Title
Fungal Ecology and Ecosystem-based Management of Special Forest Products

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FUNGAL ECOLOGY
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ECOSYSTEM-BASED MANAGEMENT OF SPECIAL FOREST PRODUCTS

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

by

Sharifa Gulamhussein Crandall

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Abstract

Fungal Ecology and Ecosystem-based Management of Special Forest Products

Sharifa G. Crandall

Fungi shape the dynamics of natural ecosystems as pathogens, nutritional mutualists, and decomposers. They are also important as Special Forest Products with cultural and economic significance. I took an interdisciplinary approach to understand how fungal reproduction varies in response to abiotic (weather) and biotic (vegetation) factors, and how forest managers in the Pacific Northwest manage collaborative activities associated with Special Forest Products. I used three complementary approaches to examine temporal and spatial variation in reproduction in fungal communities. First, I measured the phenology of airborne fungal spores in coast redwood forests, mixed-evergreen forests, and maritime chaparral in coastal California, USA. Temporal patterns in meteorological factors (relative humidity, temperature) were more important in determining airborne fungal spore abundance than was vegetation type. This suggests that overall patterns of fungal reproductive dynamics may be predictable across heterogeneous landscapes based on local weather. Second, I used novel metagenomic techniques to identify unculturable and culturable airborne fungi across a vegetation mosaic. I found that the assemblages of fungal species vary strongly over time, with little spatial structure associated with habitat types. Third, for airborne spores collected from different vegetation types, I measured physical traits that may be important for survival, dispersal, or response to environmental change. I found larger and elongated spores in dry and structurally open vegetation (chaparral) compared to smaller and rounder spores in wet and structurally closed vegetation (forests). These results suggest that fungi in chaparral possess spore traits that allow them to persist and disperse in harsh, dry, open conditions. Finally, I examined the position of Special Forest Products like mushrooms and berries, in large-scale, collaborative planning for ecosystem-based management and the role of stakeholder participation to improve natural resource management. Working in the Pacific Northwest, I conducted a regional survey and interviews with national forest managers and found that collaborative activities occur at small scales (< 20 acres) and are driven by bi-lateral stakeholder interactions and legal obligations to stakeholders such as federally recognized Native American Tribes. These findings modify existing hypotheses on collaboration of natural resources and can aid national forests in future collaborative resource management.

This dissertation is dedicated to my parents:

Nurjehan & Mansur Gulamhussein

Susan & Stephen Crandall

for their love and encouragement

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Introduction

Fungi shape ecosystem dynamics worldwide as plant and animal pathogens, mutualists, and as decomposers (Fisher et al. 2012, Bardgett and van der Putten 2014). Fungi are also valued and harvested by humans for food, medicine, ritual, and recreation (McLain and Jones 2015). Despite their ecological and cultural importance, fungal diversity and distributions are poorly understood because most taxa are unculturable or they have cryptic morphologies (Hawksworth 2010, Carroll 1988). Global estimates of fungal species are currently around 5.1 million (Blackwell 2011), however, new species are discovered each year with the advent of high throughput DNA sequencing (Caporaso et al. 2010). Fungal ecologists can now measure the diversity of entire fungal communities and at different spatial scales - from leaf to biome (Metzker 2010, Parrent et al. 2010).

From recent molecular studies, we know that although fungi are found in nearly every ecosystem on the planet, many species are dispersal limited and have restricted geographic ranges (Meiser et al. 2013, Tedersoo et al. 2014, Peay et al. 2014). However, few studies in fungal ecology combine molecular community data with ecological and environmental data to ask what might be driving the patterns of abundance and species diversity across spatio-temporal scales (Peay 2014). I combine molecular and ecological approaches in this dissertation to measure fungal reproductive and dispersal structures (spores). I analyze (1) spore density, composition, and traits together with environmental data (Pringle et al. 2015) to understand airborne spore dynamics and second, (2) fungal community composition and structure across time and space, and (3) fungal and plant collaborative resource management in national forests.

First, we know that fungal spore release into the air depends on environmental cues (e.g., temperature, relative humidity) (Burch and Leventin 2002). Spore phenology, or the timing of fungal spore release, is driven by local weather conditions and the presence of available hosts (McCartney 1994). Investigating when spores are released and modeling the response of spores to both abiotic (weather) and biotic (vegetation) factors can help us predict how fungi will respond to shifts in weather and land-use patterns. The abundance of airborne fungal spores in agricultural and urban settings increases with greater temperature, relative humidity, or precipitation. For many plant pathogens, greatest spore abundance coincides with the availability of host plant tissue. The same meteorological factors that affect temporal patterns in spore abundance also vary across natural habitats, often associated with differences in vegetation structure.

