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# Crossing the Line: Human Disease and Climate Change Across Borders

White Paper for the Environmental Working Group of the UC-Mexico Initiative

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### Introduction

Human disease epidemics are rising in concert with climate change effects. Recent models suggest that disease will undergo range shifts, rather than expanding, driving the need for international collaboration as pathogens cross borders. Of special concern are emerging infectious diseases, many of which are caused by fungal pathogens. For millions of years, fungi have had an extensive and overlooked influence on Earth's ecosystems – driving global biogeochemical cycles, facilitating the evolution of terrestrial plants, and mediating the biodiversity of plants and animals we see on Earth today. The microscopic lifestyle of fungi poses unique challenges to answering relevant ecological questions. Researchers have recently developed the technology and methods to study fungi in an ecological context. Therefore, we have both the urgent need and the effective methods to answer questions regarding fungal diseases and environmental factors that influence their dispersal and richness.

The atmosphere harbors living spores of an untold number of fungal species, and continuously moves them between nations and human populations. In fact, one cubic meter of air can harbor thousands of fungal spores representing hundreds of species. Fungi produce spores to colonize 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. Many of these fungal diseases are airborne. The prevailing winds that disperse them are likely to shift direction under climate change, threatening populations that have not developed immunity.

Most scenarios anticipate notable climate changes in the region surrounding the Mexican-U.S. border. Within this century, mean annual temperatures are predicted to increase by 2-5 °C, and droughts may become longer and more severe. Since the environmental niches of many species are strongly influenced by climate, their geographic ranges may shift accordingly. In fact, these range shifts may be particularly striking in the border region, since water scarcity and high temperatures already limit the activities of many animals, plants, and microbes. Since the border region, since water scarcity and high temperatures already limit the activities of many animals, plants, and microbes. Since the environmental niches of many species are strongly influenced by climate, their geographic ranges may shift accordingly. In fact, these range shifts may be particularly striking in the border region, since water scarcity and high temperatures already limit the activities of many animals, plants, and microbes. Since the environmental niches of many shift accordingly. In fact, these range shifts may be particularly striking in the border region, since water scarcity and high temperatures already limit the activities of many animals, plants, and microbes. Since the environmental niches of many shift accordingly. In fact, these range shifts may be particularly striking in the border region, since water scarcity and high temperatures already limit the activities of many animals, plants, and microbes. Since the environmental niches of many shifts accordingly.

Because many diseases are expected to become more prevalent under climate change<sup>1</sup>, 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, and climate change scientists who must advance research rapidly to address the new challenges. Furthermore, recent models suggest that pathogens will undergo range shifts of their habitat, further driving the need for international collaboration as pathogens cross borders.<sup>1–3</sup>

Fungal disease outbreaks can be more challenging to forecast than other diseases that are mainly transmitted by human-to-human contact, because their survival is independent of human population density. When not infecting humans, many fungal pathogens can reside in the soil as active decomposers of dead plants or animals, or as dormant spores. <sup>27,28</sup> This dimorphic lifestyle of fungal pathogens—their ability to live outside as well as inside their human hosts—is not well-studied, yet key in understanding and predicting fungal disease spread. Because the survival of these fungal pathogens is independent of human population density, these disease outbreaks

are more challenging to forecast than other diseases that are transmitted primarily via person-to-person contact. <sup>27,28</sup>

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.

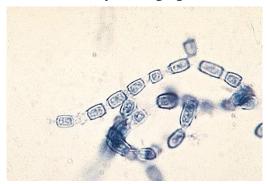


Figure 1. Spore formation in Coccidioides immitis (image courtesy of U.S. CDC)

Coccidioides causes valley fever. This disease is a "silent epidemic" because 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 (Fig. 2).<sup>29</sup> It is caused by inhalation of *Coccidioides* spp. spores, and even one spore can cause disease.<sup>30</sup> The fungus resides in the soil of arid ecosystems in the Southwest U.S. and Northern Mexico (Fig. 3). *Coccidioides* grows after rainstorms, and then forms spores during long dry periods.<sup>31</sup> Spores can cause infection once wind aerosolizes dusty soil. Climate models predict increased drought length interrupted by heavier rainstorms in the U.S. Southwestern regions, which will favor both mechanisms of spore production and dispersal of *Coccidioides*.<sup>23</sup> Much of the information regarding *Coccidioides* environmental preferences was collected and analyzed in the 1950s and 1960s. It is critical that we revisit these ideas using current data and modern techniques because lack of contemporary studies prevents informed decision-making regarding disease surveillance, vaccine development, and outbreak preparedness. In addition, a binational survey of this fungus would be unprecedented.

