UNIVERSITY OF CALIFORNIA,
IRVINE

Linking airborne fungal dispersal with ecosystem function

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Biological Sciences

by

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DEDICATION

To

My parents, Khang and Cuc, who took me on my first hikes,

My brothers, Michael and Alan, who first explored the world with me,

And to my forever co-explorer, Stephen.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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ABSTRACT OF THE DISSERTATION

Linking airborne fungal dispersal with ecosystem function

By

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Doctor of Philosophy in Biological Sciences

University of California, Irvine, 2019

Professor Kathleen K. Treseder, Chair

Fungi play critical roles in ecosystem function. Fungal pathogens, decomposers, and symbionts mediate ecosystem functions. These functions include biological control via disease, carbon emissions via decomposition rates, and carbon sequestration via plant growth rates.

Indeed, ecosystem function is partially a reflection of which fungal groups are able to disperse to and colonize in the ecosystem. Dispersal is a mechanism for fungi to follow their ideal niches as they shift under climate change. Therefore, studying fungal dispersal will allow us to understand how ecosystem function may change in concert with climate.

The goal of my dissertation is to understand airborne fungal dispersal in relation to ecosystem function. In my first chapter, I underline the importance of international cooperation when researching fungal pathogen dispersal and conducting public health surveillance on fungal diseases. I recommend actions that local, state, and national governments can take in order to improve their ability to forecast fungal dispersal and disease in humans.

My second chapter addresses differences between fungal communities in the soil versus the air across the Southwestern U.S. In order to understand dispersal differences between fungal functional groups, I sampled soil and air across Arizona, California, New Mexico, Nevada, and

Utah. Then, I compared relative abundances of functional groups in soil and air, as well as their extent of occurrence (i.e., range). I discovered that fungal pathogens tend to be found at high relative abundances in the air compared to other functional groups. Fungal pathogens also have the largest extent of occurrence in the soil.

Finally, my third chapter examines changes in fungal dispersal during normal, onshore wind conditions and Santa Ana events in Southern California. I used a high-volume sampler to capture the fraction of fungi that are small enough to be inhaled deep into human lungs. I found that Santa Ana winds bring a five-fold increase of decomposer fungi that may be pre-adapted to desert conditions. Climate change will cause Southern California to become warmer and drier, which means these fungi may alter decomposition rates and carbon cycling in the future. All together, my dissertation addresses spatial and temporal changes in fungal dispersal as it relates to ecosystem function.

INTRODUCTION

Climate change forces populations to adapt to changing conditions, move to new suitable habitats, or perish. Dispersal is one way that populations may deal with stress from climate change—they may move to a less stressful area that matches their niche as the climate changes. Indeed, plants and animals move their ranges 6.1 ± 2.4 km per decade towards the poles in order to follow their optimal habitats due to climate change (Parmesan and Yohe 2003). In the U.S. Southwest, ecosystems will get progressively drier and warmer within the next century (Seager and Vecchi 2010). We can expect that ecosystem function, including decomposition rates, will likely be altered by these changing conditions. This change may be mediated by fungi, which play critical roles in ecosystems.

Broadly, fungi can be grouped by their roles in ecosystem function. Fungal pathogens cause disease, mediating biodiversity; decomposers break down dead, organic matter; and symbionts generally increase plant growth (Wardle et al. 2004, Boddy et al. 2008, Maron et al. 2011). The fungal groups present as well as their relative abundances can mediate ecosystem function. Climate change could lead to fungal range shifts, if fungi follow their climate niches across the landscape (Kivlin et al. 2017).

Under a changing climate, long-distance dispersal will play an important role in controlling which fungi are able to move and successfully colonize new regions. While we understand how plants and animals shift under a changing climate, it is relatively unknown how far and fast fungi can disperse. Fungal spores are lightweight enough to be lofted into the air and dispersed long distances (Carlson and Prospero 1972). Currently, we do not know characteristics of fungal dispersal between different functional groups. Dispersal mode—transport via air or soil— can be a proxy for their dispersal speed. This is because air-dispersed fungi might be able

to move quickly compared to soil-dispersed fungi that rely on growth for movement. In addition, understanding these aspects of fungal dispersal can help us better parameterize trait-based and niche ecosystem models (Allison 2012, Lennon et al. 2012, Treseder and Lennon 2015). These models could help us anticipate threats to food security and human health, both of which will be exacerbated by climate change (Fisher et al. 2012).

Finally, long-distance dispersal of fungi poses societal challenges, especially under a changing climate. Fungi will likely shift their ranges across international borders, which can complicate ecological studies and, in the case of fungal pathogens, pose human health risks. For ecologists, access to soil and air sampling across the border can be difficult. Populations previously unexposed to certain fungal pathogens may be more susceptible as the disease disperses across the border. For these reasons, I focus on the Southwestern U.S. and Northwestern Mexico.

In my dissertation, I examine fungal airborne dispersal as it relates to ecosystem function. I aimed to answer the following questions:

1. What can be done to support the study of fungal dispersal research, especially in the context of policy?
2. Which fungal functional groups are better represented in air compared to the soil?
3. How does fungal dispersal change over time when the source of spores is altered?

In my first chapter, I cover fungal dispersal through the air across international borders. Ecosystems can be bisected by international borders. As a result, ecologists may be missing important data on how organismal populations disperse, including fungi. To answer the first question, I wrote recommendations for local, state, and national governments as well as for stakeholders to improve both ecological research and public health surveillance across borders.

Ecologists can achieve greater coverage and availability of data by standardizing sampling methods. Public health surveillance can be improved with mandatory reporting of fungal disease incidence that is gathered at the national level. Finally, researchers can develop models that forecast fungal disease incidence. These forecasts can be used by stakeholders to reduce exposure to fungal disease that has no vaccine and is expensive to cure. These findings were published in *Journal of Environmental Health*.

For my second chapter, I examined differences between soil and airborne fungal communities. By collecting soil and air samples across AZ, CA, NM, NV, and UT, I was able to find spatial differences in the range of various fungal groups that influence ecosystem function. Additionally, I compared relative abundances of fungal functional groups between the soil and air to understand more about their airborne dispersal ability. I found that pathogens tend to be more air-dispersed, and that decomposers tend to be more soil-dispersed. Moreover, pathogens have a significantly larger range, or extent of occurrence, in the soil than other fungal groups. This manuscript is currently in revision with *Fungal Ecology*.

In my third chapter, I compared airborne fungal communities arriving from the desert versus over the ocean in Southern California. In contrast to the mild, onshore wind patterns on the coast, Santa Ana winds bring hot, dry air from the desert (Hughes et al. 2011). Santa Ana winds are strong, seasonal winds that may bring disproportionate numbers of spores from the desert to the coast. I demonstrated that Santa Ana winds bring higher concentrations of airborne spores. Moreover, the majority of these spores are decomposer fungi. These decomposer spores may be pre-adapted to the warmer and drier conditions that will characterize Southern California in the near future. Models of Santa Ana winds under climate change suggest Santa Ana winds

will continue to bring lower humidity and higher temperatures to Southern California, particularly during the driest parts of the year (Miller and Schlegel 2006, Hughes et al. 2011).

Collectively, my dissertation outlines patterns of dispersal among fungal pathogens, decomposers, and symbionts. My research found large fluxes of potentially pre-adapted decomposer fungal spores from the desert arriving to a warming, drying coastal ecosystem. In addition, it connects ecological and public health research of fungal pathogen dispersal to societal challenges and offers solutions moving forward. Ultimately, my dissertation provides insight on how long-distance dispersal of fungi can mediate ecosystem structure and function.

CHAPTER 1

Crossing the Line: Human disease and climate change across borders

Co-Authors: Morgan Gorris, Meritxell Riquelme, Jim Randerson, and Kathleen Treseder

Introduction

Many fungi disperse through the air as spores (Ingold 1953; Roper et al. 2008). The atmosphere harbors living spores of an untold number of fungal species (Blackwell 2011), and continuously moves them between nations and human populations (Kellogg & Griffin 2006). In fact, 1 m^3 of air can harbor thousands of fungal spores representing hundreds of species (Bianchi & Olabuenaga 2006; Crawford et al. 2009; Hasnain et al. 2005; Kasprzyk & Worek 2006; Levetin 1990; Mallo et al.2011; Oliveira et al. 2009; Pyrri & Kapsanaki-Gotsi 2007; Quintero et al. 2010). Fungi produce spores able to disperse and colonize a new territory, which—in the case of pathogenic fungi—can include humans. Over 300 known fungal species can infect humans, causing more than a million human deaths each year (U.S. Center for Disease Control, 2014). Many of these fungal diseases are airborne. The prevailing winds that entrain them are likely to shift direction and magnitude under climate change, threatening populations that have not been previously exposed and therefore have not developed immunity (Yin 2005).

Climate models predict changes in the region surrounding the Mexican-U.S. border (Karl et al. 2010). Within this century, mean annual temperatures are expected to increase by 2−5 °C, and droughts may become longer and more severe (Karl et al. 2009; Schoof et al. 2010). Since the environmental niches of many species are strongly influenced by climate, their geographic ranges may shift accordingly (Whittaker 1975). In fact, these range shifts may be particularly striking in the U.S.-Mexico border region, since water scarcity and high temperatures already limit the activities of many animals, plants, and microbes (Toberman et al. 2008; Yuste et al.

2011). It would not be surprising if species follow their optimal climate envelope north or south across the border, depending in part on their ability to withstand heat or drought. A large-scale movement of diverse species would connect ecosystems in Mexico with those in the U.S., with consequences that can best be understood via collaborative research between the two nations.

Because many diseases are expected to become more prevalent under climate change (Lafferty 2009), disease ecology has recently emerged as a crisis discipline. Disease ecology requires a multidisciplinary effort by researchers with diverse expertise, including health professionals, social scientists, microbiologists, and climate change scientists who must advance research rapidly to address the new challenges. Furthermore, as pathogens cross borders, international collaboration is required to effectively anticipate and mitigate outbreaks (Bebber et al. 2013; Lafferty 2009; Raffel et al. 2012).

We use a dimorphic fungus, *Coccidioides* spp. (Fig. 1), as (1) a test case for determining what environmental factors influence the dispersal of fungal pathogens within the border region, and (2) an example of how scientists, public health specialists, and medical professionals from the U.S. and Mexico can collaborate by leveraging shared knowledge.

Two fungal species, *Coccidioides* immitis and C. posadosii cause valley fever. Valley fever has been monitored for the last several decades, but recently, this disease has become a "silent epidemic". In the southwestern U.S., its annual incidence has increased rapidly from 6 cases per 100,000 people in 1995 to a peak of 42 per 100,000 people in 2011, a >6-fold increase (Fig. 2)(Sondermeyer et al. 2013; U.S. Center for Disease Control 2011). For comparison, the incidence of new lung cancer cases was 57 per 100,000 in 2011 (U.S. Cancer Statistics Working Group 2016). A similar increase was documented in Mexico, though more data is needed to continue tracking these trends in the present day (Baptista & Riquelme 2007). Valley fever is

caused by inhalation of *Coccidioides* spores, and even one spore can cause disease (Huang et al. 2012).

The fungus resides in the soil of arid and semi-arid ecosystems in the southwestern U.S. and northern Mexico (Fig. 3). *Coccidioides* mycelia grow after rainstorms, and then forms spores during long dry periods (Lacy & Swatek 1974). Spores can cause infection once wind lofts dusty soil into the air. Climate models predict increased drought length interrupted by heavier rainstorms in the southwestern U.S., which should favor these growth and dispersal mechanisms (Schoof et al. 2010). *Coccidioides* is not dependent on host densities for infection, unlike other vector-borne disease such as Zika virus or Chagas disease. Incidence rates in humans are correlated with climate and environmental factors (Gorris et al. 2018), therefore, understanding the ecology of the causal agent is critical to forecasting outbreaks.

Much of the information regarding environmental preferences of *Coccidioides* was collected and analyzed in the 1950s and 1960s. It is critical that we revisit these ideas using current data and modern techniques because a lack of contemporary studies prevents informed decision-making regarding disease surveillance, vaccine development, and outbreak preparedness. In addition, a bi-national survey of this fungus would be unprecedented.

Human welfare impacts of valley fever

Fungal dispersal has far-reaching effects on many aspects of human welfare, ranging from health to economic concerns (Fisher et al. 2012). Human disease, including valley fever, can lead to debilitation, loss of quality of life, and a large financial burden from medical costs (Health Canada 2003). Mostly, valley fever causes only mild flu-like symptoms, but it can lead to chronic pneumonia or mortality in some patients, particularly in immunocompromised patients. In some cases, life-long medical treatment is required (Nguyen et al. 2013). Valley

fever treatment is particularly expensive, averaging $23,000 to $29,000 per patient in the U.S. (Plevin 2012). Disseminated valley fever costs $680,000 per person for hospitalization and treatment (Pappagianis et al. 2007). There is currently no vaccine for valley fever in humans. A vaccine was proven successful for mice and will be available in coming years for dogs, which are more prone than humans to inhale the fungal spores due to their proximity to the ground (Narra et al. 2016). To determine future threats of valley fever on human welfare, we need to know the extent to which it overlaps with dense human populations.

There are three distinct endemic areas for valley fever in Mexico: the northern area near the U.S. border, the Pacific coast, and the Mexican central valley (Fig. 3; (Sifuentes-Osornio et al. 2012). In California, the Central Valley is hyperendemic with parts of Southern California classified as endemic (Sifuentes-Osornio et al. 2012; U.S. Center for Disease Control 2011). In various parts of Mexico, skin testing using coccidioidin, an antigen, has revealed exposure to the fungus of 5% to 30% of the population (Sifuentes-Osornio et al. 2012).

In general, up to 40% of those exposed to valley fever spores develop the disease. Less than 1% of these patients experience severe pneumonia, which mostly affects patients with associated risk factors such as HIV, diabetes mellitus, chemotherapy, transplantation, or third-trimester pregnancy (Sifuentes-Osornio et al. 2012). For these high-risk groups, mortality rates increase up to 90% (Sifuentes-Osornio et al. 2012). Inmates imprisoned in the Central Valley of California are especially vulnerable to valley fever, because prisons are often built near *Coccidioides* spp. habitats (de Perio et al. 2015; Pappagianis et al. 2007). In addition, prison populations contain a disproportionately high number of African-American and Latino males, who have a relatively high risk of valley fever infection (Perio & Burr 2014). Many people are incarcerated for minor crimes but often leave their imprisonment with debilitating and expensive

cases of valley fever, especially since prisoners show higher rates of incidence compared to the population in neighboring cities (Pappagianis et al. 2007).

Rates of valley fever infection have now reached epidemic proportions in the border region near the states of California, Arizona, and Baja California, perhaps owing to shifts in drought severity, temperature, and dust loads (Park et al. 2005). Moreover, if climate and soil disturbance continue to change, endemic regions of valley fever could spread in the near future, potentially exposing a greater number of humans to the illness, including the 13 million people within the greater Los Angeles area (U.S. Census Bureau 2010) plus 1.3 million people in the Tijuana, Mexico area (Instituto Nacional de Estadística y Geografía 2010), as well as people in the American and Mexican states listed in Table 1. Another concern is exposure of pets and stray animals, which are more easily infected due to their proximity to the ground and behavior. Corpses of animals that die from valley fever infection are often buried or left on the spot, in the case of strays. If not cremated, those infected tissues can contribute to establishment of new sites of *Coccidioides* growth in the environment.

Fungal pathogens in a bi-national context

Epidemics of human diseases are an international concern. Ecological research answers questions about systems that cross borders. However, both epidemiological and ecological studies constrain their data by border. To overcome this limitation, it is crucial that scientists of the U.S. and Mexico collaborate to share ideas and data. Bi-national cooperation is especially critical if fungal pathogens become more wind-dispersed or change their ranges under global change. Ecologists will need to share their data in order to better understand dispersal of *Coccidioides*. In addition, epidemiologists should standardize and share incidence data of valley

fever. Research encompassing the border area could be accomplished with cooperative research and data exchange from both sides of the frontier.

For example, by working together to map and understand the distribution of fungal pathogens, researchers from Mexico and the U.S. could greatly improve preparedness for—and prevention of—disease outbreaks in the border region. While available public health and medical data from the U.S. and Mexico are too uneven to make direct comparisons, standardized environmental sampling can be conducted across borders and integrated with global climate data. Ecologists should share and standardize methods for soil sample collection so bi-national ecological data can be used across much larger areas. We support existing international meetings of researchers focused on valley fever that facilitate research collaborations, such as the Coccidioidomycosis Study Group, the California Coccidioidomycosis Collaborative Meeting, and the International Coccidioidomycosis Symposium. After research is conducted, short summaries in both English and Spanish on pertinent research should be made accessible to decision makers on both sides of the border. This could increase the use of scientific information in policy-making. We recommend that scientists from both Mexico and the U.S. share research findings with the Congreso de la Unión and Congressional offices, respectively, in order to raise awareness at the federal levels. This could lead to increased research funding for ecological projects that examine disease impacts and initiatives in inter-agency working groups at the federal level (e.g. existing partnerships between Centers for Disease Control (CDC), National Oceanic and Atmospheric Administration, National Center for Atmospheric Research, National Institutes of Health and others).

