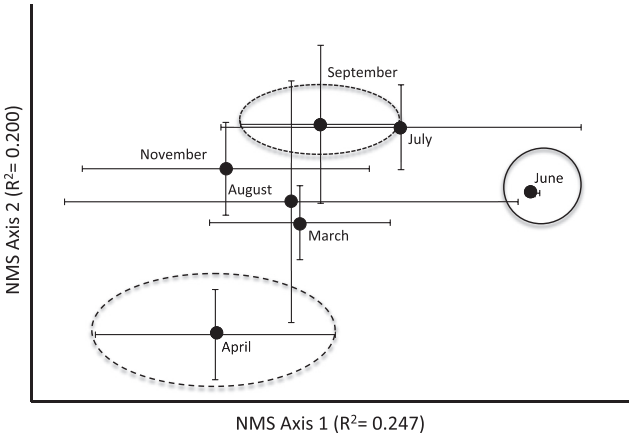

Fig 2 – NMS ordination of airborne fungal composition averaged for all sites in each month (±Standard Error). Composition differed marginally by sampling month ($T = -1.34$, $A = 0.02$, $P = 0.09$). Significant differences in composition by sampling month (corrected $P < 0.05$) are indicated by different circles.

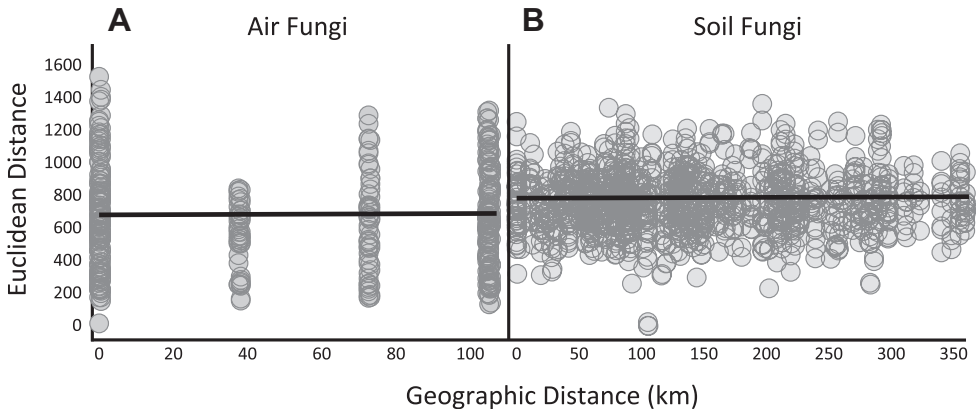

Fig 3 – Hellinger-transformed Euclidean distance versus geographic distance for all soil and airborne fungal communities. Euclidean distance of community composition was not significantly related to geographic distance between sampling sites in either air communities ($r = -0.06$, $P = 0.86$) or soil communities ($r = -0.06$, $P = 0.69$).

significantly different overall (Fig 4A, $T = -26.99$, $A = 0.03$, $P < 0.0001$) and within the same sampling site (Fig 4B, $T = -4.90$, $A = 0.03$, $P < 0.001$).

Soil composition

In contrast to air communities, soil fungal communities differed mostly by location. Overall, geographic location did not explain soil fungal distributions ($T = 0.51$, $A = -0.004$, $P = 0.68$). There was also no significant spatial autocorrelation between geographic distance and Euclidean distance of soil fungal communities at the regional scale ($r = -0.05$, $P = 0.87$) (Fig 3B), suggesting little community-wide dispersal limitation. Instead, three distinct groups of locations occurred which were driven by site-specific differences in abiotic parameters, latitude, and interactions between abiotic drivers of space (Fig 5 and Tables S2 and S3). Specifically, soil fungal community composition differed with soil nitrate concentrations ($r^2 = 0.02$, $P = 0.04$), soil C:N ($r^2 = 0.03$, $P < 0.01$) and interactions between total soil N concentrations and soil moisture, soil nitrate and ammonium concentrations, total soil C and latitude, and soil ammonium and longitude (Table S2). Other variables, such as soil pH, vegetation community and hyphal abundance, were not significantly related to soil fungal community composition (data not shown). In total, abiotic parameters explained 16 % of the variation in soil fungal community composition, even though each individual variable contributed only a small portion. Interactions between abiotic parameters and location explained an additional 4 % of the variation in fungal composition while latitude alone explained an additional 3 % of the variation in soil fungal composition (Tables S2, S3, S4).