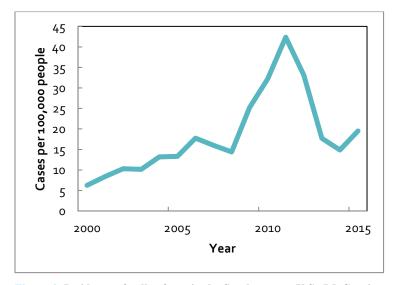


Figure 2. Incidence of valley fever in the Southwestern U.S. (M. Gorris, unpubl. data ).

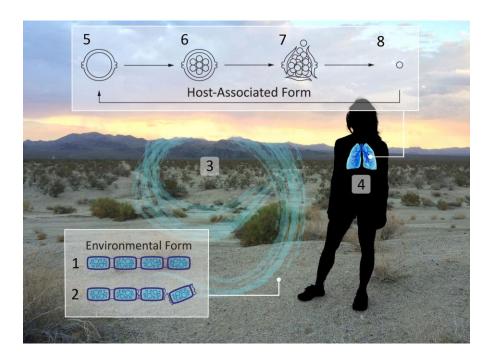


Figure 3. In the environment, *Coccidioides* spp. exists as a decomposer (1) growing in filaments. The filaments fragment into barrel-shaped arthrospores (2), which measure only 2-4 micrometers in diameter and are easily aerosolized when disturbed (3). Spores are inhaled by a mammalian host (4) and settle 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).

### Human Welfare Impacts of Valley Fever

Fungal dispersal has far-reaching effects on many aspects of human welfare, ranging from health to economic concerns.<sup>4</sup> Human disease, including valley fever, can lead to debilitation, loss of quality of life, and a large financial burden from medical costs.<sup>32</sup> Mostly, valley fever causes only mild flu-like symptoms, but it can lead to chronic pneumonia or mortality in some patients. In some cases, life-long medical treatment is required.<sup>33</sup> Valley fever treatment is particularly expensive, averaging \$23,000 to \$29,000 per patient in the U.S.<sup>34</sup> To determine future threats of valley fever on human welfare, we need to know the potential geographical range of *Coccidioides*, and 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). <sup>35</sup> In California, the central valley is hyperendemic with parts of Southern California classified as endemic. <sup>29,35</sup> Skin testing using coccidioidin, an antibody, has revealed exposure of 5% to 30% of the population in various parts of Mexico. <sup>35</sup> 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. <sup>35</sup> For these high-risk groups, mortality rates increase up to 90%. <sup>35</sup> Inmates imprisoned in the central valley of California are especially vulnerable to valley fever, because prisons are often built near *Coccidioides* habitats. <sup>36,37</sup> 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. <sup>38</sup> Many people are admitted 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.

Rates of valley fever infection have now reached epidemic proportions in the border region, perhaps owing to shifts in drought severity, temperature, and dust loads.<sup>39</sup> 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<sup>40</sup> area plus 1.3 million people in the Tijuana area.<sup>41</sup> 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 site of *Coccidioides* spp. growth in the environment. The critical question is how readily valley fever could disperse to new areas via wind transport.

### Fungal Pathogens in a Binational Context

Epidemics of human diseases are an international concern. Ecological research answers questions about systems that cross borders. Many 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. Binational cooperation is especially critical if fungal pathogens become more wind-dispersed or change their ranges under global change. Research encompassing the border area could be accomplished with cooperative research and data exchange from both sides of the frontier.

By working together to map and understand the distribution of fungal pathogens, researchers from Mexico and the U.S. can greatly improve preparedness for—and prevention of—disease outbreaks in the border region. While public health and medical data are difficult to compare between the U.S. and Mexico, environmental sampling can be conducted across borders and integrated with global climate data. This type of collaboration is the first step towards preventing loss of human life and economic costs of medical treatment.