Public health incidence data complements the ecological research by confirming infections are rising in concert with airborne spore abundance and dispersal. As with ecological

data, bi-national cooperation would increase data available for public health studies relating incidence to environmental conditions. Until 1994, valley fever incidence rates mirrored the rapid increase in the U.S., however, there is no data after 1994 when valley fever surveillance was no longer mandatory (Baptista & Riquelme 2007). The Four Corners Initiative combines incidence data from the border states of Arizona, Chihuahua, New Mexico, and Sonora. As of September 2015, this project is still in pilot stages (Dulin 2015). In addition, we suggest adding Baja California because it is in the endemic area. There is no obligation to collect data on valley fever incidence in Mexico. Therefore, we recommend that Mexico reinstate their valley fever surveillance in order to improve decision-making. To determine valley fever hotspots, researchers need consistent data collected over at least a few years. If Mexico were able to collect valley fever case data, vaccines - when they are approved for humans - could be brought to areas that need the most protection. In addition, the U.S. should require valley fever to be a reportable disease outside of the endemic zone since increased domestic travel may aid dispersal and expose additional populations (Gorris et al. 2018). After these policies are implemented, the U.S. and Mexico should coordinate with their local and state public health departments to consolidate incidence data. Then, the federal governments should share the bi-national data for analysis by public health departments that currently have resources to do so. There are some limitations because incidence data collection will differ between the U.S. and Mexico. However, states in the U.S. also exhibit variations in data collection due to delays in diagnoses, incubation time variation, and reporting requirements. Even with these limitations, we are still able to find significant relationships between valley fever incidence and environmental factors including precipitation, temperature, soil moisture, and dust concentration (Gorris et al. 2018). Recommendations stemming from ecological data and public health surveillance would be

important steps towards preventing loss of human life, reducing morbidity, and lowering the economic costs of medical treatment by improving predictions of outbreaks of valley fever.

Climate change and fungal pathogen dispersal: A macrosystems approach

Coccidioides dispersal lends itself well to a "macrosystems theory" framework (Fig. 4). In macrosystems ecology, ecological processes are examined at the regional scale by considering mechanisms that occur at smaller scales (Heffernan et al. 2014). We expect that changes in precipitation regimes and soil disturbance will each increase the connectivity of *Coccidioides* across the border region, leading to more frequent deposition of *Coccidioides* in downwind ecosystems. In this case, dust transport is the medium of connectivity (Field et al. 2010).

Specifically, as regional climate shifts toward alternating cycles of heavier rainfall followed by longer droughts, we hypothesize that *Coccidioides* spore production should likewise increase. This is because *Coccidioides* may grow quickly after heavy rains, and then produce spores to endure the following drought. Furthermore, *Coccidioides* may become dormant as dry spells proceed (Treseder et al. 2010), and then produce spores as protective resting structures (Allen 1965; Gottlieb 1950). As a result, the predicted shift in precipitation regime may augment the soil spore bank.

Drought and soil disturbance will each reduce the cohesion of soil particles and spores, allowing spores to become windborne. *Coccidioides* spores can then be transported and deposited in downwind ecosystems. In addition, the dispersal of *Coccidioides* among ecosystems could elicit shifts in their geographical range if the climate favors their survival. The result would be an increase in the introduction of *Coccidioides* to new ecosystems. Thus, we could potentially see an increase in case numbers as a result of pathogenic fungi successfully establishing in areas with dense human populations. It is important that we increase bi-national collaboration on two

fronts: 1) increased collaboration between Mexican and American ecologists, and 2) coordinated valley fever surveillance between the public health offices of Mexico and the U.S.

Fungi and climate change: What do we know?

Regional climate change

Numerous local-scale studies have found that fungi respond to climate. For example, lower water availability frequently and quickly leads to declines in fungal growth (Wardle, 1992) and changes in community composition (Castro et al. 2010; Hawkes et al. 2011; Schimel et al. 1999). This issue is relevant for the border region, since climate models predict that this region should experience longer, more severe droughts interspersed with larger, less frequent storms by the end of this century (Karl et al. 2009; Schoof et al. 2010). Overall, mean annual precipitation may decline 10–20% by the end of the century (Schoof et al. 2010). In addition, mean annual temperatures are expected to increase 2 to 5 °C during the same time frame (Karl et al. 2009). These projections are consistent with empirical trends documented in this region over the past several decades (Karl et al. 2009; Pal et al. 2013). The border region has recently experienced an exceptionally severe drought unprecedented in historical records (U.S. Drought Monitor, http://droughtmonitor.unl.edu/). *Coccidioides* could respond to these variations in climate by proliferating during the heavy rainstorms, and then forming spores to achieve dormancy as soils dry. As the soils dry out, it becomes easier for the spores to become airborne.

Soil disturbance and hotspots

Dust storms are common in the region causing spores to become windborne (Nickling & Brazel 1984; Reheis & Kihl 1995; Reheis & Urban 2011; Sweeney et al. 2011). Dust storms in the western U.S. are increasing in frequency owing to anthropogenic soil disturbances such as off-road vehicle use, construction, road maintenance, military activities, grazing, and agriculture

(Neff et al. 2013) It has been shown that workers at solar panel construction sites in California's Central Valley are exposed to and infected by valley fever at higher rates than average (Colson et al. 2017). In 2015, cropland area was positively correlated with valley fever incidence in the Southwestern U.S. (Gorris et al. 2018). Dust emissions over disturbed soils can be 10–100 times greater than undisturbed soil for a given wind speed (Belnap & Gillette 1997; Gillette 1978). Since the human population is growing faster in the Southwest than in any other region of the U.S (U.S. Census Bureau 2010), soil disturbance should increase in concert.

Wind transport

Many fungi—even human pathogens such as valley fever—have a life stage in the soil (Roszak & Colwell 1987). Therefore, they could be potentially entrained in winds and transported as dust. Indeed, microbes are abundant in the atmosphere (Womack et al. 2010). Globally, it is estimated that fungal spores account for about 23% of organic aerosols (Heald & Spracklen 2009). Moreover, the richness of fungal species in air is on the same order as richness in soils (Fröhlich-Nowoisky et al. 2009; Fröhlich-Nowoisky et al., 2012; Kivlin et al. 2014).

Typically, fungi disperse over relatively long distances and many fungal species actively launch spores into the air (Ingold 1953; Roper et al. 2008). About half of fungal species produce fairly small spores—less than 10 μm diameter at their longest axis (Robert et al. 2005). These species are most likely to be wind transported (Wilkinson et al. 2012), since dust particles smaller than 10 μm in diameter can remain airborne long enough to travel significant distances (Zender et al. 2003). Moreover, fungal spores can be particularly resistant to UV radiation and desiccation (Griffin 2004; Levetin 1990; Potts 1994; Roszak & Colwell 1987; Ulevicius et al. 2004). As a result, fungi can remain viable in the atmosphere long enough to cross continents or oceans (Kellogg & Griffin 2006; Lighthart 1997; Womack et al. 2010). For example, Smith and

collaborators were able to cultivate viable spores of the fungus Penicillium that were collected from an Asian dust plume 20 km above the Pacific Ocean (Smith et al. 2010). In addition, clinical strains of valley fever occasionally differ from the environmental strains of the disease extracted from the putative site of exposure (Barker et al. 2007). This indicates that patients may be exposed to valley fever spores from locations hundreds of kilometers away (Barker et al. 2007). Altogether, it seems likely that viable *Coccidioides* can be wind-dispersed across the border region, although this idea has not yet been directly assessed.

Policy responses and challenges against disease

By better understanding movement of fungi across borders at a regional scale, researchers could build more powerful models to forecast prevalence of fungal disease in the environment. These models can help develop an early warning system of potential outbreaks of valley fever. Currently, environmental niche models are used to map valley fever (Baptista-Rosas et al. 2010; Baptista-Rosas, Hinojosa, & Riquelme 2007). Suitable living conditions for *Coccidioides* are input as parameters (i.e., soil moisture, maximum or minimum temperature, pluviometry, etc.). The relationships between *Coccidioides* presence and environmental and climate conditions are typically governed by regression or other statistical methods. The mathematical model is mapped out in geographical space and represents the extent of where a species can live. In future steps, environmental niche models for *Coccidioides* could be altered to reflect changing climate conditions in order to predict which new ecosystems and human populations could be exposed to valley fever in the future.

This system would be used by stakeholders, community members, and health care providers (Table 1). It could also be useful as a decision support tool for policy makers to build capacity to respond to global change. The challenge is conveying the information quickly and

effectively to vulnerable communities, on both sides of the border. In the future, when valley fever immunizations are approved for human use, this system can help authorities allocate vaccines efficiently.

Coccidioides ecology as a research priority

Coccidioides is a test case for fungal pathogens; studying its ecology and epidemiology can broadly inform policy in the U.S. and Mexico. Fungal pathogens are of special concern, because they are emerging faster than other types of diseases as climate change accelerates. Many of them share *Coccidioides'* bi-modal life cycle in the soil and air. Thus, knowledge gained from *Coccidioides* research can be leveraged to predict dispersal of other fungal human pathogens, such as *Cryptococcus*, *Aspergillus*, and *Histoplama* species as well as pathogens of agricultural crops, which threaten food security (Anderson et al. 2004; Fisher et al. 2012). Environmental niche models, like the ones for valley fever, can be applied to any type of disease that has an environmental stage, or for diseases that have living vectors that are sensitive to environmental changes (i.e. yellow fever, Zika virus, West Nile virus, all carried by mosquitoes).

It is critical that we prioritize bi-national collaborations to fully characterize fungal pathogens on both sides of the border. We should do so via annual meetings between researchers of both countries to exchange data and protocols. In addition, coordination of soil sample collection between Mexican and U.S. researchers would allow us to maximize coverage of species distribution maps. Coordination of local and state public health organizations will provide valley fever incidence data to complement our knowledge of *Coccidioides* in the environment. Then, we can combine ecological data and valley fever incidence rates into models to uncover drivers of valley fever outbreaks. In the future, forecasts of valley fever outbreaks can be communicated to stakeholders of both nations. Climate change directly affects us as a species,

by changing the ecosystems we live in and the diseases we are exposed to. In this way, it is necessary to cultivate international cooperation to face future challenges

Table 1. 1.

Stakeholders with an interest in valley fever forecasts.	
Arizona Valley Fever Center for Excellence	https://vfce.arizona.edu/
Binational Border Infectious Disease Surveillance Program (BIDS)	https://www.cdc.gov/usmexicohealth/bids/index.html
California Division of Occupational Safety and Health (Cal-OSHA)	https://www.dir.ca.gov/dosh/
California Valley Fever Network	http://valleyfever.ucmerced.edu/
Public Health Departments of Northern Mexico	Including states of Baja California, Baja California Sur, Sonora, Chihuahua
Public Health Departments of the Southwestern U.S.	Including counties of AZ, CA, NM, NV, UT
State and local health agencies	Including state of AZ, CA, NM, NV, UT
U.S. Center for Disease Control (CDC) Mycotic Diseases Branch (MDB)	https://www.cdc.gov/fungal/cdc-and-fungal.html
World Health Organization	http://www.who.int/topics/infectious_diseases/en/

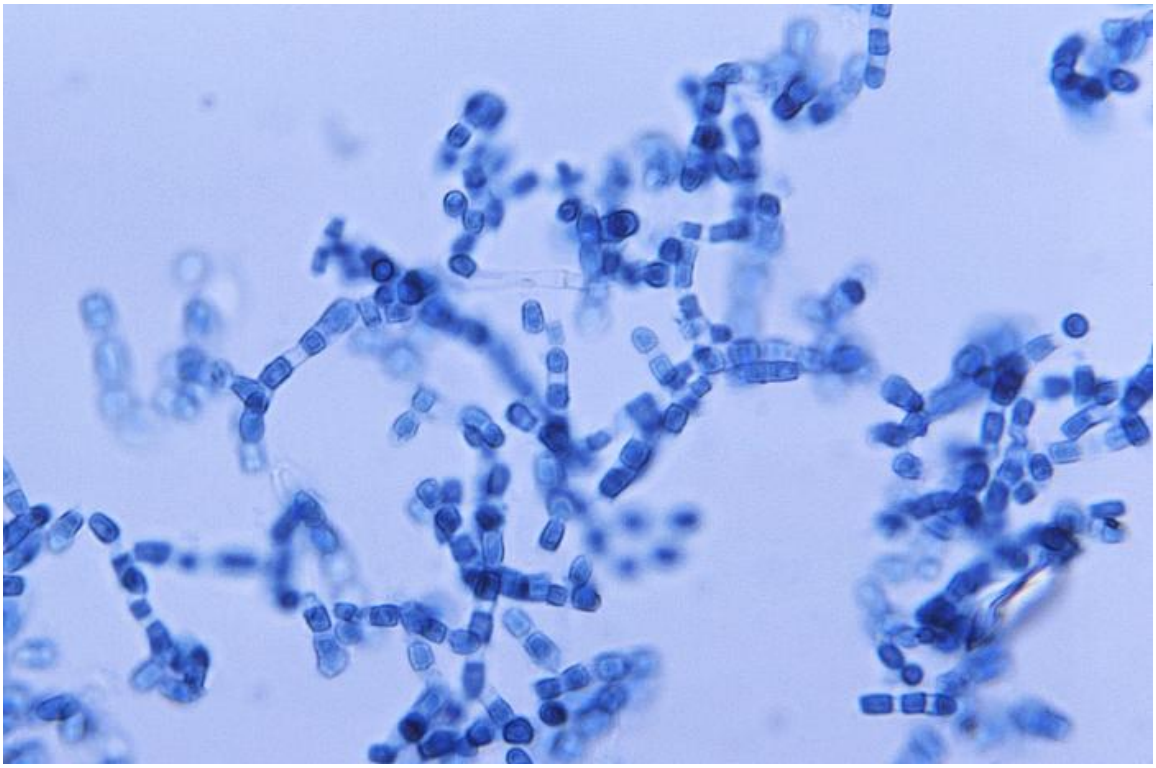


Figure 1.1. Spore formation in *Coccidioides immitis*. Image courtesy of the Centers for Disease Control and Prevention.

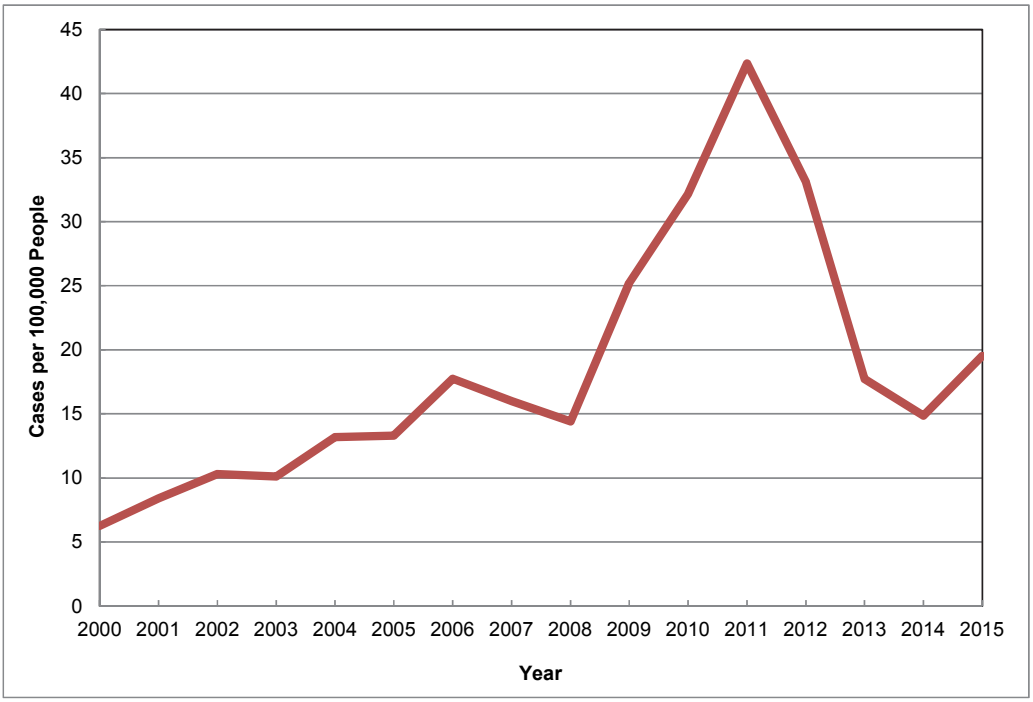


Figure 1.2. Incidence of valley fever in the Southwestern United States.