In Chapter 1, I investigated how temporal and spatial variation in aerial spore abundance is affected by abiotic (weather) and biotic (vegetation) factors as a foundation for predicting how fungi may respond to changes in weather and land-use patterns. I measured the phenology of airborne fungal spores across a mosaic of naturally occurring vegetation types at different time scales to describe 1) how spore abundance changes over time, 2) which local meteorological variables are good predictors for airborne spore density, and 3) whether spore abundance differs across vegetation types. Using an air volumetric vacuum sampler, we collected spore samples at 3-hour intervals over a 120-hour period in a mixed-evergreen forest and coastal prairie to measure diurnal and nocturnal spore abundance and total airborne abundance between vegetation types. Spore samples were also collected at weekly and monthly intervals in mixed-evergreen forest, redwood forest, and maritime chaparral vegetation types from 12 field sites across two years. We found greater airborne spore densities during the wetter winter months compared to the drier summer months. Mean total spore abundance in the mixed-evergreen forest was twice that in the coastal prairie, but there were no significant differences in total airborne spore abundance among mixed-evergreen forest, redwood forest, and maritime chaparral vegetation types. Weekly and monthly peaks in airborne spore abundance corresponded with rain events and peaks in soil moisture. Overall, temporal patterns in meteorological factors were much more important in determining airborne fungal spore abundance than was habitat type. This suggests that overall patterns of fungal spore dynamics may be predictable across heterogeneous landscapes based on local weather patterns.

In Chapter 2, I used next-generation DNA sequencing techniques to identify unculturable and culturable airborne fungi across a vegetation mosaic. I found that the airborne fungal spore composition varies temporally over a wet season; however, we see little spatial structure associated with vegetation types. Spore traits are important for survival, dispersal, or response to environmental change (Pringle et al. 2015). I also measured continuous spore traits from airborne spores that were sampled across the vegetation mosaic. I found larger and more elongated spores in dry and structurally open shrub-like vegetation compared to smaller and rounder spores in wet and structurally closed forests. These results suggest that fungi in shrub-like environments possess spore traits that may facilitate persistence and dispersal in harsh, dry, open conditions.

Finally, some fungi and plant species are important economic and cultural resources. In the United States, mushrooms and berries for example, are called Special Forest Products (SFPs) or Non-timber Forest Products (NTFPs) (McLain and Jones 2005). Special Forest Products are harvested extensively in national forests in northern California, Oregon, and Washington. Ecosystem-based management is one approach that uses landscape-scale assessment and collaborative multi-stakeholder participation to inform environmental planning (Layzer 2013). For instance, information about large-scale ecological processes is incorporated into environmental plans and policies to manage for multiple species, especially those with large ranges or at the scale of entire watersheds or regions. Collaboration between stakeholders (e.g., governmental agencies, non-governmental organizations, the public, Native American tribes) can be used to incorporate people's values and needs, in addition to ecological information, into the decision-making process (Wondolleck and Yaffee 2000). An ecosystem-based approach was integrated into public land use policy and plans in the 1980s and 1990s as a way to improve natural resource management. Today, environmental institutions across the nation and globally use an ecosystem-based approach to manage natural resources. Despite the requirement for landscape-scale assessment and collaborative planning on public land, however, some natural resource management projects depart from the ecosystem-based ideal depending on the natural resource in question, who uses it, the legal framework that allows access and use, and the socio-cultural context under which the resource is managed and harvested (Layzer 2008). The Pacific Northwest Forest Plan (1994) was written and used to improve forest resource management in national forests through using an ecosystem-based management approach during a time when clear-cutting and other timber practices were degrading ecosystems in the Pacific Northwest.

In Chapter 3, I ask 1) how does ecosystem-based management guide the incorporation of SFPs for forest planning in national forests under the Pacific Northwest Forest Plan and 2) how do landscape-scale and multi-stakeholder collaboration, two essential elements of ecosystem-based management, are incorporated into SFP management in the Willamette National Forest under the Pacific Northwest Forest Plan. First, I define ecosystem-based management and describe landscape-scale assessment and collaborative planning. Then, I present the benefits and challenges of collaboration within the context of ecosystem-based management. I review pertinent federal regulations and policies for SFP management in national forests as well as the rights of harvesters to access and harvest products on public land. Next, I present results from a survey on SFP management that I administered to USFS resource managers in the Pacific Northwest; the survey provided information about the current state of SFP programs in national forests and pointed to the Willamette National Forest as an appropriate case study to examine collaborative activities between forest service staff and harvesters. Finally, I examine if the case study findings support, reject, or modify existing hypotheses on collaboration of natural resources. I find departure from the original ecosystem-based goals in the Northwest Forest Plan: there are small-scale SFP management projects with bilateral rather than multi-lateral stakeholder collaboration. I situate these results in the current literature on collaboration and ecosystem-based management and highlight best practices for future collaborative activities for SFP management in US national forests.