Under the auspices of the UC-Mexico Initiative, researchers from University of California Irvine (L. Cat, M. Gorris, J. Randerson, and K. Treseder) reached out to Meritxell Riquelme and her colleagues at the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE) in Baja California, Mexico. Dr. Riquelme generously led the UCI group to a previously-mapped hotspot of valley fever in Valle de las Palmas. This area was home to an orphanage that had previously suffered an outbreak of valley fever. Together, we sampled topsoil as well as rodent burrows, which are thought to serve as a reservoir for the pathogen in the soil. Dr. Riquelme shared her laboratory protocols for identifying *Coccidioides* in environmental samples, and the UCI group was able to replicate her results. This way, the two groups developed a common sampling protocol for future surveys in the border region. This field campaign also allowed Mexican and U.S. graduate students to compare how they approached similar research questions and enabled us to learn more from each other.

## Climate Change and Fungal Pathogen Dispersal: A Macrosystems Approach

The next step is to examine *Coccidioides* dispersal within 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. <sup>45</sup> 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. <sup>46</sup>

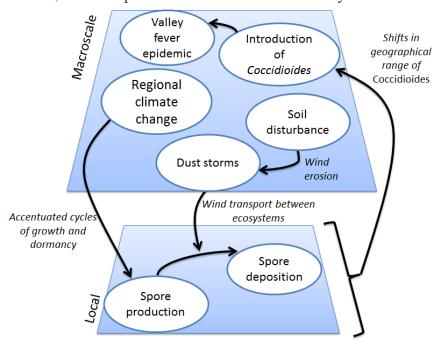


Figure 4. Conceptual framework of fungal movement within the border region.

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<sup>47</sup>, and then produce spores as protective resting structures. 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.

### Policy Responses and Challenges Against Disease

Our research aims to better understand movement of fungi across borders at a regional scale to build more powerful models that can be used 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. Suitable living conditions for *Coccidioides* are input as parameters and are typically governed by linear regression relationships or other statistical methods describing the climate conditions in which *Coccidioides* lives (i.e., soil moisture, maximum or minimum temperature, etc.). The model is mapped out in geographical space and represents the extent of where a species can live. Due to the difficulty of obtaining positive isolates and "true" negative isolates of *Coccidioides*, the amount of data points incorporated into the models is low. Including the results from our soil samples in Mexico with Dr. Riquelme and our sampling transect in the U.S. will increase the model's power and thus make it more robust. The environmental niche model for *Coccidioides* can then 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.

Table 1. Stakeholders with an interest in valley fever forecasts.

U.S. Center for Disease Control (CDC) Mycotic Diseases Branch (MDB)
Binational Border Infectious Disease Surveillance Program (BIDS)
State and local health agencies
Public Health Departments of Northern Mexico
Public Health Departments of the Southwestern U.S.
California Division of Occupational Safety and Health (Cal-OSHA)
Arizona Valley Fever Center of Excellence
World Health Organization
California Valley Fever Network

In addition, international research collaborations on fungal diseases can be fostered through formal meetings. With respect to valley fever, university researchers, CDC microbiologists, scientists, medical professionals, public health epidemiologists, and political activists meet on an annual basis at the *Coccidioides* Study Group and *Coccidioides* Collaborative Meeting. These inperson gatherings are hosted in California or Arizona each year. The agendas cover all aspects of how to screen, diagnose, and treat valley fever, as well as environmentally-oriented research on predicting and mitigating human exposure. These small groups are an excellent example of binational collaboration, because Mexican scientists and doctors share their findings and strengthen research partnerships. The intimate meetings allow individuals to exchange unpublished yet valuable data that can direct future lines of research. During research talks, scientists and researchers are encouraging and willing to share specific techniques and tips, especially since it is quite challenging to find and study *Coccidioides* in the environment. Additionally, many individuals, who have been involved in valley fever research since the 1960s, attend and offer input that cannot be gleaned from reading peer-reviewed articles. Much of the

documented knowledge of the pathogenesis, mycology, and clinical aspects of valley fever originated from studies performed by the *Coccidioides* Study Group.