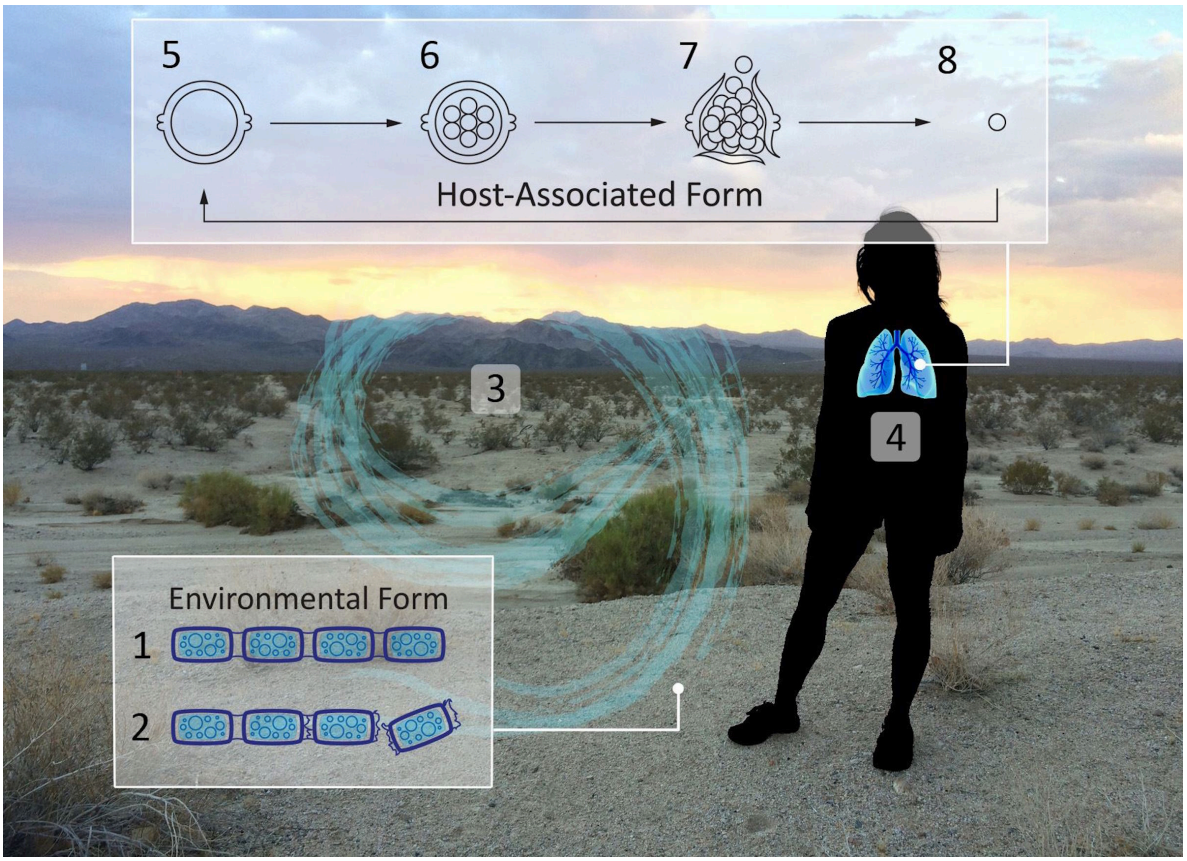


Figure 1.3. Life Cycle of *Coccidioides*: In the environment, *Coccidioides* spp. exist as a decomposer (1) growing in filaments. The filaments fragment into barrel-shaped arthrospores (2), which measure 2–4 µm in diameter and are easily aerosolized when disturbed (3). Spores are inhaled by a mammalian host (4) and settle into the lungs where they switch to a pathogenic lifestyle (5). *Coccidioides* grows in its pathogenic form as spherules (6). When a spherule ruptures (7), *Coccidioides* endospores are released and spread into surrounding tissue where the cycle repeats (8).

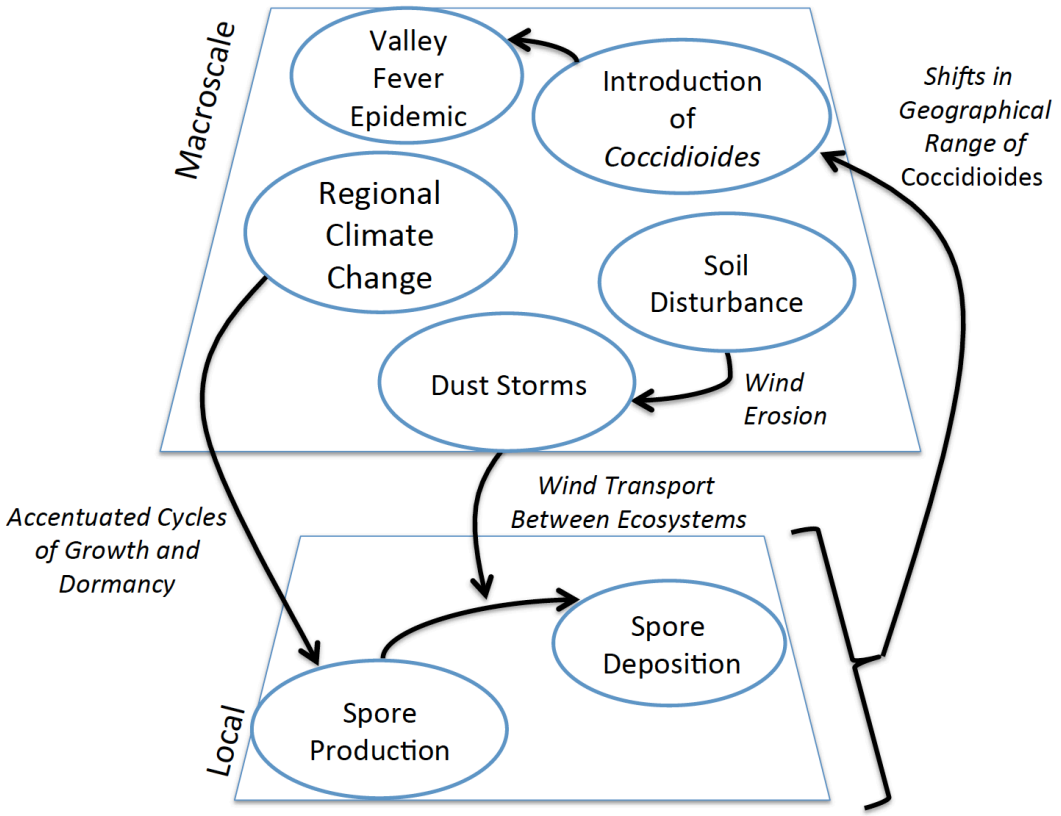


Figure 1.4. Conceptual framework of fungal movement within the border region

CHAPTER 2

Fungal pathogen dispersal in the soil and air across the U.S. Southwest

Co-Authors: Morgan Gorris, Jim Randerson, and Kathleen Treseder

Introduction

Fungi can be transported globally through the air, especially through airborne soil dust that can rise over 5 km in altitude and contribute to long-distance dispersal (Carlson and Prospero 1972). Fungal spores are extremely resilient to UV, desiccation, and temperature extremes as they disperse to a new location (Deems et al. 2013, Wyatt et al. 2013, Tong et al. 2017). Indeed, most of the viable biomass in the air are fungi (Fröhlich-Nowoisky et al. 2009). Moreover, long-distance dispersal of spores include those of pathogenic fungi (Weil et al. 2017).

Fungal diseases are a serious threat to food security and human health (Fisher et al. 2012). Many pathogenic fungi are dimorphic, and can become soil decomposers if there are no viable hosts. Since their growth rate is decoupled from host populations, dimorphic fungi are more likely to eliminate host populations than diseases that rely exclusively on the host (Fisher et al. 2012). Each year, fungal pathogens destroy enough food crops to feed 600 million people. Moreover, fungal diseases directly kill 1-2 million people - more than tuberculosis or malaria (Brown et al. 2012, Meyer et al. 2016). Nevertheless, the airborne dispersal of fungal diseases is not well understood.

Understanding which groups of fungi are able to become airborne for long distances is crucial to understanding dispersal, a fundamental aspect of the fungal life cycle. Currently, we do not know broad patterns of dispersal mode for fungal pathogens or other groups, and by proxy, their dispersal speed. This issue is important, because air-dispersed fungi might be able to move quickly compared to soil-dispersed fungi that rely on growth for movement. Most studies on

fungal diversity and community composition are performed in either soil or air only (Yoo et al. 2016). Furthermore, with respect to airborne microbes, numerous studies have examined temporal fluctuations in community composition within one location (Lin and Li 2000, Jones and Harrison 2004, Fierer et al. 2008, Crawford et al. 2009, Fröhlich-Nowoisky et al. 2009, Bowers et al. 2011). By contrast, regional-scale studies of airborne fungi are rare.

Our study area covers ~86,000 sq km within the U.S. Southwest. The U.S. Southwest will experience increased temperature, and potentially increased drought under climate change (Easterling et al. n.d., Wehner et al. n.d., Seager and Vecchi 2010). These factors increase dust storm formation by killing vegetation that keeps soil anchored. The frequency of dust storms in this region has more than doubled in the last 20 years and will continue to increase (Tong et al. 2017). With significantly reduced winter precipitation, it is highly likely that the U.S. Southwest will be drier in this current century than the past century (Seager and Vecchi 2010). Climate change in the U.S. Southwest will threaten organisms that are already limited by water scarcity and high temperatures (Toberman et al. 2008, Yuste et al. 2011).

Indeed, soil fungal communities are often sensitive to moisture (Allison and Treseder 2008; Hawkes *et al.* 2011; Looby *et al.* 2016). Thus, climate change within the U.S. Southwest may shift the ranges of certain fungal species (Parmesan and Yohe 2003). Differences in dispersal ability through soil and air might influence how fungal species can respond to future climate change. For example, hyphal growth through soil is much slower compared to long-distance air dispersal, where fungal spores can traverse hundreds to thousands of kilometers within days (Stein et al. 2015).

This study is one of the first to examine air and soil fungal community composition at a regional scale. Here, we address three questions regarding fungal community composition and

function in the soil and air. First, what environmental factors structure fungal community composition in the soil and the air? For the soil, we hypothesized that soil moisture, soil pH, soil density, and soil salinity influence soil fungal community composition. For the air, we hypothesized that mean annual precipitation (MAP), mean annual temperature (MAT), and maximum vapor pressure deficit (VPD) structure airborne fungal community composition. Second, how are fungal functional groups distributed in the soil and in the air? Fungi can be categorized into broad "functional groups" such as pathogens, mutualists (i.e., mycorrhizal or lichen fungi), or decomposers. We hypothesized that pathogens would be more abundant in the air compared to other groups because their evolutionary success depends on infecting as many hosts as possible. We hypothesize symbionts and decomposers will be the most abundant groups in the soil because their success depends on being located within proximity to their plant host and/or nutrient sources in the environment. Third, how does fungal functional group affect extent of occurrence in the soil? We hypothesized that pathogens would have greater extent of occurrence (EOO) because they are likely to be abundant in air and therefore will disperse greater distances compared to dispersal by water or animals.

To test our hypotheses, we sampled both air and soil at 60 sites across the U.S. Southwest. We used next-generation sequencing techniques and a bioinformatics pipeline to analyze airborne and soil fungal community composition in the context of functional groups. We determined factors controlling communities and which functional groups are most abundant in soil and air. Finally, we compared EOO for the functional groups across the region.

Methods

Field sites

We conducted our study in the U.S. southwestern region, covering approximately 86,000 km^2 and 11 Holdridge life zones (Lugo et al. 1999). Over five days in July 2015, we collected soil and air samples at 60 sites across Arizona, California, Nevada, New Mexico, and Utah. We selected sites that followed an approximate north-south and east-west transect and were at least 1 km away from major highways (Figure 1). We used a global positioning system to record latitude, longitude and elevation at each site. We took mean annual temperature (MAT), mean annual precipitation (MAP), and maximum vapor pressure deficit (VPD) for each site from the PRISM Climate Group at Oregon State University (Daly et al. 2008). Maximum VPD data was based on the month of July 2015. We selected maximum VPD because it is a particularly physiologically stressful condition. Holdridge life zone was assigned by the IRI/LDEO Climate Data Library (Leemans 1990). For soil samples, we assessed soil pH, soil moisture, soil density, and soil salinity as detailed below.

Sample Collection

Within each site, we collected a 2.5 cm-diameter by 10 cm deep soil core from each of two random locations (processed independently until data analysis). We deployed a Biostage air sampler (SKC, Inc., Eighty Four, PA) to capture air samples. With this technique, fungal spores as small as ~0.6 μm were captured on plain agar (with no nutrients) in a Petri dish. The sampler ran for five minutes at a sampling rate of 20 L/min, for a total of 100 L of air sampled. We kept air and soil samples on dry ice during the duration of the sampling trip, and stored the samples at −80°C upon return to the lab.

Soil properties

We measured soil pH on a 1:1 ratio (w/v) of soil to deionized water. We determined soil moisture gravimetrically by drying subsamples for 48 hours at 65 °C. Soil density was assessed

by weighing 5 ml of soil. We measured soil salinity as the conductivity of a 1:5 w/v soil to deionized water mix.

DNA Extraction

We processed air and soil samples using the MoBio PowerSoil Extraction kit (MoBio, Carlsbad,CA). For soil samples, we extracted DNA according to manufacturer recommendations. For air samples, we removed a sub-sample of the agar from a 2 cm by 2 cm surface of the Petri dish, and then followed manufacturer directions for all other steps. Both soil and air samples required concentration using the Zymo DNA Concentrator kit (Zymo Research Corp., Irvine, CA). We standardized DNA concentrations to 10 ng/uL before PCR.

PCR amplification and sequencing

We amplified a ~340 bp region of the fungal ITS2 region in the 5.8S encoding gene. This shorter amplicon reduces species bias and chimera formation without compromising inferences of species diversity (Ihrmark et al. 2012). We used a staggered primer design to improve overall sequence quality in the Illumina MiSeq flowcell as described in Looby et al. 2016 (Tremblay et al. 2015, Looby et al. 2016). The forward primer (ITS9f; AATGATACGGCGACCACCGAGATCTACAC TC TTTCCCTACA CGACGCTCTTCCGATCT NNNNNGAA CGCAGCRAAIIGYGA) was standard across all samples and reverse primer (CAAGCAGAAGACGGCATACGAGAT) also had a 12 bp barcode to identify unique samples, pad (AGTCAGTCAG), linker sequences (CC), and the ITS4 primer (TCCTCCGCTTATTGATATGC).

Reactions contained 0.75 ng of each forward and reverse primer, 21.5 ng of Platinum PCR SuperMix (Invitrogen, Carlsbad, CA), 1 uL of BSA, and ~10 ng of template DNA for a total volume of 25 uL. We amplified each sample in triplicate and the reaction ran for 35 cycles

of 94°C for 45 s, 50°C for 1 min, and 72°C for 90 s with a hot start at 94°C for 7 min and a final extension step at 72°C for 10 min. We pooled and purified triplicates to remove primer-dimers and non-target DNA using Agencourt AmPure XP beads (Beckman-Coulter, Brea, CA) mixed with PCR product at a 1:1 ratio. To create a multiplexed library, we quantified DNA concentrations with a spectrophotometer and the Qubit dsDNA High Sensitivity Assay Kit (Life Technologies, Grand Island, NY) and then pooled samples in equi-molar concentrations. Samples were sequenced at the University of California, Riverside Institute for Integrative Genome Biology on the Illumina Mi-Seq platform on a single flowcell lane at 2 x 300 bp paired end reads.

We obtained ~8.6 million total sequences from one lane of the Mi-Seq run. Using the open-source Quantitative Insights into Microbial Ecology (QIIME) pipeline, raw sequence data were demultiplexed (Caporaso et al. 2011). We filtered low quality reads using the following parameters: 1) a minimum Phred quality threshold of Q30, 2) elimination of sequences with three consecutive low quality base reads, and 3) a minimum ratio of 0.75 for high quality base calls to input read length. We removed chimeras by comparing against reference sequences for fungi from the UNITE database, the most comprehensive database for fungal taxa (v.7, updated 01/31/2016, https://unite.ut.ee/repository.php)(Abarenkov et al. 2010). Following open reference picking of OTUs by 97% similarity, OTUs were assigned taxonomy using BLAST (version 2.2.22) and the UNITE database. The 97% cutoff is equivalent to species or genus (Nilsson et al. 2009). To reduce noise from sequencing errors or chimeras, we removed global singletons. After taxonomical assignment, non-fungal OTUs were filtered out. Following quality control, our dataset contained ~2.1 million fungal sequences. We rarefied samples to standardize the number of OTUs for each site through random sub-sampling. Rarefaction levels were different between

soil and air samples, because soil samples had higher sequence reads than air samples. To use data from the majority of our air samples, we rarefied at a lower level. We used samples from 51 out of 60 sites for soil, and 40 out of 60 sites for air. Rarefaction levels were as follows: 5,000 sequences for analyses of soil communities only, 400 sequences for analyses involving both air and soil communities, and 400 sequences for analyses of air communities only. After rarefaction, sequence reads from soils samples that were collected in duplicate were averaged between samples from the same site.

We used FUNGuild to assign fungal OTUs to functional groups, based on their taxonomic identities (Nguyen et al. 2016). FUNGuild assigned OTUs into broad "trophic modes" - pathotroph, symbiotroph, and saprotrophs. Here, we call these modes pathogens, symbionts, and decomposers, respectively. Within these broad trophic modes were more specific functional guilds: animal pathogens, arbuscular mycorrhizal fungi, ectomycorrhizal fungi, lichenized fungi, plant pathogens, undefined decomposers, and wood decomposers. Dimorphic fungal species were assigned two trophic modes and functional guilds (e.g., “pathogen-decomposer” and “animal pathogen-decomposer”). Here, we treated joint trophic mode assignments of dimorphic fungi as additional trophic modes if there were at least 50 OTUs within a dimorphic FUNGuild assignment. Thus, trophic modes for this study included pathogens, pathogen-decomposers, decomposers, and symbionts). FUNGuild also assigned confidence rankings for each classification, based on primary research literature. We only used FUNGuild classifications that were associated with confidence ratings of “probable” or “highly probable”.