Abundance versus spatial range

When comparing all sampling sites and dates, fungal taxa that were abundant in the air were also abundant in soils ($r = 0.33$, $P < 0.001$), indicating that abundance-dependent, neutral dispersal and establishment may play a role in community assembly of air-dispersed taxa at the landscape scale. To understand if airborne and soil fungal communities differed in their distributions, we regressed the mean abundance of

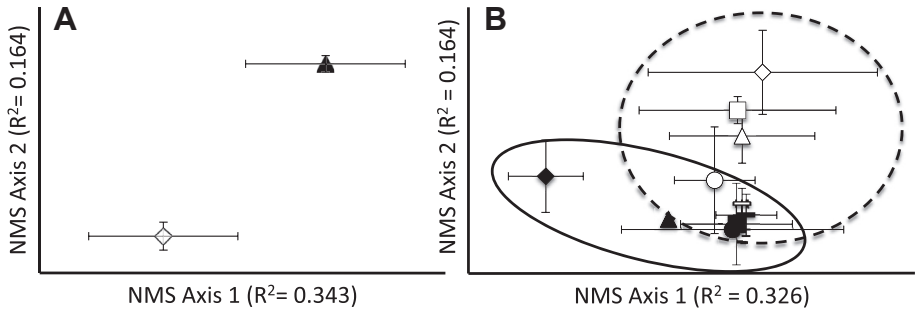

Fig 4 – (A) NMS ordination comparing composition of all soils averaged across all sampling sites and dates (closed shape, bounded by solid line)(±Standard Error) and all air samples averaged across all sampling sites and dates (open shape, bounded by dashed line)(±Standard Error). Composition significantly differed between soil and air samples ($T = -26.99$, $A = 0.03$, $P < 0.0001$) (B) NMS ordination comparing composition of soils (closed shapes)(±Standard Error) and air samples (open shapes)(±Standard Error) at the same geographic location. Soil samples were significantly different from airborne samples ($T = -4.90$, $A = 0.03$, $P < 0.001$). Sites are as follows: squares Irvine Ranch Grassland; triangle Irvine Ranch scrubland; circles James Reserve; diamonds Boyd Pinyon; rectangles Boyd Chaparral.

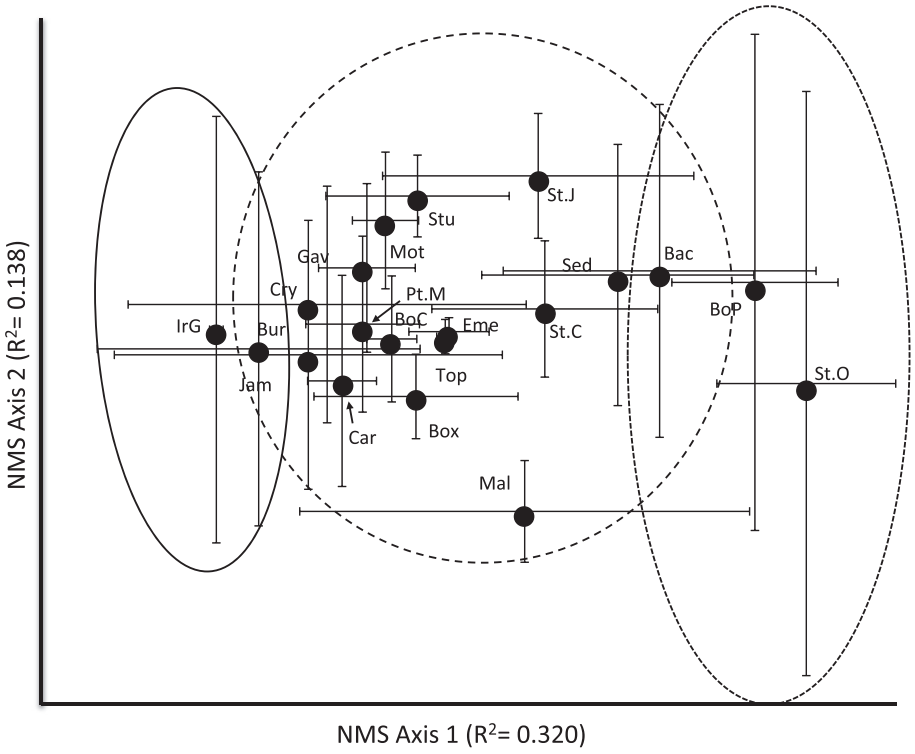

Fig 5 – NMS ordination of soil fungal community composition averaged for all sampling times at each site (±Standard Error). Composition varied by site with three distinct groups of sites, but not overall by space ($T = 0.51$, $A = -0.004$, $P = 0.68$). Significant differences in composition by location (corrected $P < 0.05$) are indicated by different circles.