### 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<sup>53</sup> and changes in community composition.<sup>54–56</sup> 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.<sup>22,23</sup> Overall, mean annual precipitation may decline 10–20% by the end of the century.<sup>23</sup> In addition, mean annual temperatures are expected to increase 2 to 5 °C during the same timeframe.<sup>22</sup> These projections are consistent with empirical trends documented in this region over the past several decades.<sup>22,57</sup> The border region is currently experiencing 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

These spores can become windborne, especially because dust storms are common in the region. <sup>58–61</sup> 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. <sup>62</sup> 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 (Lauer et al. 2016, in press). Dust emissions over disturbed soils can be 10–100 greater than undisturbed soil for a given wind speed. <sup>63,64</sup> Since the human population is growing faster in the Southwest than in any other region of the U.S., soil disturbance should increase in concert. <sup>40</sup>

### Wind transport

Many fungi—even human pathogens such as valley fever—have a life stage in the soil. 65 Therefore, they could be potentially entrained in winds and transported as dust. Indeed, microbes are abundant in the atmosphere. 66 Globally, it is estimated that fungal spores account for about 23% of organic aerosols. 67 Moreover, the richness of fungal species in air is on the same order as richness in soils. 68–70

Typically, fungi disperse over relatively long distances and many fungal species actively launch spores into the air. <sup>71,72</sup> About half of fungal species produce fairly small spores—less than 10 μm diameter at their longest axis. <sup>73</sup> These species are most likely to be wind transported <sup>74</sup>, since dust particles smaller than 10 μm in diameter can remain airborne long enough to travel significant distances. <sup>75</sup> Moreover, fungal spores can be particularly resistant to UV radiation and desiccation. <sup>11,65,76–78</sup> As a result, fungi can remain viable in the atmosphere long enough to cross continents or oceans. <sup>66,79,80</sup> 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. <sup>81</sup> In addition, clinical strains of valley fever occasionally differ from the environmental strains of the disease extracted from the putative site of exposure. <sup>82</sup> This indicates

that patients may be exposed to valley fever spores from locations hundreds of kilometers away.<sup>82</sup> Altogether, it seems likely that viable *Coccidioides* can be wind-dispersed across the border region, although this idea has not yet been directly assessed.

### Research Void: Airborne Fungi

Airborne fungi are highly diverse and difficult to observe. As a result, we know very little about the pathogenic fungi in the border region and how easily they disperse, which species disperse most readily, what physiological traits improve dispersal, and how evolutionary history can influence their success in new territories. In addition, we need to discover which ecosystems are "hotspots" that form important sources of pathogens and other critical fungal species, which climate conditions spur the production of spores, and how prevailing winds can influence their transport through the air. By examining these issues, we will learn much about a poorly understood, basic process and improve our ability to predict—and potentially avoid—outbreaks of airborne fungal diseases like valley fever.

We are currently using next-generation DNA sequencing to map the distributions of fungal pathogens in soil of the border region. We will use these maps to determine the range of climate conditions that individual species can tolerate. We will incorporate this information into a new spore transport model to simulate the production and air dispersal of fungal pathogens in the environment. In addition, the spore transport model will be integrated with a global climate model, allowing us to link spore dispersal with climate change.

### Disease Ecology as a Research Priority

Overall, we expect climate change to be an important driver of the dispersal of airborne pathogens within the border region. Soil disturbance from farming and construction will almost certainly become more prevalent as the human population expands, resulting in greater mobilization of fungal spores. This mechanism alone would increase movement of fungi across the region. Regional climate change could amplify its effects by accelerating spore production and allowing longer-range transport of spores. Altogether, these responses should interact to increase the transport of pathogenic fungi to new areas. *Coccidioides* is a special concern, since shifts in the geographical range of this pathogen could expose new human populations to valley fever. This fungus is just one of many that might alter human health and well-being by dispersing more readily within the region.

Coccidioides is a test case for fungal pathogens; studying its ecology and epidemiology will bring new ecological data to the surface as well as better human welfare in the U.S. and Mexico. Fungal pathogens are of special concern because they are emerging faster than other types of disease 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. Environmental niche models, like the ones we are improving for valley fever, can be applied to any type of disease that has an environmental stage, or for diseases that have living vectors (i.e. yellow fever, Zika virus, West Nile virus, all carried by mosquitoes).