Statistics

Hypothesis 1

We hypothesized that soil moisture, soil pH, soil density, and soil salinity would structure soil fungal community composition. In addition, we hypothesized that in the air, fungal communities would be structured by MAP, MAT, and VPD. Community composition for Hypothesis 1 was represented by the Bray-Curtis dissimilarity metric. In order to maximize the number of samples we used, we tested Hypothesis 1 on soil community composition data rarefied to 5000 sequences, and air community composition data rarefied to 400 sequences.

We used a series of perMANOVAs in the vegan package in R to compare soil or airborne fungal composition to one environmental factor at a time (Oksanen et al. 2011). For soil samples, independent variables were latitude, longitude, elevation, soil pH, soil salinity, soil density, soil moisture, maximum VPD, MAP, MAT, or Holdridge life zone. For air samples, we used the same set of independent variables, except we omitted soil pH, soil salinity, soil density, soil moisture.

In addition, we examined environmental factors driving individual OTUs. We examined the top 5 most prevalent OTUs in the soil and the top 5 in the air. OTU prevalence was measured as number of site occurrences. For each of the 10 selected OTUs, we used the pscl package in R to fit a linear model to OTU abundance and an environmental factor (Jackson 2017). For both soil and air OTUs, environmental factors were latitude, longitude, elevation, MAP, MAT, or VPD. In addition, we checked for relationships between soil OTUs versus soil moisture, soil pH, soil conductivity, soil salinity, or soil density. We noted OTUs that had an environmental factor significantly driving its abundance ($p < 0.05$), and then selected the environmental factor with the greatest influence (based on r^2 value).

Hypothesis 2

We hypothesized that pathogens would be more abundant than other groups in the air, while decomposers and symbionts would be the most abundant trophic modes in the soil. Abundance data were square root transformed to meet assumptions of normality using built-in function in R (R Core Team 2013). We used ANOVA to check for differences between trophic mode within air or soil, followed by the Tukey HSD post-hoc tests for pairwise differences. Hypothesis 2 would be supported if pathogens had a significantly higher abundance than other trophic modes in the air, and decomposers and symbionts were the most abundant trophic modes in soil.

Hypothesis 3

We hypothesized that pathogens, if found in higher abundance in the air (see Hypothesis 2), would have a greater geographic range in the soil. Since our study was regional, we used extent of occurrence (EOO) as a proxy for geographic range. We estimated EOO by calculating the furthest distance between sites in which a given OTU was detected. To calculate distance between latitude/longitude coordinates, we used the distCosine function within the Geosphere package in R (Hijmans 2016). This package is accurate within a margin of ~1 m. It uses the Law of Cosines and accounts for the curvature of Earth. We performed this calculation for all air samples, and then repeated the calculation for all soil samples.

Following EOO calculation for each OTU, we used an ANOVA to check for significant differences in EOO between trophic modes. We then used another ANOVA to test for differences between functional guilds within air. We then repeated this process for soils. If differences were significant between groups, we conducted Tukey HSD post-hoc tests to test for significant pairwise differences between trophic mode groups and then functional guild groups. Our hypothesis would be supported if OTUs that were either 1) broadly classified as pathogens

for trophic mode or 2) specifically classified as animal pathogens and plant pathogens under functional guild, had significantly larger EOOs than other functional groups in the soil.

Results

Hypothesis 1

We found that several environmental factors structure fungal community composition in either air and soil. In the soil, latitude, longitude, elevation, MAT, MAP, max VPD, soil density, and HLZ were significantly related to fungal community composition (Table 1). Moreover, the geographical factor that explained the most variance in soil fungal communities was latitude (Table 1, Figure 2). Furthermore, the climatic factor with the strongest relationship to soil community composition was maximum VPD (Table 1, Figure 2). We did not find support for our hypothesis that environmental factors based on soil characteristics structure soil fungal communities (with the exception of soil density). Instead, other environmental factors we did not originally predict more strongly drove soil fungal community composition.

In the air, longitude was the geographical factor with the most significant relationship to airborne fungal community composition (Table 1, Figure 3). Among the climate factors, MAP explained the greatest variation in airborne fungal communities (Table 1, Figure 3). Thus, we found partial support for our hypothesis regarding airborne fungal communities.

We also investigated the effect of environmental factors on the five most prevalent OTUs in soil, then air (Table 2). The most prevalent soil OTUs that were significantly related to environmental factors were *Alternaria planifunda* and *Giberella tricinta*, both plant pathogens. The abundances of the other three abundant OTUs in soil were not significantly related to any

environmental factors. *A. planifunda* abundance in soil increased most significantly with latitude (among the geographic factors) and maximum VPD (among the climatic factors) (Figure S1). Accordingly, *A. planifunda* was relatively abundant in soil within the Mojave Desert (Figure S2). In contrast, *G. tricinta* was most abundant in soils of mountains and plateaus (Figure S2). Correspondingly, *G. tricinta* abundance in soil was greatest as higher elevations (geographic factor) and lower mean annual temperature (climatic factor)(Figure S3). We did not find significant relationships between environmental factors and the five most abundant OTUs in air.

Hypothesis 2

With respect to broad trophic mode, in the air, pathogens were significantly more abundant than were decomposers, pathogen-decomposers, or symbionts (Figure 4 $F = 27.05$, $p < 0.001$). Moreover, pathogens were distributed relatively uniformly across the region, compared to the other trophic modes (Figure 1). In the soil, decomposers were significantly more abundant than the other trophic modes (Figure 4, $F = 51.76$, $p < 0.001$). Moreover, decomposers were present in the soil in every site that we sampled (Figure 5). Altogether, the distribution of trophic modes supported our hypothesis that pathogens should be particularly abundant in the air.

Hypothesis 3

We found support for our hypothesis that pathogens have greater geographic ranges than do other groups, at least in the soil. We used EOO as a proxy for OTU range in order to understand differences in range between functional groups. In the soil, EOO varied significantly between broad trophic modes ($F = 16.79$, $p < 0.001$) (Figure 6) as well as specific functional guilds ($F = 11.12$, $p < 0.001$) (Figure 7). Among trophic modes in the soil, pathogens and pathogen-decomposers had a relatively large EOO, while symbionts had the smallest EOO. These patterns were also reflected at the functional guild level: in the soil, animal pathogens-

decomposers displayed the greatest range, while symbionts such as lichenized fungi, arbuscular mycorrhizal fungi, and ectomycorrhizal fungi had the smallest ranges (Figure 7). In the air, differences in EOO were non-significant at the broad trophic mode level. We did not calculate EOO at the functional guild level in the air because there were too few OTUs present in two or more sites within each functional guild classification.

Discussion

We discovered that pathogens are the most abundant functional group in the air. Furthermore, in the soil, they had the largest EOO at both the broad trophic mode and specific functional guild levels. In other words, pathogens appeared to be more air-dispersed than other groups, which might have been tied to larger geographical ranges over the soil. We were able to uncover these patterns because our study is one of a few that examines both air and soil fungal communities – most fungal ecology studies are typically performed exclusively in either soil or air (Wardle and Lindahl 2014, Lymperopoulou et al. 2016, Yoo et al. 2016). Although Kivlin et al. 2014 compared fungal community composition between air and soil at a regional scale, they did not specifically compare pathogens versus other trophic modes.

Air dispersal of pathogens has potential consequences for other organisms, especially if pathogens spread to new areas (Fisher et al. 2012). For example, pathogen "pollution" occurs when disease is introduced to naïve populations (Daszak et al. 2000). Pathogen pollution can create catastrophic loss of biodiversity in invaded areas (Vitousek et al. 1997, Daszak et al. 2000). In addition, if pathogens shift away from former habitats, they can release their previous hosts from a source of population regulation (Harvell 2002). Biodiversity loss may result. This scenario may be especially relevant for fungal pathogens that rely on environmental transmission rather than direct transmission between hosts (Dobson 2004, Fisher et al. 2012).

Pathogens and pathogen-decomposers displayed the most extensive EOOs, potentially associated with their greater air dispersal. The ability to air disperse may be evolutionary advantageous to certain pathogens, if it increases reproductive success via infection of more hosts (Dobson 2004). In our study, decomposers were most dominant in the soil, yet exhibited an intermediate EOO. Long-distance air dispersal may be less critical for this group, and they may rely more upon hyphal growth or animal dispersal to move between resources (Hudson 1968, Boddy et al. 2009). Symbionts displayed the smallest EEO, potentially because their geographic ranges are constrained by availability of hosts (Dhillion 1992, Sanders 2003, Croll et al. 2008).

It is interesting to note that animal pathogens-decomposers had the highest EOO of the specific functional guilds. *Coccidioides immitis* and *posadaii* are animal-pathogen decomposers that infect mammals, causing valley fever (Nguyen et al. 2013). *Coccidioides* spp. can decompose protein from an infected host animal and then later become wind-dispersed (Del Rocío Reyes-Montes et al. 2016) *Coccidioides* could proliferate to an expanded range via animal migration, such as that of humans, bats, and armadillos (Eulalio et al. 2001, Fisher et al. 2001, Cordeiro et al. 2012). Indeed, *Coccidioides* appears to have reached North America from South America through human migration (Fisher et al. 2001). The combination of host movement and ability to grow in soil or animal carcasses may help *Coccidioides* proliferate (Cordeiro et al. 2012, Del Rocío Reyes-Montes et al. 2016). These dispersal patterns could be mirrored in other animal pathogen-decomposer species, resulting in the high EOO we observed.

We examined various environmental factors on fungal community composition in both the air and soil. In our study, we found that MAP and maximum VPD were influential; both are related to water availability. Water can be limiting to growth in semi-arid and arid ecosystems like those in the U.S. southwest (Anderson 1936). Our soil results were consistent with those

reported in an earlier study based in Southern California, where latitude and soil moisture each influenced soil fungal community composition (Kivlin et al. 2014). In contrast, air fungal communities in the Southern California study did not vary with climate (Kivlin et al. 2014), potentially owing to its smaller geographical coverage.

Fungal dispersal is salient when considering climate change effects on community composition and function. Plants and animals can move their ranges 6.1 ± 2.4 km per decade towards the poles in order to follow their optimal habitats due to climate change (Parmesan and Yohe 2003). Fungi that air disperse could be able to match or exceed this rate. This can lead to changes in community composition if dispersing fungi land in areas favorable to their growth. Though our study did not assess if fungi were successful at colonizing new habitats, previous studies have observed changes in microbial community composition under global change (Allison and Treseder 2008, Hawkes et al. 2011, Xiong et al. 2014, Looby et al. 2016, Van Diepen et al. 2017). Thus, fungal long-distance dispersal might contribute to shifts in microbial communities and their function under climate change.

There are some limitations to our study. Although we were not able to sample the entire airborne community, we captured a "snapshot" of the fungal community in the air as we simultaneously sampled the soil community. The abiotic factors we measured did not fully explain variation in soil fungal community composition in this study. Indeed, other factors may also be structuring soil fungal communities that were not included in this study, such as nitrogen, phosphorus, carbon, or calcium nutrient availability (Lauber et al. 2008, Kivlin et al. 2014, Tedersoo et al. 2014). In addition, we were unable to assign function to all of the fungal OTUs we collected. Continuing to update and expand the FUNGuild database will increase the number

of fungal species that can be assigned a functional group, thus improving the power of future analyses.

In conclusion, we discovered that both air and soil fungal communities were influenced by spatial and environmental factors. Our study found that fungal pathogens were more air dispersed than decomposers or symbionts. Pathogens also had larger EOOs in the soil than other functional groups. Our data provide evidence that pathogens may have an advantage over other groups of fungi that may not be able to move to a suitable environment as quickly. This has even more serious implications under the increasing pressures of climate change. It is critical we understand the speed and extent of fungal migration. Our study suggests that fungal migration might differ between pathogens and other groups. This information could ultimately help develop models that will forecast fungal pathogen spread. These models could be used to prepare for effects on human health and food security in the future.

Table 2.1. perMANOVA results for relationships between soil and airborne fungal community composition versus environmental factors.†

Parameter	Soil			Air		
	F	r^2	P	F	r^2	P
Latitude	2.34	0.053	**<0.001**	2.20	0.055	**0.004**
Longitude	2.33	0.053	**<0.001**	2.37	0.059	**0.003**
Elevation	1.64	0.037	**0.017**	1.44	0.036	0.075
MAT	1.85	0.042	**0.006**	1.25	0.032	0.152
MAP	1.69	0.039	**0.007**	1.84	0.046	**0.018**
Max VPD	2.21	0.050	**<0.001**	1.28	0.033	0.155
Soil pH	1.25	0.029	0.099	NA	NA	NA
Soil density	1.53	0.035	**0.025**	NA	NA	NA
Soil salinity	1.05	0.024	0.346	NA	NA	NA
Soil moisture	1.31	0.030	0.091	NA	NA	NA
Holdridge life zone	1.41	0.243	**<0.001**	1.17	0.026	0.069

†Significant results are in bold. NA: parameter was not tested against community composition

Table 2.2 Top five most prevalent OTUs for soil and air.

Type	Species	Trophic Mode	Prevalence (% of sites)	OTU ID
soil	*Alternaria alternata*	pathogen	84.1	278
	Alternaria planifunda	pathogen	81.8	15
	Ulocladium chartarum	pathogen	79.5	348
	Didymella phacae	pathogen-decomposer	79.5	4
	Gibberella tricincta	pathogen	68.2	447
air	*Pleosporaceae sp.*	not assigned	92.5	411
	Dothideomycetes sp.	not assigned	75	239
	Alternaria alternata	pathogen	70	278
	Alternaria planifunda	pathogen	65	15
	Alternaria alternata	pathogen	55	349

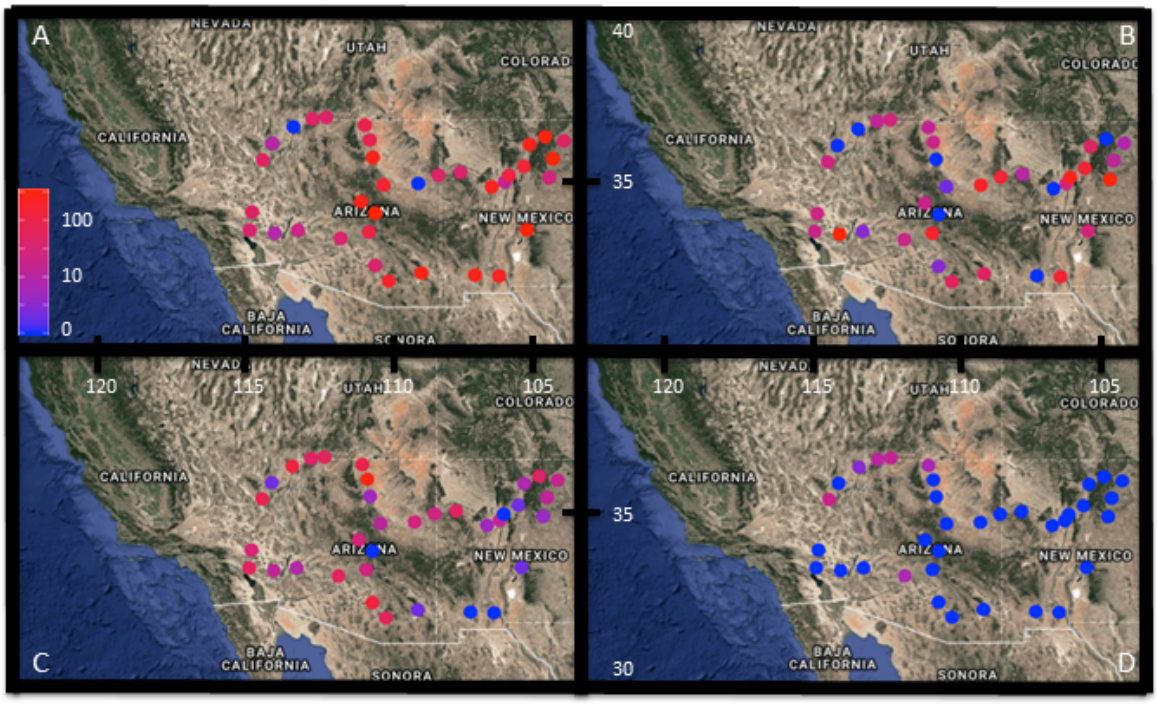


Figure 2.1. Map of abundance in air of (A) pathogens, (B) pathogen-decomposers, (C) decomposers, and (D) symbionts. Color of dot indicates abundance, with the scale bar showing number of sequence reads on a logarithmic scale, rarified to 400 sequence reads per sample. Map degrees for latitude are N and for longitude are W.