This dissertation contributes 1) empirical evidence on the structure and diversity of fungal communities at the landscape level and 2) finds evidence for successful management projects that depart from a strict ecosystem-based view of resource management. First, while others show that fungal spore composition and abundance is tightly coupled to vegetation type, I find that at coarse spatial scales (2-4 km), environmental factors (i.e., meteorology and edaphic conditions) rather than vegetation drive the reproductive phenology of fungal communities. These results suggest that temporal patterns in airborne fungal spore abundance and structure are generalizable across heterogeneous landscapes. Spore traits may also provide an explanation for fungal dispersal and survival among vegetation types. Second, small-scale projects with bi-lateral stakeholder participation can produce improved social and ecological outcomes for Special Forest Product management; national forest personnel must retain experts trained in policy and sociology and invite all potential stakeholders to the planning table to ensure the success of collaborative projects.

Chapter 1
Meteorological factors predict airborne fungal spore abundance over natural vegetation

Introduction

Fungi are important as pathogens, mutualists, and decomposers of plants and animals in ecosystems worldwide (Brown and Hovmøller 2002, Daszak et al. 2000, Leake 1994, Bardgett and van der Putten 2014). Fungi disperse to new hosts and substrates by producing and releasing spores - small structures (2-20 μm) that serve for fungal reproduction and survival (Moore-Landecker 2011). Once spores are produced and released (sporulation), spores travel through the air (Elbert et al. 2007, Glickson et al. 1995), water or soil (Fitt et al. 1989), or are carried by animals (Lilleskov and Bruns 2005). Although some fungi can disperse over short distances through the growth of thread-like hyphae (Agerer 2001), spore release into the air is the most common mode of fungal dispersal (Gregory 1967, Egan et al. 2014). The primary source of airborne spores are fungi growing on plants (Burgess 2002), and high abundances of airborne spores of plant associates such as *Alternaria* spp. or *Aspergillus* spp. can increase the risk of plant disease in crops (Langenberg et al. 1977, Bock et al. 2004) as well as respiratory illness in humans (Pringle 2013, D'Amato et al. 2015).

Previous studies from agriculture and urban environments point to the importance of meteorological conditions in driving airborne spore density (Burch and Leventin 2002, Hock et al. 1995, Manstretta and Rosi 2015). As a general rule, airborne spore abundance increases when there is a marked increase in air temperature (Langenberg et al. 1977), relative humidity (Webster et a. 1989), and precipitation (Gregory 1967, Velez-Pereira 2016). Warm air temperatures are positively correlated with high airborne spore densities of *Alternaria* spp. (Aira et al. 2013, Corden et al. 2003) and other pathogens such as *Cladosporium* spp. or *Epicoccum* spp. (Troutt and Leventin 2001, Grinn-Gofron and Strzelczak 2013). An increase in relative humidity can trigger spore release thereby increasing the abundance of spores in the air (Leyronas and Nicot 2013, Gabey et al. 2010). Rain also triggers spore release (Aylor and Sutton 1992); the moist soil and leaf conditions that persist after a rain event contribute to an increase in airborne fungal spore densities (Ganthaler and Mayr 2015).

In order to understand the epidemiology of fungal disease and predict threats to crops, agricultural scientists have long measured the timing of spore release, or spore phenology (McCartney 1994). Disease forecasting models are often based on spores released during a host plant's growing season (Huber and Gillespie 1992, Small et al. 2015); airborne spore abundance can reach a peak during plant flowering and/or fruiting time (Fouré and Gantry 2008, Xu and Berrie 2014). A sudden rise in air temperature and relative humidity can cue fungal sporulation from aerial leaves and shoots of crops as well as from leaf litter or the soil surface (Levetin and Dorsey 2006, Fernández-González et al. 2009). Once in the air, spores can land on a leaf surface through either dry or wet deposition (Fuentes and Gillespie 1992, Grove and Biggs 2006). Leaf wetness is also correlated with spore germination (Guyader et al. 2013); the longer a leaf is wet, the greater the disease severity (Bradley et al. 2003, Huber and Gillespie 1992). Coordinated measurement of airborne spore density, host fruiting and flowering time, and the timing, duration, and magnitude of local meteorological conditions (e.g., precipitation, leaf wetness) are critical foundations for plant disease forecasting models (Wu et al. 2002).