It is critical that we prioritize binational collaborations to fully characterize fungal pathogens on both sides of the border. We can do so via annual meetings (e.g., *Coccidioides* Study Group)

between researchers to exchange data and protocols. In addition, coordination of sample collection between Mexican and U.S. researchers would allow us to maximize coverage of species distribution maps. Finally, 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.

### Acknowledgements

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### References

- 1. Lafferty, K. The ecology of climate change and infectious diseases. **90**, 888–900 (2009).
- 2. Raffel, T. R., Ruiz-Moreno, D. & Thomas, M. B. Frontiers in climate change-disease research. **2011**, 270–277 (2012).
- 3. Bebber, D. P., Ramotowski, M. a. T. & Gurr, S. J. Crop pests and pathogens move polewards in a warming world. *Nat. Clim. Chang.* **3**, 985–988 (2013).
- 4. Fisher, M. C. *et al.* Emerging fungal threats to animal, plant and ecosystem health. *Nature* **484**, 186–94 (2012).
- 5. Desirò, A. *et al.* Detection of a novel intracellular microbiome hosted in arbuscular mycorrhizal fungi. *ISME J.* **8,** 257–70 (2014).
- 6. Treseder, K. K. *et al.* Integrating microbial ecology into ecosystem models: challenges and priorities. *Biogeochemistry* **109**, 7–18 (2012).
- 7. Rizzetto, L., De Filippo, C. & Cavalieri, D. Richness and diversity of mammalian fungal communities shape innate and adaptive immunity in health and disease. *Eur. J. Immunol.* **44,** 3166–81 (2014).
- 8. Desprez-Loustau, M.-L. *et al.* The fungal dimension of biological invasions. *Trends Ecol. Evol.* **22**, 472–80 (2007).
- 9. García-Guzmán, G. & Heil, M. Life histories of hosts and pathogens predict patterns in tropical fungal plant diseases. *New Phytol.* **201**, 1106–1120 (2014).
- 10. Peay, K. G., Kennedy, P. G. & Bruns, T. D. Fungal Community Ecology: A hybrid beast with a molecular master. **58**, 799–810 (2008).
- 11. Levetin, E. Studies on airborne basidiospores. *Aerobiologia (Bologna)*. **6,** 177–180 (1990).
- 12. Hasnain, S. M., Fatima, K., Al-Frayh, A. & Al-Sedairy, S. Prevalence of airborne basidiospores in three coastal cities of Saudi Arabia. *Aerobiologia (Bologna)*. **21**, 139–145 (2005).
- 13. Bianchi, M. & Olabuenaga, S. A 3-year airborne pollen and fungal spores record in San Carlos de Bariloche, Patagonia, Argentina. *Aerobiologia (Bologna)*. **22**, 247–257 (2006).
- 14. Kasprzyk, I. & Worek, M. Airborne fungal spores in urban and rural environments in Poland. *Aerobiologia (Bologna)*. **22,** 169–176 (2006).
- 15. Pyrri, I. & Kapsanaki-Gotsi, E. A comparative study on the airborne fungi in Athens, Greece, by viable and non-viable sampling methods. *Aerobiologia (Bologna)*. **23**, 3–15 (2007).
- 16. Crawford, C. *et al.* Temporal and spatial variation of indoor and outdoor airborne fungal spores, pollen, and  $(1\rightarrow 3)$ -β-d-glucan. *Aerobiologia (Bologna)*. **25,** 147–158 (2009).
- 17. Oliveira, M., Ribeiro, H., Delgado, J. L. & Abreu, I. Seasonal and intradiurnal variation of allergenic fungal spores in urban and rural areas of the North of Portugal. *Aerobiologia* (*Bologna*). **25**, 85–98 (2009).
- 18. Quintero, E., Rivera-Mariani, F. & Bolaños-Rosero, B. Analysis of environmental factors and their effects on fungal spores in the atmosphere of a tropical urban area (San Juan, Puerto Rico). *Aerobiologia (Bologna)*. **26**, 113–124 (2010).
- 19. Mallo, A., Nitiu, D. & Gardella Sambeth, M. Airborne fungal spore content in the atmosphere of the city of La Plata, Argentina. *Aerobiologia (Bologna)*. **27**, 77–84 (2011).
- 20. U.S. Center for Disease Control. Types of fungal diseases. **2016**, (2014).
- 21. Yin, J. H. A consistent poleward shift of the storm tracks in simulations of 21st century climate. *Geophys. Res. Lett.* **32**, 1–4 (2005).
- 22. Karl, T. R., Melillo, J. M. & Peterson, T. C. Global Climate Change Impacts in the United