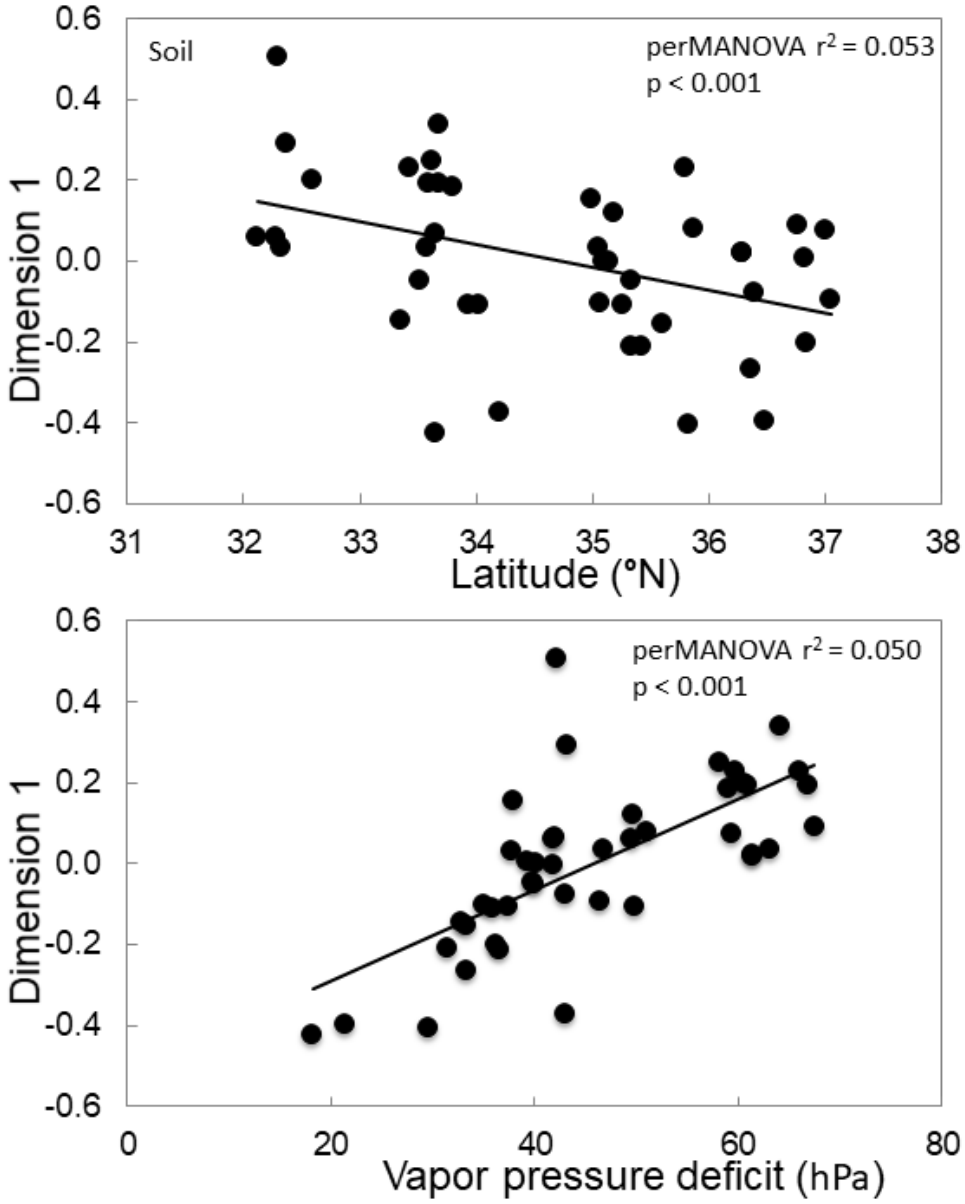


Figure 2.2. Drivers of fungal community composition in the soil. Dimension 1 is the NMDS dimension that explains the most variance between communities. Circles indicate soil fungal communities from each site. The line shows linear regression, however, r^2 is measured by ANOVA.

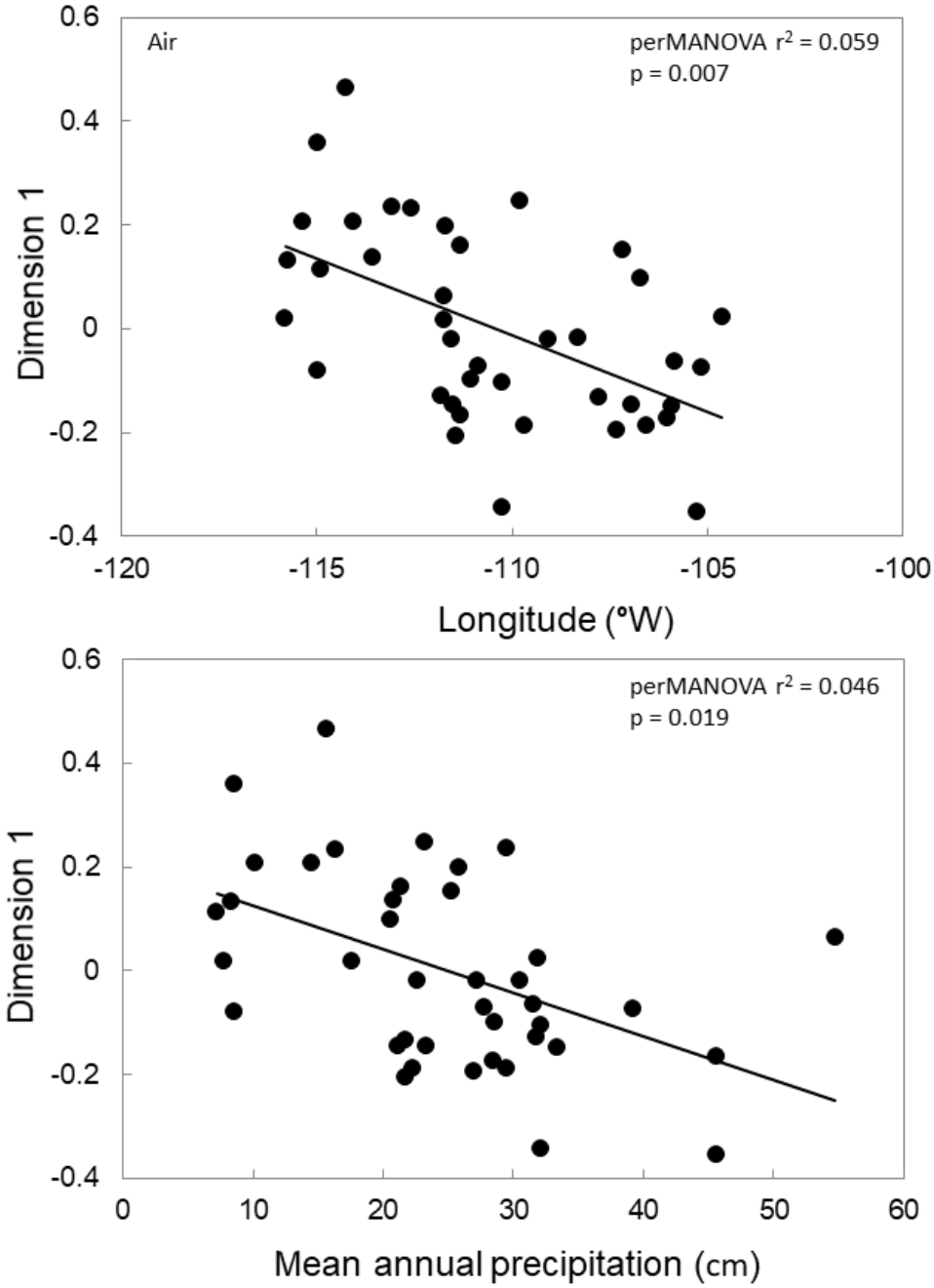


Figure 2.3. Drivers of fungal community composition in the air. Dimension 1 is the NMDS dimension that explains the most variance between communities. Circles indicate airborne fungal communities from each site. The line shows linear regression, however, r^2 is measured by ANOVA.

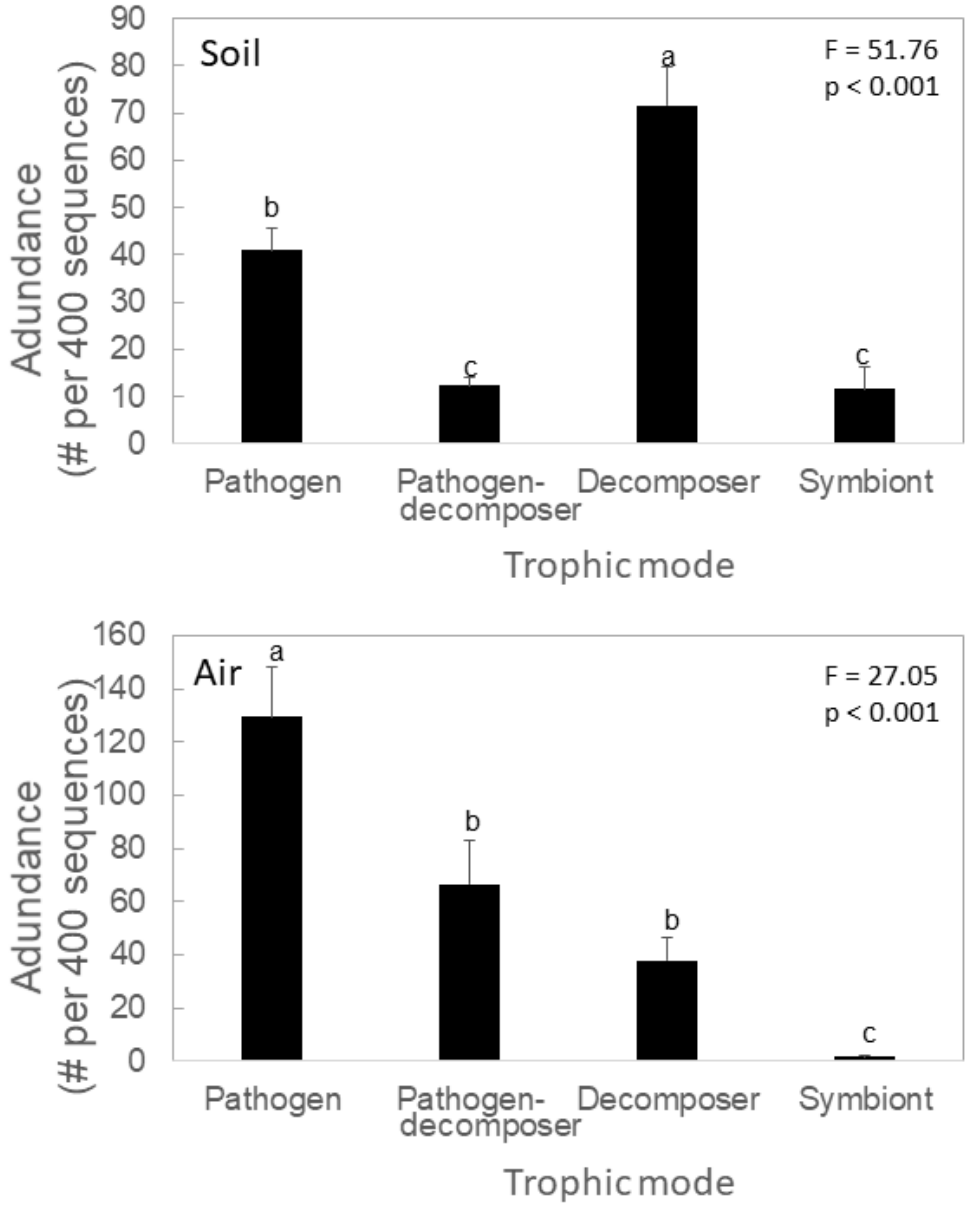


Figure 2.4. Abundances of trophic modes in both the soil and the air, rarified to 400 sequences. Values are averaged abundances across OTUs within a trophic mode. Error bars represent SE. Letters indicate significant pairwise differences between each group. P-values were determined by ANOVA.

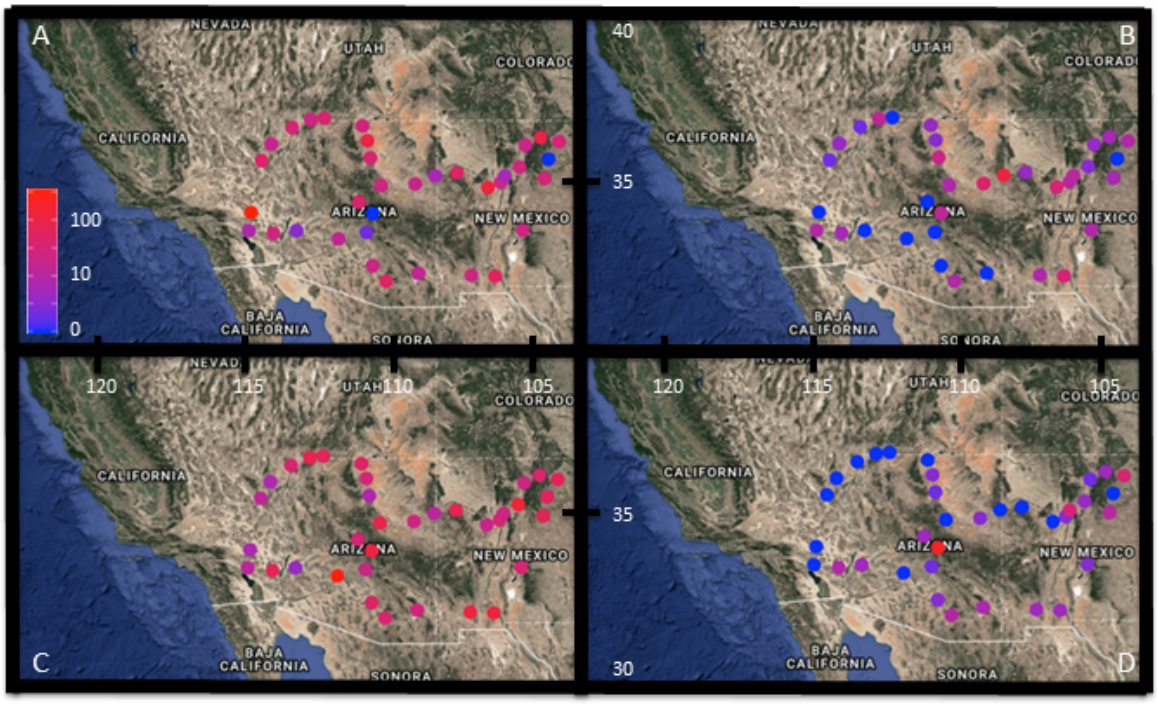


Figure 2.5. Map of abundance in soil of (A) pathogens, (B) pathogen-decomposers, (C) decomposers, and (D) symbionts. Color of dot indicates abundance, with the scale bar showing number of sequence reads on a logarithmic scale, rarified to 5,000 sequence reads per sample. Map degrees for latitude are N and for longitude are W.

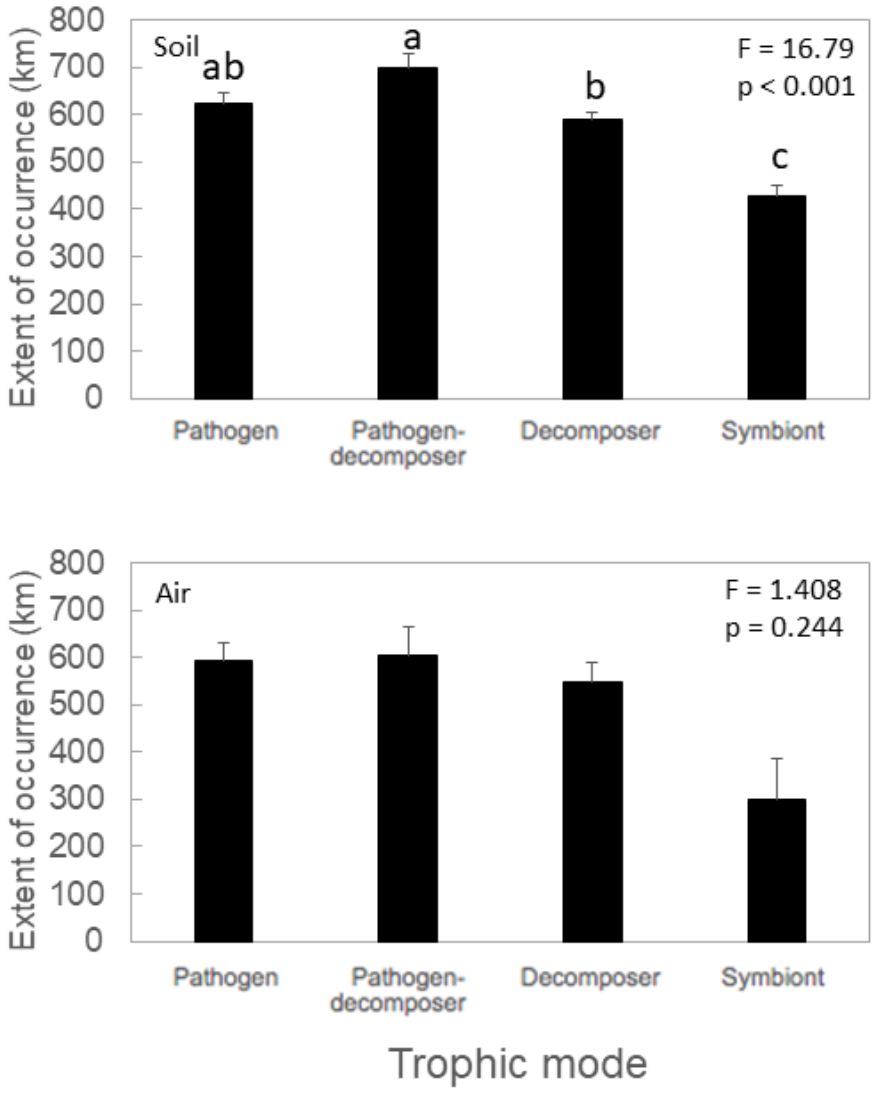


Figure 2.6. Extent of occurrence (EOO) of trophic modes in both the soil and the air. Values are averaged EOOs of across OTUs within a trophic mode. Error bars represent SE. Letters indicate significant pairwise differences.