Most research on fungal spore phenology has focused on agricultural or human pathogens. From these studies we know that meteorological factors (Burch and Leventin 2002) and vegetation type (Skjøth et al. 2016) drive the timing of spore release and the quantity of airborne spore loads (Stepalska and Wolek 2009); we would expect similar patterns to hold in less heavily managed land-use types or natural systems where fewer spore phenology studies have been conducted (e.g., forests, shrub-lands) (Bowers et al. 2013, Alexander 2010, Gilbert and Reynolds 2005). Understanding how spore phenology responds to abiotic (weather) and biotic (vegetation) factors in natural systems can help us predict how fungi will respond to changes in climate (D'Amato et al. 2015, Velez-Pereira et al. 2015) and land-use patterns (Bowers et al. 2013) and the implications of such changes for disease incidence.

Based on our understanding of spore production, we expected that spore loads would be the highest during the moist winter growing season compared to the summer dry season, and that at shorter time scales, spore abundance would increase along with air temperature and relative humidity and following rainfall events. We also expected that spore abundance should be higher in forested habitats compared to open-vegetation-like prairie or chaparral because structurally complex forests typically have more available plant biomass as substrate for fungal growth. To test these expectations we measured the phenology of airborne fungal spores across a mosaic of natural vegetation types in Mediterranean-climate California at different time scales and asked 1) how does spore abundance change over time? 2) which meteorological variables are good predictors for airborne spore loads, and 3) how does spore abundance differ across vegetation types?

Materials and Methods

Field Sites

This research was conducted on the University of California, Santa Cruz (UCSC) Natural Reserve and in adjacent Wilder Ranch State Park in Santa Cruz County, California, USA (Figure 1.1, Appendix 1A). The region experiences a Mediterranean type climate with mild, wet winters and hot, dry summers with a total average annual precipitation of approximately 745 mm (Appendix 1B). Although maritime fog inundates the coast of California between July and September (Johnstone and Dawson 2009), approximately 745 mm of precipitation falls as rain in the winter and spring months from October to April, and approximately 45 mm as summer fog (Appendix B, Gilbert et al. 2010). Various terrestrial coastal vegetation types form a natural mosaic across the landscape: redwood forest, mixed-evergreen forest, coastal prairie, and maritime chaparral (Sawyer and Keeler-Wolf 2009, Haff et al. 2008).