- States. (Cambridge University Press, 2009).
- 23. Schoof, J. T., Pryor, S. C. & Surprenant, J. Development of daily precipitation projections for the United States based on probabilistic downscaling. *J. Geophys. Res. Atmos.* **115**, D13106 (2010).
- 24. Whittaker, R. H. Communities and Ecosystems. (Macmillan Publishing Company, 1975).
- 25. Yuste, J. C. *et al.* Drought-resistant fungi control soil organic matter decomposition and its response to temperature. *Glob. Chang. Biol.* **17**, 1475–1486 (2011).
- 26. Toberman, H., Freeman, C., Evans, C., Fenner, N. & Artz, R. R. E. Summer drought decreases soil fungal diversity and associated phenol oxidase activity in upland Calluna heathland soil. *FEMS Microbiol. Ecol.* **66**, 426–436 (2008).
- 27. Sánchez-Martínez, C. & Pérez-Martín, J. Dimorphism in fungal pathogens: *Candida albicans* and *Ustilago maydis* similar inputs, different outputs. *Curr. Opin. Microbiol.* **4,** 214–221 (2001).
- 28. Klein, B. S. & Tebbets, B. Dimorphism and virulence in fungi. *Curr. Opin. Microbiol.* **10**, 314–9 (2007).
- 29. U.S. Center for Disease Control. *Fungal pneumonia: a silent epidemic. Coccidioidomycosis (valley fever).* (2011).
- 30. Huang, J. Y., Bristow, B., Shafir, S. & Sorvillo, F. Coccidioidomycosis-associated deaths, United States, 1990-2008. *Emerg. Infect. Dis.* **18**, 1723–1728 (2012).
- 31. Lacy, G. H. & Swatek, F. E. Soil Ecology of *Coccidioides immitis* at Amerindian Middens in California. **27**, 379–388 (1974).
- 32. Health Canada. Methods of assessing human health vulnerability and public health adaptation to climate change.
- 33. Nguyen, C. *et al.* Recent advances in our understanding of the environmental, epidemiological, immunological, and clinical dimensions of coccidioidomycosis. *Clin. Microbiol. Rev.* **26**, 505–25 (2013).
- 34. Plevin, R. Taxpayers spend millions on valley fever in prisons. *Reporting On Health Collaborative* (2012).
- 35. Sifuentes-Osornio, J., Corzo-Leon, D. E. & Ponce-De-Len, L. A. Epidemiology of invasive fungal infections in Latin America. *Curr. Fungal Infect. Rep.* **6**, 23–34 (2012).
- 36. de Perio, M. A., Niemeier, R. T. & Burr, G. A. *Coccidioides* exposure and coccidioidomycosis among prison employees, California, United States. *Emerg. Infect. Dis.* **21**, 1031–1033 (2015).
- 37. Pappagianis, D. *et al.* Coccidioidomycosis in California State correctional institutions. *Ann. N. Y. Acad. Sci.* **1111,** 103–111 (2007).
- 38. Perio, M. A. De & Burr, G. A. Evaluation of *Coccidioides* Exposures and Coccidioidomycosis Infections among Prison Employees. (2014).
- 39. Park, B. J. *et al.* An epidemic of coccidioidomycosis in Arizona associated with climatic changes, 1998-2001. *J. Infect. Dis.* **191**, 1981–1987 (2005).
- 40. U.S. Census Bureau. in *Census 2010* (http://factfinder2.census.gov/, 2010).
- 41. Instituto Nacional de Estadística y Geografía. Censo de Población y Vivienda 2010. **2016**, 1–3 (2010).
- 42. Baptista-Rosas, R. C. *et al.* Molecular detection of *Coccidioides* spp. from environmental samples in Baja California: Linking Valley Fever to soil and climate conditions. *Fungal Ecol.* **5**, 177–190 (2012).
- 43. Catalán-Dibene, J. *et al.* Detection of coccidioidal antibodies in serum of a small rodent community in Baja California, Mexico. *Fungal Biol.* **118,** 330–339 (2014).
- 44. Vargas-Gastelum, L. *et al.* Impact of seasonal changes on fungal diversity of a semi-arid ecosystem revealed by 454 pyrosequencing. *FEMS Microbiol. Ecol.* **91,** fiv044-fiv044