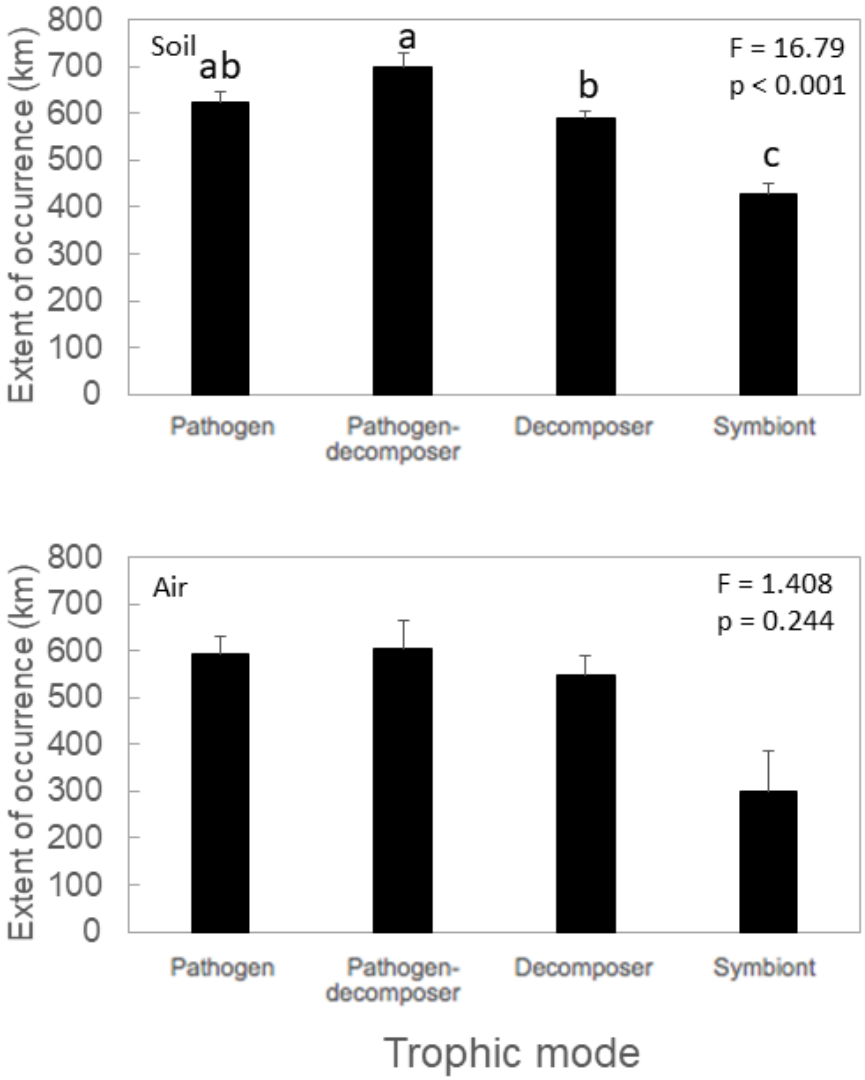


Figure 2.7. Extent of occurrence (EOO) of functional guilds in the soil only. Values are averaged EOOs of across OTUs within a functional guild. Error bars represent SE. Letters indicate significant pairwise differences.

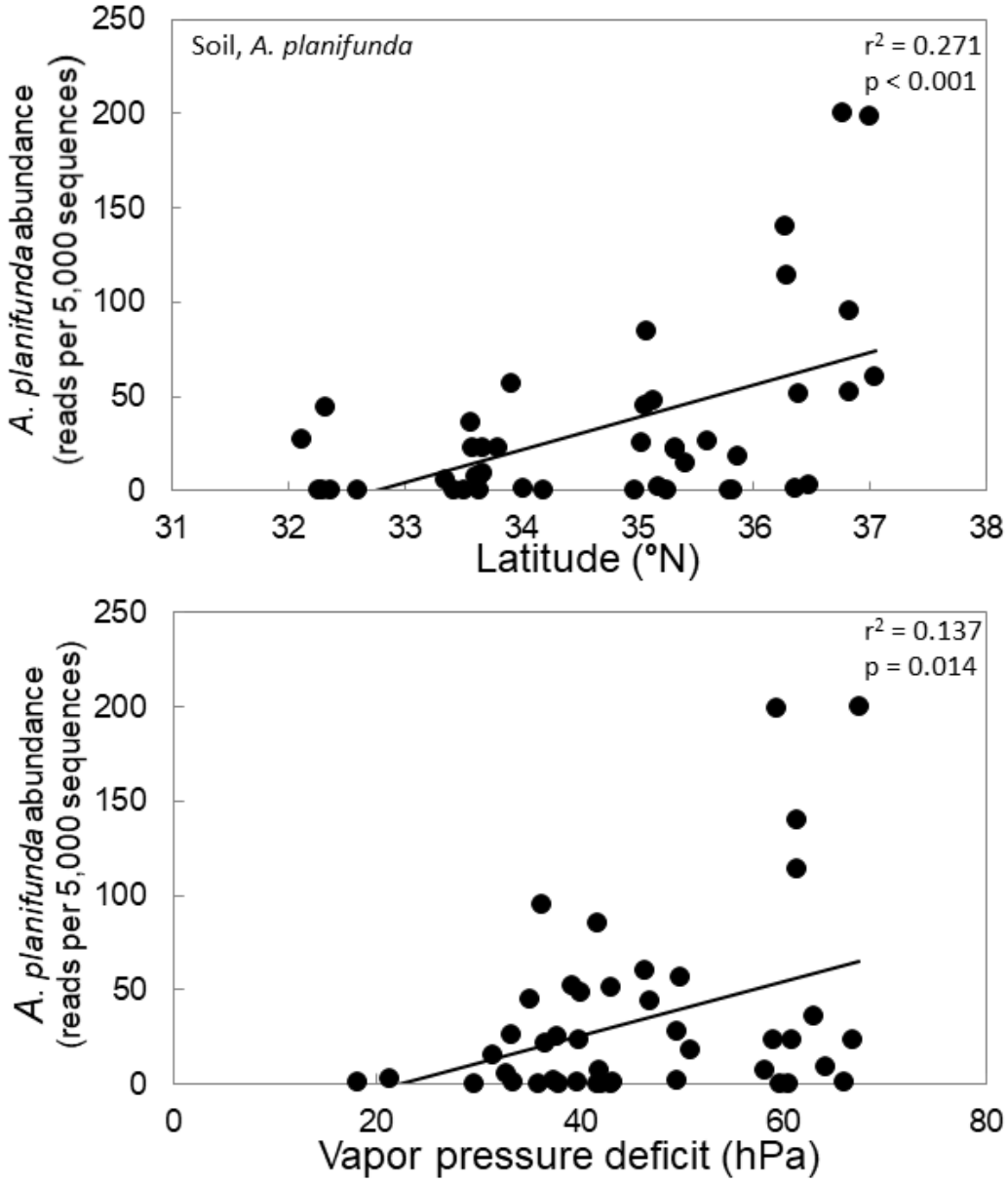


Figure 2.S1. Spatial and climatic factors driving *A. planifunda* abundance in the soil. Circles indicate *A. planifunda* abundance from various sites. The line shows linear regression.

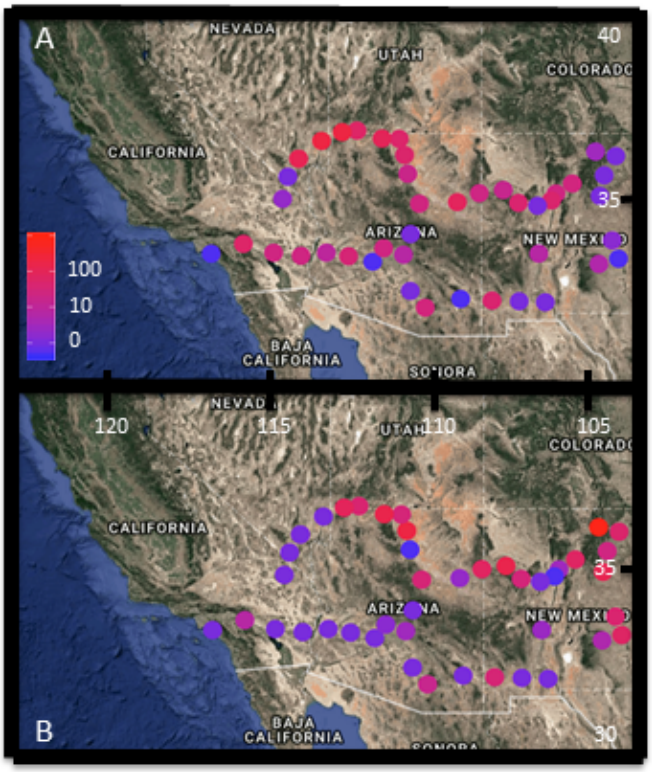


Figure 2.S2. Map of abundance in soil of (A) *Alternaria planifunda* and (B) *Giberella tricinta*. Color of dot indicates abundance, with the scale bar showing number of sequence reads on a logarithmic scale, rarefied to 5,000 sequence reads per sample. Map degrees for latitude are N and for longitude are W.

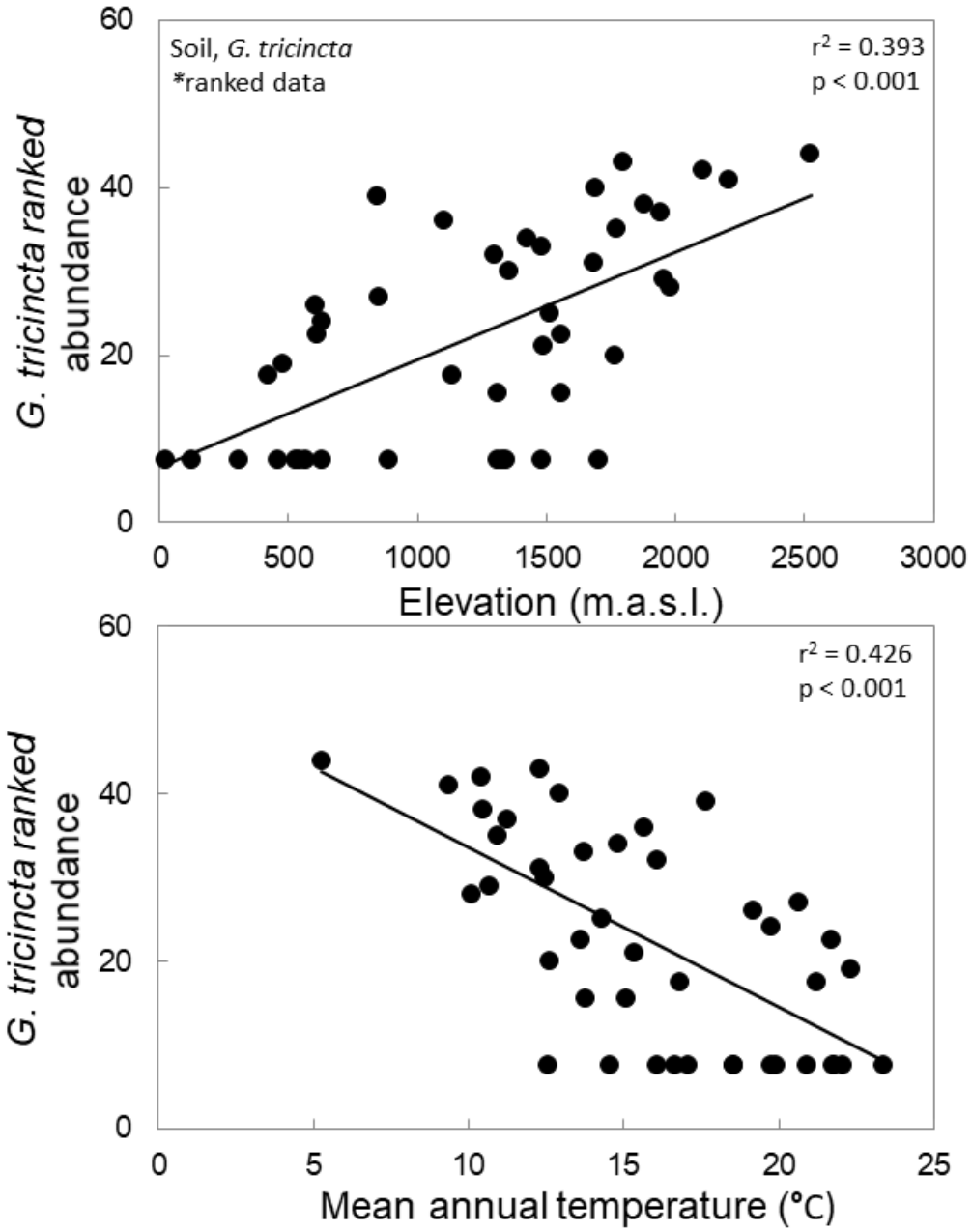


Figure 2.S3. Spatial and climatic factors driving *G. trincinta* abundance in the soil. Circles indicate *G. trincinta* abundance from various sites. The line shows linear regression.

CHAPTER 3

Santa Ana winds shift airborne fungal communities in Southern California

Co-Authors: Claudia Czimczik and Kathleen Treseder

Introduction

Climate change is altering ecosystem structure and function (Grimm et al. 2013). In particular, fungi perform many critical ecosystem functions, such as decomposing plant material, increasing plant growth, and causing diseases (Wardle et al. 2004, Boddy et al. 2008, Maron et al. 2011). Climate change could lead to range shifts of fungi, if fungi can follow their climate niches across the landscape (Kivlin et al. 2017). Long-distance dispersal of fungi can play an important role in these transitions (McGuire and Treseder 2010).

Southern California is predicted to become drier and warmer under climate change (Seager and Vecchi 2010). Strong seasonal winds could be carrying fungi from desert to coastal ecosystems. These fungi might colonize coastal ecosystems undergoing drying and warming, because they are likely pre-adapted to the arid desert ecosystems. Moreover, the functional groups of fungi that colonize coastal ecosystems may mediate ecosystem function. Currently, we do not know if there are changes in the functional groups dispersing to coastal ecosystems, especially when sources of airborne fungi change from the ocean to the desert. Understanding long-distance fungal dispersal from the desert to the coast could inform models of current and future predictions of ecosystem function (Allison 2012, Lennon et al. 2012, Treseder and Lennon 2015).

Santa Ana winds bring dry, hot air towards the coast, originating from inland mountains and deserts (Hughes and Hall 2010). In contrast, normal onshore, wind conditions blow from the ocean onto the coast. Santa Ana winds are seasonal and generally occur between September and

April (Raphael 2003). These winds are caused by two mechanisms: synoptic forcing and temperature gradients (Hughes et al. 2009, Hughes and Hall 2010). Synoptic forcing is the result of higher atmospheric pressure over the deserts of the southwestern U.S., combined with lower pressure near the coast. In addition, warmer temperatures near the coast and cooler temperatures in the desert can create a temperature gradient that triggers Santa Ana winds. Either temperature gradients alone, or both mechanisms acting simultaneously, can cause Santa Ana winds to form (Hughes et al. 2009). Models of Santa Ana winds under climate change suggest Santa Ana winds will continue to bring lower humidity and higher temperatures to Southern California, particularly during the driest parts of the year (Miller and Schlegel 2006, Hughes et al. 2011). However, we do not know how many spores and which groups of fungi are dispersed during Santa Ana winds.

Spores are resistant to UV radiation and desiccation and can remain viable after long-distance dispersal (Wyatt et al. 2013). Spores under 2.5 microns are of particular importance. Spores under 2.5 microns are more readily dispersed long distances through the air, because they can stay entrained for a longer time period (Roper et al. 2008, 2010). Indeed, fungal spores represent 4–11% of total particulate mass under 2.5 microns in sampled air in urban and rural areas (Womiloju et al. 2003). In addition, particles under 2.5 microns can be inhaled deep into the lungs of humans and pose a threat of disease (U.S. EPA 2009). Due to associated health risks and longer duration spent in the atmosphere, we focus on the dispersal of smaller spores.

This study is one of the first to examine fungi entrained in the air during Santa Ana winds. We addressed four questions regarding the airborne fungal community during Santa Ana winds. First, do Santa Ana winds carry more airborne fungal spores than do onshore winds? We hypothesized that airborne spore abundance would rise during Santa Ana winds, owing to a

greater amount of dust entrained by winds blowing over desert ecosystems. Second, does the structure of airborne fungal communities differ between normal, onshore wind conditions and Santa Ana wind events? We hypothesized that fungal community composition will shift, because the source of fungi will change from the ocean to inland, likely dispersing different fungi. Moreover, if fungal community composition shifts, we hypothesized that there would be specific indicator species driving the shift. Third, which fungal functional group is most abundant during Santa Ana winds? We hypothesized that fungal pathogens would be the most abundant functional group during the Santa Ana winds, because fungal pathogens tend to rely on air dispersal more than decomposers or symbionts (Cat et al. 2019). Finally, do airborne fungal communities differ across dispersal studies conducted in the same region? We hypothesized that airborne fungal communities would be similar at the phyla level because the mixing of air, especially at the timescale of days to weeks, would allow for mixing and homogenizing of airborne fungal communities.