each fungal taxon at each site where it was present in Jul. 2010 (i.e., regional abundance) against their spatial range. First we considered fungi only collected in air samples. For those fungi that occurred only in air, the spatial range of OTUs was not significantly related to their landscape-scale abundance (Fig 6A, $r = 0.04$, $P > 0.05$). Airborne fungi, sequenced from air filters that were also found in soils also had spatial ranges that were not significantly related to their landscape-scale abundance in air samples (Fig 6A, $r = 0.09$, $P > 0.05$). Next we considered fungi only collected in soils. For soil fungi that were only found in soils, not airborne samples, the regional abundance of OTUs was positively related to their spatial range

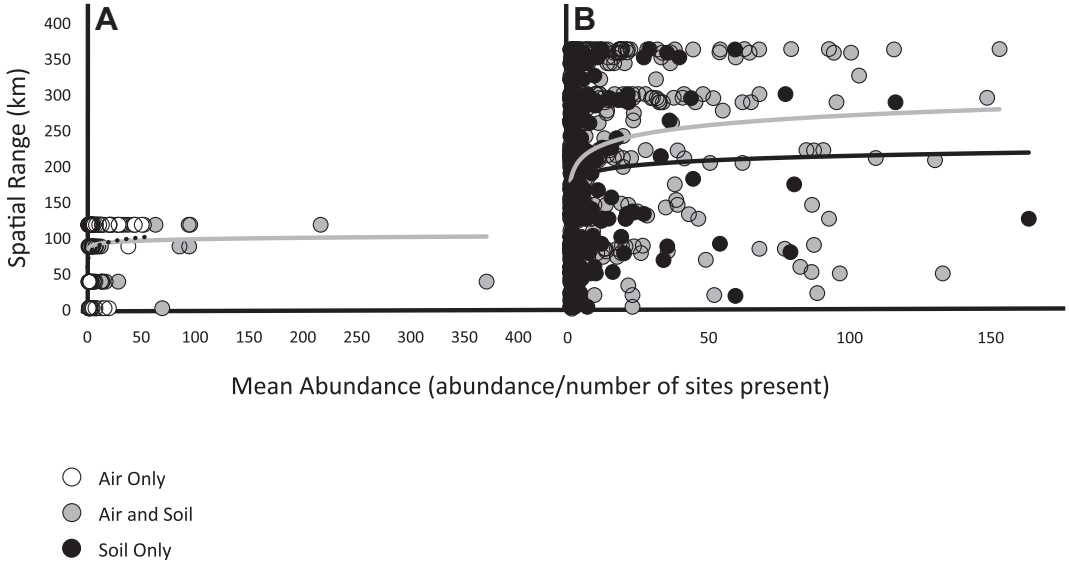

Fig 6 – Mean regional abundance of air (A) and soil (B) fungi by sampling site. All soil fungal abundances were significantly correlated with spatial range while air fungal abundance was not correlated with spatial range (air only ($r = 0.04$, $P > 0.05$); air samples also found in soil ($r = 0.09$, $P > 0.05$); soil samples also found in air ($r = 0.18$, $P < 0.001$); and soil only ($r = 0.10$, $P = 0.05$)).

(Fig 6B, $r = 0.10$, $P = 0.05$). However, fungal OTUs sequenced from the soil that were also found in airborne samples had a stronger positive relationship between their abundance in the soil and spatial range (Fig 6B, $r = 0.18$, $P < 0.001$).

Spatial range and abundance and spore morphology

The average volume of sexual spores for each OTU was negatively related to dispersal ability (Independent Contrast, $r = -0.43$, $P < 0.001$). This result indicates that taxa with smaller volume spores (<50 μm^3) dispersed more readily than those with larger spores (>1 000 μm^3), given similar abundances. Fungal taxa that produce aboveground spores also displayed higher dispersal ability than fungal taxa that produced belowground spores (Variance Contrast = 35.16 ± 8.57, $P < 0.001$). There was no difference in dispersal ability based on spore shape (i.e. ellipsoid v. crescent) ($P > 0.05$), or on spore surface texture (i.e. smooth v. warted) (Table S5, $P > 0.05$).