- (2015).
- 45. Heffernan, J. B. *et al.* Macrosystems ecology: understanding ecological patterns and processes at continental scales. *Front. Ecol. Environ.* **12,** 5–14 (2014).
- 46. Field, J. P. *et al.* The ecology of dust. *Front. Ecol. Environ.* **8,** 423–430 (2010).
- 47. Treseder, K. K., Schimel, J. P., Garcia, M. O. & Whiteside, M. D. Slow turnover and production of fungal hyphae during a Californian dry season. *Soil Biol. Biochem.* **42**, 1657–1660 (2010).
- 48. Allen, P. J. Metabolic aspects of spore germination in fungi. *Annu. Rev. Phytopathol.* **3**, 313- (1965).
- 49. Gottlieb, D. The physiology of spore germination in fungi. *Bot. Rev.* **16,** 229–257 (1950).
- 50. Baptista-Rosas, R. C., Hinojosa, A. & Riquelme, M. Ecological niche modeling of *Coccidioides* spp. in western North American deserts. *Ann. N. Y. Acad. Sci.* **1111,** 35–46 (2007).
- 51. Baptista-Rosas, R. C., Arellano, E., Hinojosa, A. & Riquelme, M. Bioclimatologia de la Coccidioidomicosis en Baja California, Mexico. *Investig. Geogr.* **71**, 21–30 (2010).
- 52. Ocampo-Chavira, L. unpubl. data.
- 53. Wardle, D. A. A comparative assessment of factors which influence microbial biomass, carbon, and nitrogen levels in soil. *Biol. Rev. Camb. Philos. Soc.* **67**, 321–358 (1992).
- 54. Schimel, J. P., Gulledge, J. M., Clein-curley, J. S., Lindstrom, J. E. & Braddock, J. F. Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. **31**, 831–838 (1999).
- 55. Castro, H. F., Classen, A. T., Austin, E. E., Norby, R. J. & Schadt, C. W. Soil microbial community responses to multiple experimental climate change drivers. *Appl. Environ. Microbiol.* **76**, 999–1007 (2010).
- 56. Hawkes, C. *et al.* Fungal community responses to precipitation. *Glob. Chang. Biol.* **17**, 1637–1645 (2011).
- 57. Pal, I., Anderson, B. T., Salvucci, G. D. & Gianotti, D. J. Shifting seasonality and increasing frequency of precipitation in wet and dry seasons across the U.S. *Geophys. Res. Lett.* **40**, 4030–4035 (2013).
- 58. Nickling, W. G. & Brazel, A. J. Temporal and spatial characteristics of Arizona dust storms (1965–1980). *J. Climatol.* **4,** 645–660 (1984).
- 59. Reheis, M. C. & Kihl, R. Dust deposition in southern Nevada and California, 1984-1989 Relations to climate, source area, and source lithology. *J. Geophys. Res.* **100**, 8893–8918 (1995).
- 60. Reheis, M. C. & Urban, F. E. Regional and climatic controls on seasonal dust deposition in the southwestern U.S. *Aeolian Res.* **3,** 3–21 (2011).
- 61. Sweeney, M. R., McDonald, E. V & Etyemezian, V. Quantifying dust emissions from desert landforms, eastern Mojave Desert, USA. *Geomorphology* **135**, 21–34 (2011).
- 62. Neff, J. C., Reynolds, R. L., Munson, S. M., Fernandez, D. & Belnap, J. The role of dust storms in total atmospheric particle concentrations at two sites in the western US. *J. Geophys. Res.* **118**, 11201–11212 (2013).
- 63. Gillette, D. A wind tunnel simulation of the erosion of soil: Effect of soil texture, sandblasting, wind speed, and soil consolidation on dust production. *Atmos. Environ.* **12**, 1735–1743 (1978).
- 64. Belnap, J. & Gillette, D. A. Disturbance of biological soil crusts: impacts on potential wind erodibility of sandy desert soils in southeastern Utah. *L. Degrad. Dev.* **8**, 355–362 (1997).
- 65. Roszak, D. B. & Colwell, R. R. Survival strategies of bacteria in the natural environment. *Microbiol. Rev.* **51**, 365–379 (1987).