To test our hypotheses, we stationed a high-volume air sampler to collect air during normal, onshore wind conditions versus Santa Ana wind events. We examined spores under 2.5 microns carried by these winds. We used high throughput sequencing to characterize the airborne fungal community, as well as a bioinformatics pipeline to determine fungal functional groups.

Methods

Sample collection

From March 2015 to September 2015, we deployed a high-volume total suspended particulate sampler equipped with $PM_{2.5}$ impactor plates (TE-230-QZ, Tisch Environmental, Cleves, OH, USA) on top of a five-story building on the University of California, Irvine campus (33.646206 N, -117.845014 W). Particulate matter smaller than 2.5 microns was collected on a

20 cm by 25 cm quartz microfiber filter (2500 QAT-UP, Pallflex Tissuquartz, Pall, Port Washington, NY, USA) after pre-filtering of larger particles using a slotted microquartz fiber filter installed in the impactor head (TE-230-QZ, microquartz slotted collection substrates, Tisch). Before collection, we sterilized sample filters at 500°C for 4 h. After collection, we stored sample filters at -20 °C until processing within three months.

Currently, there is no standard Santa Ana winds index (Hughes et al. 2009). Santa Ana winds have been defined by a number of parameters – both individually or combined – including: speed, direction, local pressure gradients, air temperatures, and relative humidity (Raphael 2003, Hughes et al. 2009). Santa Ana winds can also vary in scale from localized to generalized events. In this study, we defined localized Santa Ana events as periods where all of these three criteria were met at our study site: 1) the average air temperature was greater than 25° C, 2) wind speeds were faster than 4 km per hr, and 3) relative humidity was below 30%. Climate data, including air temperature, relative humidity, wind speed, wind direction, and precipitation were recorded every 30 minutes at the Cattle Crest weather station, located 4 km from the sampler. We collected samples during Santa Ana wind events (n=2) and normal onshore wind conditions or rainfall (n=15). We obtained only 2 Santa Ana wind samples, because we followed conservative criteria to define the localized Santa Ana events. The 2 Santa Ana wind samples were collected from March 13 to March 16, 2015 and April 27 to May 1, 2015. Moreover, we confirmed that spores sampled during Santa Ana wind events were dispersed from inland (Figure 1a) as opposed to the ocean (Figure 1b) using modeled trajectories from NOAA HYSPLIT (Stein et al. 2015). Atmospheric sampling intervals ranged from approximately 2 to 25 days.

To obtain the fungal spores from the filters, we cut a quarter piece from the filters and immersed the subsample in sterile 1X phosphate buffered saline solution in a Whirl-Pak bag (sensu Chow, Griffin, Barker, Loparev, & Litvintseva, 2016). The filters were shaken on a tabletop shaker for 30 min at 450 RPM to wash the spores off the filter. The filters collect black carbon, a large fraction of the airborne particulate matter due to burning of fossil fuels. To remove the black carbon, we pelleted the black carbon, but not the spores, from the filters by transferring the PBS buffer (which contained the spores), plus the filter, to 50 mL Falcon tubes and centrifuging at 200g for four hours (Jiang et al. 2015). This relatively slow speed allowed the spores to remain in the PBS buffer while removing most of the black carbon.We counted spore abundance using aliquots of the PBS solution containing spores using a hemocytometer under a microscope. Spore concentrations were standardized to spores per cubic meter of air using flow rate of the air sampler and sampling time period.

DNA extraction, PCR amplification, sequencing, and bioinformatics

We processed the air filters using the MoBio PowerSoil Extraction kit (MoBio, Carlsbad,CA). We followed manufacturer recommendations for all steps, except we used 250 uL of the PBS solution containing spores instead of the recommended 0.25 g of soil. Then, we amplified a ~340 bp region of the fungal ITS2 region in the 5.8S encoding gene (Ihrmark et al. 2012). This shorter amplicon reduces species bias and chimera formation without compromising inferences of species diversity (Ihrmark et al. 2012). We used a staggered primer design to improve overall sequence quality (Tremblay et al. 2015, sensu Looby et al. 2016).

Reactions contained 0.75 ng of each forward and reverse primer, 21.5 ng of Platinum PCR SuperMix (Invitrogen, Carlsbad, CA), 1 uL of BSA, and ~10 ng of template DNA for a total volume of 25 uL. We amplified each sample in triplicate, and ran the reaction for 35 cycles

of 94°C for 45 s, 50°C for 60 s, and 72°C for 90 s with a hot start at 94°C for 7 min and a final extension step at 72°C for 10 min. We pooled and purified triplicates to remove primer-dimers and non-target DNA using Agencourt AmPure XP beads (Beckman-Coulter, Brea, CA) mixed with PCR product at a 1:1 ratio. To create a multiplexed library, we quantified DNA concentrations with a spectrophotometer and the Qubit dsDNA High Sensitivity Assay Kit (Life Technologies, Grand Island, NY) and then pooled samples in equi-molar concentrations. Samples were sequenced at the University of California, Riverside Institute for Integrative Genome Biology on the Illumina Mi-Seq platform on a single flowcell lane at 2 x 300 bp paired end reads.

We obtained ~16.2 million total sequences. Then, we demultiplexed raw sequence data using Quantitative Insights into Microbial Ecology (QIIME)(Caporaso et al. 2011). We chose QIIME in order to customize our parameters for QC. We removed low quality reads that were below a Phred quality threshold of Q30, and eliminated sequences with three consecutive low quality base reads. We required a minimum ratio of 0.75 for high quality base calls to input read length. We removed chimeras by removing singleton OTUs as well as comparing against reference sequences from the UNITE database, the most comprehensive database for fungal taxa (v.7, updated 01/12/2017, https://unite.ut.ee/repository.php) (Abarenkov et al. 2010). Following open reference picking of OTUs by 97% similarity, OTUs were assigned taxonomy using BLAST (version 2.2.22) and the UNITE database. The 97% cutoff is equivalent to species or genus, contingent on fungal phyla (Nilsson et al. 2009). After taxonomical assignment, non-fungal OTUs were filtered out. Following quality control, our dataset contained ~12.7 million fungal sequences. We rarefied to 18,000 reads per sample through random sub-sampling to standardize the number of OTUs for each air sample.

In order to assign fungal species to functional groups, taxonomic identities of OTUs were uploaded to FUNGuild (Nguyen et al. 2016). FUNGuild assigns OTUs into broad "trophic modes" - pathotroph, symbiotroph, and saprotrophs – that are supported by primary literature. Here, we call these modes pathogens, symbionts, and decomposers, respectively. Some fungal species are assigned two or more trophic modes (e.g., “pathogen-decomposer” and “animal pathogen-decomposer”). Our criterion to include these groups was met if there were greater than 30 species present within a group. No trophic mode groups with three or more assignments met this requirement, so they were not included in the following analyses.

Statistics

Hypothesis 1

We hypothesized that airborne spore concentration will rise during Santa Ana winds. We used an ANOVA to check for significant differences in spore concentration during onshore winds and Santa Ana winds. In addition, we tested relationships between spore concentration and climate variables by using ANOVA.

Hypothesis 2

We hypothesized that fungal community composition will differ between Santa Ana events and normal, onshore winds. We used the metaMDS function in the vegan package in R to visualize the fungal community in each sample in two dimensions (stress = 0.162 after 50 iterations) (R version 1.0.136, R Core Team 2017, Oksanen et al. 2011). Then, we used the ordiellipse function to group communities within samples based on similarity using the 99% confidence interval around the mean calculated by standard error. In order to compare fungal community composition with climate factors, we compared the OTU table with averaged climate

conditions over each individual sampling period in a series of perMANOVAs using the vegan package in R (Oksanen et al. 2011).

In order to understand which species were driving changes in fungal community composition, we determined indicator species for normal, onshore wind conditions and for Santa Ana winds. Indicator species are used as ecological indicators of environmental conditions, in this case, normal, onshore conditions versus Santa Ana winds. Indicator species were defined as OTUs with a positive, significant Pearson residual during one type of event and a negative, significant Pearson residual during the opposite type of event.

Hypothesis 3

We hypothesized that fungal pathogens will be the most abundant functional group during the Santa Ana winds. We used ANOVA to check for differences between trophic modes between onshore and Santa Ana winds, followed by the Tukey HSD post-hoc tests for pairwise differences.

Hypothesis 4

We hypothesized that airborne fungal communities would be similar across airborne fungal communities from different dispersal studies. We calculated the relative abundance of phyla in the air for Chapter 3 data, then Chapter 2 data. Next, we calculated the relative abundance of phyla in soil samples from Chapter 2. We used supplementary data available from Kivlin et al. 2014, which looked and regional airborne and soil fungal communities sampled over 2-3 months. We included the top 3 most abundant phyla across all sample types.

Results

Hypothesis 1

In support of our hypothesis, spore concentrations significantly increased during Santa Ana winds, compared to onshore winds (Figure 2). In fact, spores were about 2.5 times as abundant during Santa Ana winds. In addition, spore concentration decreased significantly with relative humidity (Figure S1). There was no significant relationship between spore abundance and temperature, wind speed, wind direction, or precipitation (Table S1).

Hypothesis 2

Airborne fungal community composition significantly shifted during Santa Ana winds (Table 1, Figure 3), which supported our hypothesis. We tested all measured climate factors against changes in fungal community composition. We found a weak but significant relationship between fungal community composition and relative humidity, along with weak and marginally significant associations with wind speed and precipitation (Table 1).

Since community composition shifted, we checked for indicator species of Santa Ana winds. We found that one strain of *Exophiala xenobiotica* was the strongest indicator species for Santa Ana events (Table 2). Four other strains of *E. xenobiotica* were also indicator species for Santa Ana events (Table 2). An unidentified species from class *Tremellomycetes* was the strongest indicator species for normal, onshore wind conditions (Table 2).

Hypothesis 3

Decomposers were the most abundant functional group during Santa Ana wind events (Figure 4). Neither pathogen nor decomposer abundance differed significantly between Santa Ana and onshore winds (Figure 4). These results did not support our third hypothesis that pathogen abundance would increase during the Santa Ana winds.

Hypothesis 4

In support of our hypothesis, we found that airborne fungal communities generally have a higher proportion of basidiomycetes than soil fungal communities (Figure 3.5).

Discussion

We discovered that the abundance of decomposer fungi increased during Santa Ana wind events. This change was driven by a ~2.5-fold increase in absolute abundance of fungal spores, in addition to a ~6-fold increase in relative abundance of decomposer fungi. Moreover, fungal community composition differed between normal, onshore wind conditions and Santa Ana events. This shift in community composition was weakly related to relative humidity, wind speed, and precipitation. To our knowledge, our study is the first to broadly examine airborne fungi in Santa Ana winds, especially with regard to their ecological functions. Other prior studies have focused on the inorganic dust transported by Santa Ana winds or changes in air quality (Guazzotti et al. 2001, Bytnerowicz et al. 2010).

We confirmed that Santa Ana winds carried a higher abundance of spores compared to normal, onshore wind conditions. In our study, spore abundance was negatively correlated with relative humidity. Other studies have found relationships between spore abundance and relative humidity, even at different temporal scales and across ecosystem types. For example, seasonal fluctuations of airborne spore concentrations can be negatively related to relative humidity in Europe (Lewis et al. 2000, Grinn-Gofroń and Strzelczak 2013). Moreover, airborne spore concentrations at finer time-scales in the Midwest are linked to dew point (a measurement related to relative humidity) (Burch and Levetin 2002). Therefore, the relationship between spore abundance and relative humidity appears to hold across temporal scales and ecosystem type.

Our study examined dispersal to Southern California from two different areas –the ocean and the desert. This observational study is in contrast to a similar study using high-throughput sequencing of the ITS region to examine airborne fungi. That study found that airborne communities are similar over a large area with a similar climate, and that variations in community composition are mainly driven by seasonal rather than spatial factors (Nicolaisen et al. 2017). In the current study, we were able to capture—in one location—fungi arriving from geographic areas with contrasting climates. As a result, we discovered that decomposer fungi adapted to warm, dry desert conditions were dispersing to Southern California ecosystems, which are currently warming and drying due to climate change.

Interestingly, an opportunistic black yeast – *Exophiala xenobiotica* – was an indicator species that significantly contributed to changes in community structure during Santa Ana winds. *Exophiala xenobiotica* is a member of the ascomycete order *Chaetothyriales*, which includes degraders of monoaromatic hydrocarbons such as toluene (Prenafeta-Boldu et al. 2001, De Hoog et al. 2006). Toluene is one of the most abundant components of the water soluble fraction of crude and refined oils (Prenafeta-Boldu et al. 2001). Environmental strains of *E. xenobiotica* are commonly found in hydrocarbon polluted soil, and they can also act as an opportunistic pathogen of humans or other animals (De Hoog et al. 2006). Other members of Exophiala, such as *E. jeanselmei* and *E. dermatitidis*, are well-documented agents of subcutaneous or lung infections (Vicente et al. 2008, Kirchhoff et al. 2017). *Exophiala xenobiotica* is able to resist UV light (De Hoog et al. 2006), which can act as an environmental stressor for airborne microbes (Womack et al. 2010, DasSarma and DasSarma 2018). Santa Ana winds may have facilitated the dispersal of *E. xenobiotica,* with potential implications for human and environmental health.

Our finding that decomposer fungi dominated the airborne fungal community during Santa Ana winds contrasted with a previous study that found pathogenic fungi tend to be more air-dispersed within the Southwestern U.S. (Cat et al. 2019). Strong Santa Ana winds may have lifted soil (and its associated decomposer fungi) from inland and desert areas (Figure 1). Onshore winds from the ocean would have had less opportunity to do so. During Santa Ana winds, fungi that may have been adapted to arid inland ecosystems were deposited in coastal ecosystems that are expected to become drier and warmer during this century (Seager and Vecchi 2010). This movement could potentially cause shifts in carbon cycling in this system if fungi better adapted to drier and warmer conditions outcompete local decomposers.

We observed that basidiomycetes have a larger relative abundance in the air, across studies that vary from the local to regional scale, as well as from one timepoint to weeks to months. Overall, we observed that basidiomycetes have a larger relative abundance in local (Chapter 3) and regional (Chapter 2 and Kivlin et al. 2014) air samples compared to regional soil samples. Although both members of Basidiomycota and Ascomycota use active and passive methods of air dispersal, our results suggest that basidiomycetes are able to keep their spores airborne more effectively than ascomycetes. Variations in abundance between air samples, notably the lower relative abundance of ascomycetes in Kivlin et al. 2014, could be caused by primer bias against certain phyla. For example, the primers used in Chapter 2 and Chapter 3 were designed to reduce bias against members of ascomycetes (Ihrmark et al. 2012).

Our study has some limitations. First, the climate factors recorded did not fully explain variations in the airborne fungal community in this study. Second, we focused our analyses on the $PM_{2.5}$ fraction, because this fraction tends to capture fungi that can travel longer through the air (Pickersgill et al. 2017). A previous study found that decomposer fungi tend to be <3 microns

while pathogens may be slightly larger (Pickersgill et al. 2017). This restriction may explain why decomposer fungi were prevalent in our samples. Yet, this restriction applied to onshore as well as Santa Ana winds, so it likely did not account for the disproportionate increase in decomposer fungi during Santa Ana winds. Third, ecological function was not assigned to all the OTUs captured by this study, as the FUNGuild database is still undergoing development. Fourth, we found a relatively low concentration of airborne fungal spores in the environment (~6-15 spores per cubic meter). Desert environments often display lower spore concentrations (~400 per cubic meter) than those of temperate and tropical regions (Lacey 1981). We sampled during a historic severe drought in California (He et al. 2017, Luo et al. 2017), which may have contributed to the low spore concentrations. Lastly, we caution that our results are likely only applicable to a <100 km radius, as previous studies have found that airborne fungal communities differ at a greater distance (Abrego et al. 2018).

Climate change may alter the frequency and strength of Santa Ana winds. Some studies suggest that the deserts may heat faster than the coast, thereby reducing the strength of Santa Ana winds (Hughes et al. 2009, 2011). This prediction, however, is not necessarily consistent with historic records (Guzman-Morales et al. 2016). Regardless, climate models predict that Santa Ana winds will continue to expose Southern California to lower relative humidity and higher temperatures, especially during the driest parts of the year (Miller and Schlegel 2006, Hughes et al. 2011). Since lower relative humidity coincided with greater concentrations of airborne spores in our study, it is possible that climate change could increase the dispersal of fungal spores during Santa Ana winds.

In conclusion, we discovered that Santa Ana events increased overall spore concentrations, especially for decomposer fungi. Indeed, decomposer fungi increased in both

relative and absolute abundance during Santa Ana winds, leading to an overall 5-fold increase in decomposer fungi. At the same time that Southern California ecosystems undergo drying and warming from climate change, decomposer fungi from the desert could be carried to coastal ecosystems by Santa Ana winds. Ecosystem function may change as decomposers adapted to arid ecosystems disperse to and colonize these coastal ecosystems (Seager and Vecchi 2010). Moving forward, it is critical we understand how arid-adapted fungi may alter decomposition rates in coastal ecosystems undergoing drying and warming under climate change.