Discussion

Overall, airborne and soil fungal diversity was of the same order of magnitude in our study and equivalent to fungal diversity found in other systems (Frohlich-Nowoisky et al., 2009; Meisner et al., 2014). Because airborne fungal communities were so abundant and diverse, the potential for airborne fungal dispersal between geographic locations is appreciable. Indeed, one third of soil fungal taxa appeared to be air-dispersed as the same taxa were found in air samples throughout our study area. Furthermore, airborne fungal communities varied temporally and not spatially, indicating that there was no significant geographically based turnover in composition within our study area. Moreover, because airborne fungal communities were consistently distinct from nearby soil fungal communities, soil point sources near our air sampling towers were likely not the primary contributors to the airborne fungal composition (or *vice versa*). Therefore, airborne fungi did not seem to be dispersal limited over the landscape range (~3 000 km^2). Our survey, however, may have inflated living fungal diversity by assaying spores that suffered UV damage (Ulevicius et al., 2004) or desiccation (Griffin, 2004) and, therefore, were not viable. Alternatively, the use of 18S primers may have caused us to underestimate OTU diversity in both air and soil samples. Furthermore, while most previous studies of airborne fungal communities have been conducted at single sites (Fierer et al., 2008; Frohlich-Nowoisky et al., 2009), some culture-dependent approaches have suggested that airborne fungal composition may vary spatially (Shelton et al., 2002). Thus, airborne fungal composition, at least for viable, culturable fungi, may vary geographically over spatial scales that are larger than the 3 000 km^2 represented in our study system.

Airborne fungal diaspora are often temporally variable (Lin and Li, 2000; Jones and Harrison, 2004; Fierer et al., 2008; Frohlich-Nowoisky et al., 2009; Bowers, 2014). These temporal variations have been attributed to shifts in daily temperature (di Giorgio et al., 1996; Calderón et al., 1997; Lin and Li, 2000; Burch and Levetin, 2002), wind direction (di Giorgio et al., 1996), relative humidity (Calderón et al., 1997; Lin and Li, 2000; Burch and Levetin, 2002) and rainfall (Venables et al., 1997; Burch and Levetin, 2002). We did not find support that airborne fungal community composition shifted with abiotic variables in southern California. However, the lengthy sampling time may have integrated airborne fungal diaspora produced throughout a variety of abiotic conditions.

Fungal diaspora are known to travel transcontinental distances via wind currents (Brown and Hovmoeller, 2002; Munoz et al., 2004; Kellogg and Griffin, 2006). Previous evidence also suggests that soil fungal communities differ over continental scales (Kivlin et al., 2011). Thus, we expected to see differences in airborne fungal communities based on changing wind patterns, and therefore points of origin, throughout the year (Conil and Hall, 2006). Instead, fungi in wind currents in our area may be thoroughly mixed, disrupting any signal of diaspora origin. Alternatively, our 2–3 month sampling scheme may have integrated fungal spores from a variety of sources, also effectively disguising diaspora origins. Mushroom-producing fungal species are also known to vary temporally in fruiting time and spore production, dependent on abiotic cues (Kauserud et al., 2011). While we do not have any direct evidence of differences in spore production over time in this system, mushroom phenology could be driving the temporal patterns we observed in airborne fungal composition.

Soil fungi that were dispersed via the air seemed to largely experience stochastic dispersal in our study. Generally, air-dispersed fungi that were common at any given site were also widespread across the region in the soil. The regional abundance of fungal OTUs in the soil explained 18 % of the variation of the range in which fungi were located, as long as the taxon was air-dispersed. Similar patterns of abundance and occupancy can be seen for animals (Gaston et al., 1997) and bacteria (Nemergut et al., 2011): the most regionally abundant taxa also have the largest ranges. Many mechanisms such as niche breadth, habitat breadth, metapopulation dynamics, density dependent growth and sampling artifacts have been posited as explanatory factors for these trends in animal communities (Gaston et al., 1997). The extent to which these processes shape microbial communities is unknown, although this trend suggests that similar mechanisms may affect the distribution of all organisms.