- 66. Womack, A. M., Bohannan, B. J. M. & Green, J. L. Biodiversity and biogeography of the atmosphere. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 3645–3653 (2010).
- 67. Heald, C. L. & Spracklen, D. V. Atmospheric budget of primary biological aerosol particles from fungal spores. *Geophys. Res. Lett.* **36,** L09806 (2009).
- 68. Fröhlich-Nowoisky, J. Pickersgill, D. A. Despres, V. R. Pöschel, U. High diversity of fungi in air particulate matter. *Proc. Natl. Acad. Sci.* **106**, 12814–12819 (2009).
- 69. Fröhlich-Nowoisky, J. *et al.* Biogeography in the air: fungal diversity over land and oceans. *Biogeosciences* **9**, 1125–1136 (2012).
- 70. Kivlin, S. N., Winston, G. C., Goulden, M. L. & Treseder, K. K. Environmental filtering affects soil fungal community composition more than dispersal limitation at regional scales. *Fungal Ecol.* **12**, 14–25 (2014).
- 71. Ingold, C. T. *Dispersal in Fungi*. (Clarendon Press, 1953).
- 72. Roper, M., Pepper, R. E., Brenner, M. P. & Pringle, A. Explosively launched spores of ascomycete fungi have drag-minimizing shapes. *Proc. Natl. Acad. Sci.* **105**, 20583–20588 (2008).
- 73. Robert, V., Stegehuis, G. & Stalpers, J. The MycoBank engine and related databases. http://www.mycobank.org. (2005).
- 74. Wilkinson, D. M., Koumoutsaris, S., Mitchell, E. A. D. & Bey, I. Modelling the effect of size on the aerial dispersal of microorganisms. *J. Biogeogr.* **39**, 89–97 (2012).
- 75. Zender, C. S., Bian, H. S. & Newman, D. Mineral Dust Entrainment and Deposition (DEAD) model: Description and 1990s dust climatology. *J. Geophys. Res.* **108**, (2003).
- 76. Potts, M. Desiccation tolerance of prokaryotes. *Microbiol. Rev.* **58,** 755–805 (1994).
- 77. Griffin, D. W. Terrestrial microorganisms at an altitude of 20,000 m in Earth's atmosphere. *Aerobiologia (Bologna)*. **20,** 135–140 (2004).
- 78. Ulevicius, V., Peciulyte, D., Lugaukas, A. & Andrijauskiene, J. Field study on changes in viability of airborne fungal propagules exposed to UV radiation. *Environ. Toxicol.* **19**, 437–441 (2004).
- 79. Lighthart, B. The ecology of bacteria in the alfresco atmosphere. *Fems Microbiol. Ecol.* **23,** 263–274 (1997).
- 80. Kellogg, C. A. & Griffin, D. W. Aerobiology and the global transport of desert dust. *Trends Ecol. & Comp. Evol.* **21**, 638–644 (2006).
- 81. Smith, D., Griffin, D. & Schuerger, A. Stratospheric microbiology at 20 km over the Pacific Ocean. *Aerobiologia (Bologna)*. **26,** 35–46 (2010).
- 82. Barker, B. M., Jewell, K. A., Kroken, S. & Orbach, M. J. The population biology of *Coccidioides*: Epidemiologic implications for disease outbreaks. *Ann. N. Y. Acad. Sci.* **1111,** 147–163 (2007).