Table 3.1. perMANOVA results for relationships between airborne fungal community composition versus climate factors and spore concentrations.*

Parameter	**F**	**r^2**	**P**
Relative humidity	1.79	0.095	**0.019**
Wind speed	1.44	0.078	0.104
Wind direction	0.71	0.040	0.858
Temperature	0.96	0.053	0.465
Precipitation	1.40	0.076	0.098
Event	2.16	0.113	**0.009**
Spore concentration	1.66	0.089	0.057

*Significant relationships are in bold. Marginally significant results are underlined.

Table 3.2. Pearson residuals for indicator species analysis.

Species	OTU ID	Onshore	Santa Ana	Abundance*
E. xenobiotica	New.ReferenceOTU109	-88.38	257.66	25703
E. xenobiotica	SH194487.07FU_DQ182587_refs	-21.69	63.25	924
E. xenobiotica	New.ReferenceOTU149	-7.91	23.07	203
E. xenobiotica	New.ReferenceOTU266	-4.55	13.27	124
E. xenobiotica	New.ReferenceOTU269	-3.74	10.92	111
Tremellomycetes spp.	New.ReferenceOTU248	19.29	-56.24	31733

*Abundance measured as number of sequence reads

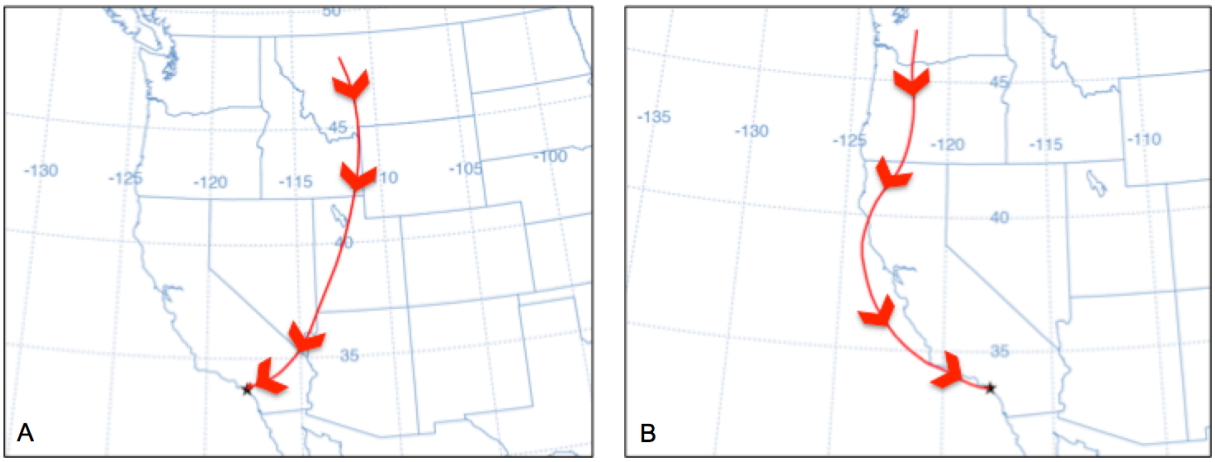


Figure 3.1. Likely trajectory of spores 48 h before the air sampler captured spores on April 29, 2015, during a Santa Ana event that lasted from April 27 to May 1, 2015 (A). Likely trajectory of spores 48 h prior to sampling during normal onshore wind conditions on May 15, 2015 (B). The star is the location of the air sampler. Based on the NOAA HYSPLIT model, the red line represents the likely trajectory of spores before being deposited on the air sampler.

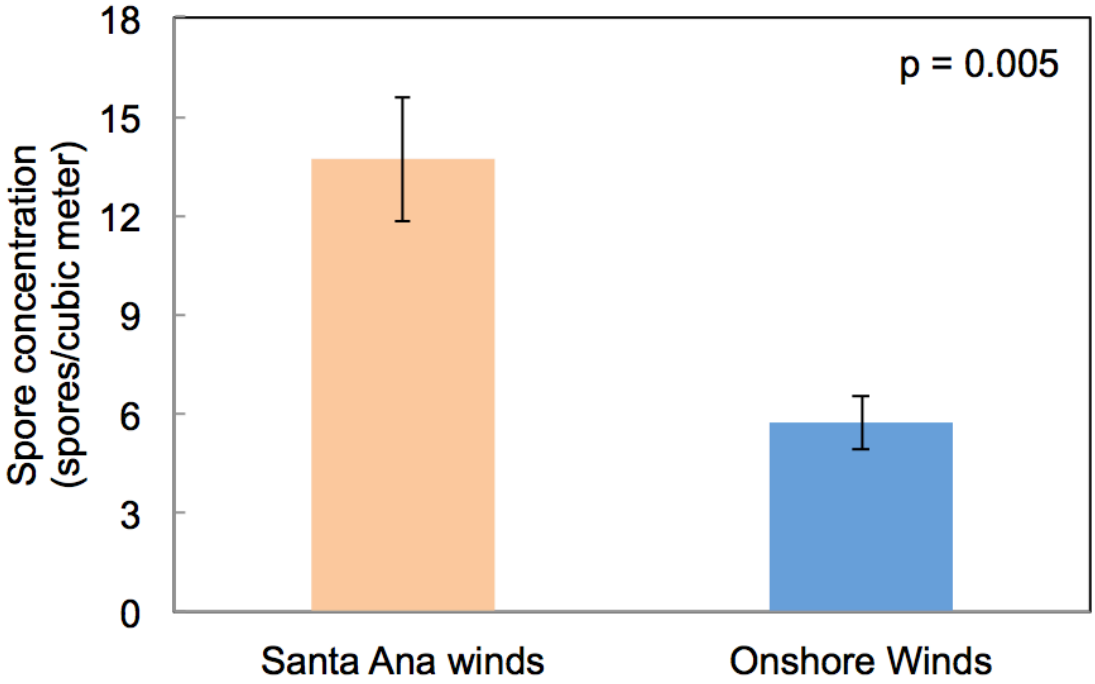


Figure 3.2. Spore concentrations per cubic meter of sampled air during Santa Ana and onshore wind conditions. Values are averaged spore concentrations from samples taken during each event type. Error bars represent ±1 SE.

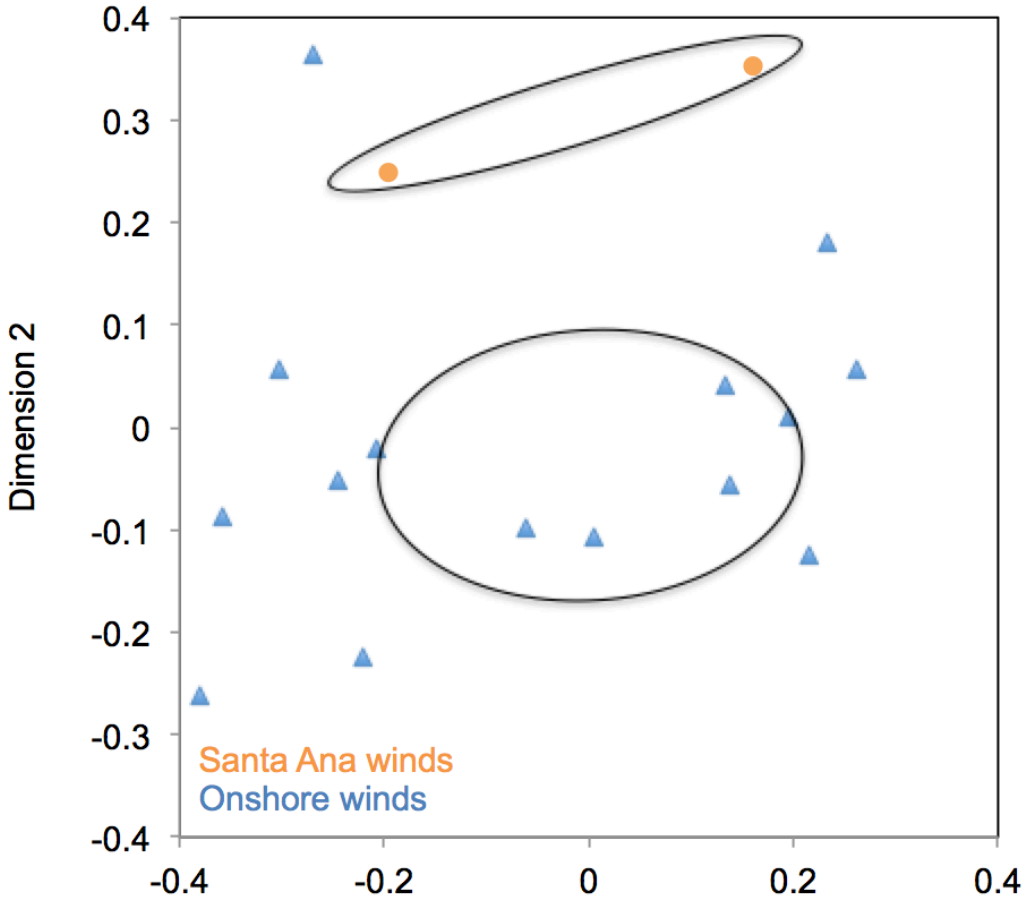


Figure 3.3. NMDS Dimension 1 and 2 each combine weather factors that explain variation between fungal communities. Circles represent fungal communities from each sample. Ellipsis indicate the 99% confidence interval around the mean calculated by SE for communities during Santa Ana and onshore winds.

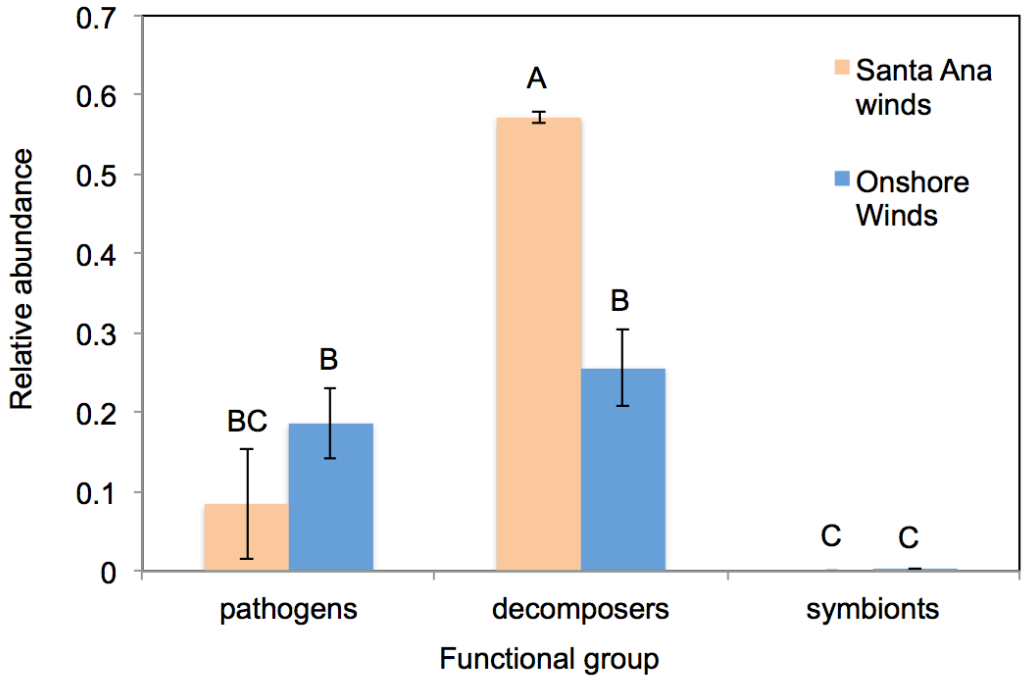


Figure 3.4. Relative abundance of trophic modes during Santa Ana and onshore winds. Values are averaged relative abundances across OTUs within a trophic mode. Error bars represent ±1 SE. Letters indicate significant pairwise differences.

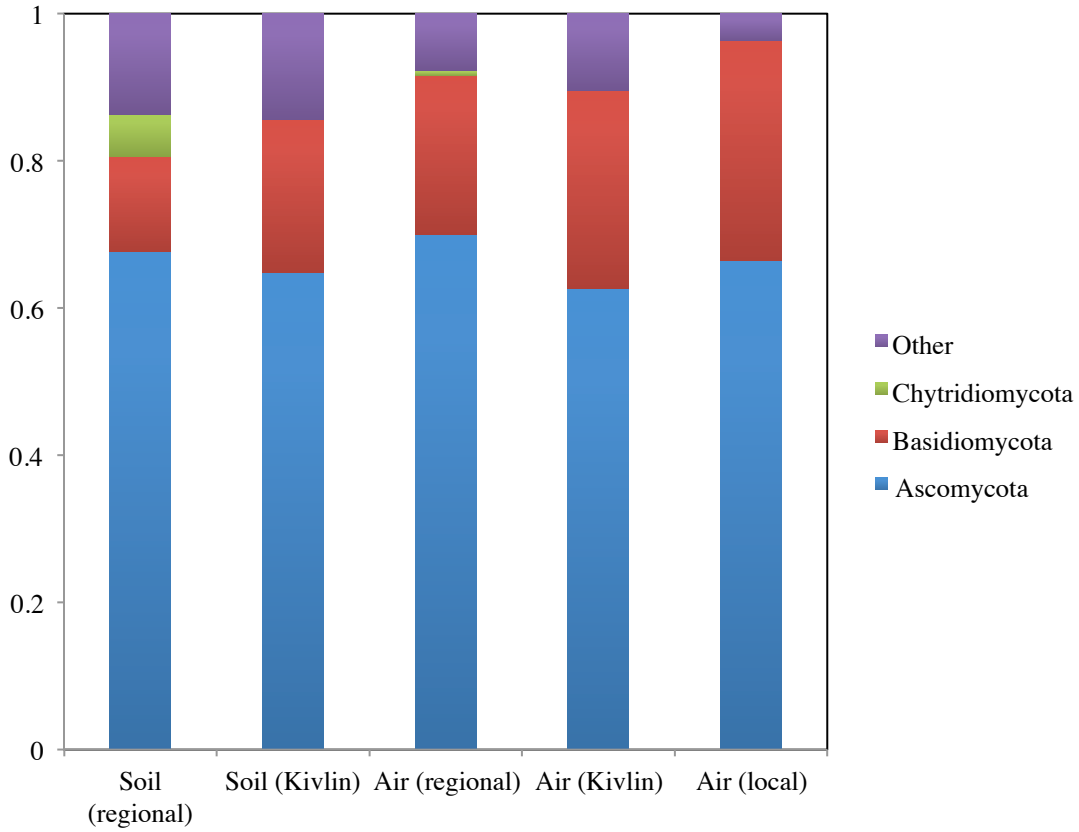
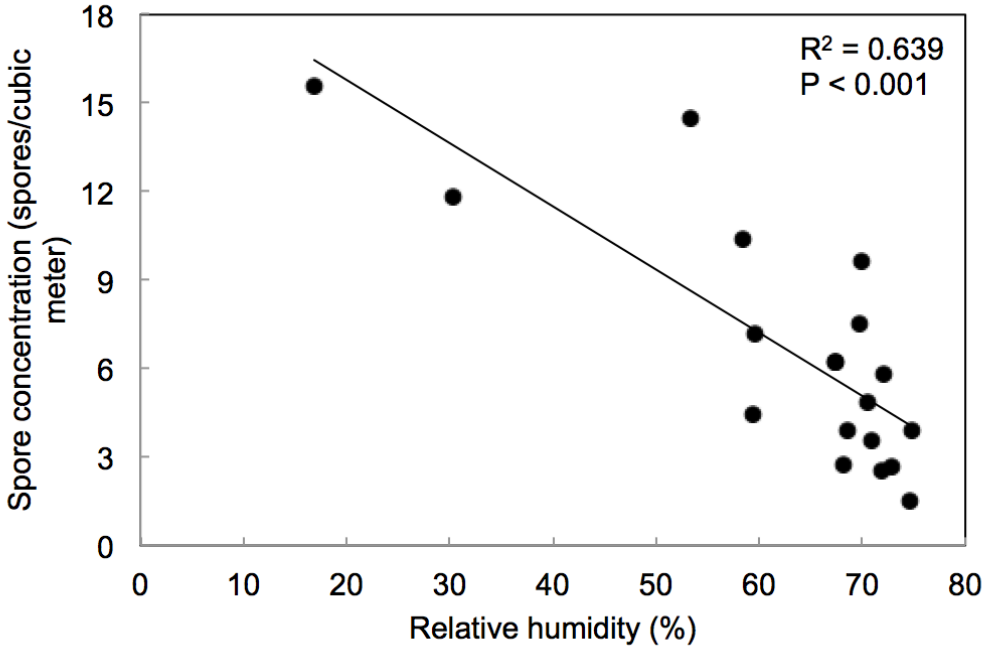


Figure 3.5. Comparison of relative abundance of fungal phyla between soil sampled at a regional scale (Chapter 2 & Kivlin et al. 2014), air sampled at a regional scale (Chapter 2 & Kivlin et al. 2014), and all local air samples during both Santa Ana winds and onshore conditions (Chapter 3).



3.S1. Spore abundance is correlated with the relative humidity at time of sampling. Circles indicate spore concentration at different relative humidity levels. The line is a linear regression.

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