Deterministic, niche-based processes may also influence fungal dispersal, as there was variation in regional abundance and dispersal range for soil fungi. Some taxa were very abundant at a few sites, but were not widespread. These taxa were predominantly hypogeous fungi with poor long-range dispersal, but may also be poor competitors that cannot establish easily in new communities. Examples of this archetype that occurred frequently in our study system are fungi in the genus *Glomus*. These fungi occur as arbuscular mycorrhizal symbionts in many ecosystems, and are known to experience dispersal limitation at even small scales (<3 km) (Lekberg et al., 2007). Many fungi with hypogeous spore production are dispersed via animal ingestion (Janos et al., 1995; Klironomos and Kendrick, 1996; Mangan and Adler, 2000), which may also explain their reduced range sizes. Conversely, fungal taxa with aboveground fruit bodies had significantly larger ranges than those that reproduce belowground. There were also numerous rare taxa that were found in many locations. These fungi tended to have smaller spores, which is

consistent with the expectation that smaller particles have longer residence times in the air and will travel farther (Wilkinson et al., 2012). An example of this archetype in our study is a *Suillus* sp. This fungus is ectomycorrhizal and can invade areas where its host, *Pinus* sp., have been introduced (Hynson et al., 2013). While we have focused on spore-based dispersal, some fungal taxa can be aerially dispersed via hyphal fragments and colonized root fragments (Green et al., 2006). We did not detect any of these in our air filters at 200x magnification, but since our study focused on fungal spore dispersal, we may not have captured all of the airborne dispersal dynamics.

While we observed mostly neutral fungal dispersal for fungal taxa that were aerially dispersed, on the whole, environmental filtering influenced soil fungal community assembly. There was no discernable distance–decay relationship over the regional scale of our soil fungal communities, even though soil fungal communities varied significantly among sites. Soil fungal communities may be relatively well-mixed over this region, and the variation among sites could be due to site-specific abiotic factors. For example, in our study soil nitrate, ammonium, soil C:N, and interactions between these factors and soil moisture, latitude and longitude correlated with fungal community composition. Belowground fungal composition is affected by soil moisture in other systems (Lekberg et al., 2007; Allison and Treseder, 2008; Kivlin et al., 2011). Moreover, soil nutrient concentrations have been linked to shifts in fungal composition in a variety of ecosystems (Dickie et al., 2002; Lilleskov et al., 2002; Hoffland et al., 2004; Allison et al., 2007; Johnson et al., 2010), and are particularly relevant in southern California where nitrogen deposition can affect fungal communities (Egerton-Warburton and Allen, 2000). Since fungal taxa are known to specialize on different nutrients (McGuire et al., 2010) and environmental conditions (Hawkes et al., 2011; Kivlin et al., 2011), it is not surprising that these same abiotic factors largely controlled the composition of soil fungi in our sites. The interactions between environmental filtering over space that we observed may indicate reduced dispersal capabilities for some fungal taxa, especially for the 2/3rds of the soil fungal taxa that were not found in airborne samples. However, the distributions of these taxa were not strictly spatially structured, as latitude only predicted 3 % of the variance in fungal composition and longitude was not significant.

The abiotic factors that we measured did not explain all of the variation in soil fungal community composition in our dataset. Other drivers may also be structuring soil fungal communities. One set of factors that we did not measure, but is known to influence fungal communities, is biotic interactions. Biotic interactions between fungi (Maherali and Klironomos, 2007; Kennedy, 2010; Tucker and Fukami, 2014), predation, or interactions between fungi and other microorganisms (Fitter and Garbaye, 1994) or plants (Davison et al., 2011) could be structuring soil fungal communities. Other abiotic factors that we did not measure, such as soil texture (Lekberg et al., 2007), can also affect fungal community composition. Furthermore, since we observed neutral distribution patterns for a majority of fungal taxa, neutral or stochastic assembly of fungal taxa may explain some of the residual variation in soil fungal community composition.

Overall, we found support for soil fungal communities being assembled via a combination of deterministic environmental filtering and stochastic or neutral processes. We found no evidence that the majority of airborne fungal taxa were dispersal limited over the landscape scale in our study system. Instead, fungal dispersal was mostly a stochastic process that varied over time. Soil fungal distributions for most fungal taxa were correlated with their regional abundance, which suggests that neutral community assembly may also be occurring in this system. For a minority of taxa, however, fungal spore traits and growth forms also influenced their regional abundance and spatial range. In future climates, changes in abiotic parameters such as soil moisture and nutrient concentration, not dispersal limitation, will likely have the largest influence on fungal composition and ecosystem-level nutrient cycling.

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Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.funeco.2014.04.004.

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