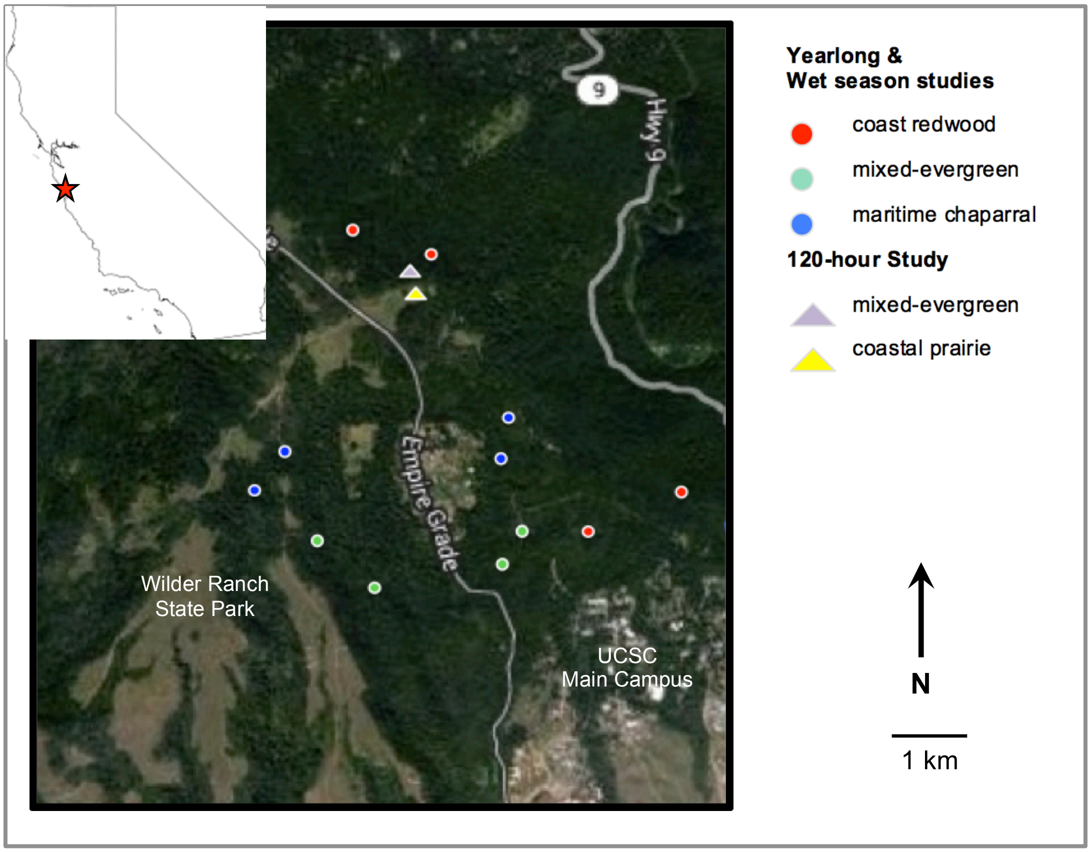

Figure 1.1. Field sites on the central coast of California, USA (inset); locations volumetric air samples data and meteorological data were collected in 2013 and 2014.

We selected field sites using topographic maps and vegetation data that were obtained from reserve and state park managers. In order to find suitable sites to sample, we visualized our maps as geospatial layers in a Geographic Information System (GIS) (ArcGIS version 9.0) Spore sampling locations were chosen based on common coastal vegetation types: coast redwood forest, mixed-evergreen forest, maritime chaparral, and coastal; locations were at least 200 m apart and accessible from hiking trails, but at least 10 m from a trail or paved road to minimize any disturbance from human activity.

Sampling Design

To examine spore abundance patterns over a year across a vegetation mosaic, we collected volumetric airborne spore samples once a month throughout 2014 (see collection methods below). We selected 12 field sites in redwood forest, mixed-evergreen forest, and maritime chaparral (3 vegetation types × 4 replicate field sites/vegetation type = 12 sites total; Figure 1.1). We standardized the spatial distance between replicate collection points in the field in order to make it logistically feasible to travel to each replicate field site within the sampling time interval, while still accounting for habitat heterogeneity across replicate sites in our sampling design. The distance between nearest neighbor sites ranged from 200 m to 4000 m. Airborne spore samples were collected for 10 min at each site between 09:00 h - 14:00 h. To evaluate the influence of weather during the wet season, we collected spore samples at the same 12 field sites once a week for 9 weeks during the wet season (January - March) in 2013 and again in 2014. Finally, to measure diurnal and nocturnal patterns in spore density in the coastal prairie and mixed-evergreen forest, we selected 3 replicate field sites each (6 sites total); sites were arranged at the vertices of an equilateral triangle 10 m apart (Figure 1.1). We measured volumetric airborne spore samples for 10 min at each site every 3 h over a 120-h period (January 7-11, 2013).

Spore & Weather Data Collection Methods

We collected quantitative samples of airborne spores using a Buck Bioslide™ model 1020 Sampling Pump (A.P. Buck Inc., Orlando, Florida, USA). A standard glass microscope slide (25 mm × 75 mm × 1 mm) was coated on one side with a thin film of petroleum jelly using a clean cotton swab (Q-tip™) to provide an adhesive surface for spores to attach. Slides were placed in the sampling pump on a tripod 1 m above the ground. Air pumped through the device for 10 min at a steady volumetric rate of 15 L min^{-1} (A.P. Buck Inc.). Air entered the device through a slit and left an impact trace of spores and other particulates on the greased slide surface. The procedure was repeated sequentially at each site. There was a 15-20 min sampling time lapse between field sites depending on the time needed to travel from site to site. Microclimate data were collected during each 10-min sampling period: ambient air temperature (°C) was measured using a Weatherwise Instruments™ digital field thermometer (Wise Brands LLC, Jupiter, Florida, USA) and relative humidity (%) was recorded using a portable Weems & Plath hygrometer (Weems & Plath, Annapolis, Maryland, USA). Meteorological data were obtained as averages from 12 Decagon™ model EM 50 weather stations (Decagon Devices, Pullman, Washington, USA) in the understory from the nearby University of California, Santa Cruz Forest Ecology Research Plot (Gilbert et al. 2010, http://ferp.ucsc.edu). We obtained average hourly and daily measurements for seven meteorological variables: solar radiation (W m^{-2}), air temperature (°C), soil temperature (°C), relative humidity (%), precipitation (mm), leaf moisture hours (h), and soil moisture (%).

Spore Density Counts

Between January - March 2013 and 2014, we collected spore samples once a week for 9 weeks at 12 sites (Figure 1.1) for a total of 108 spore samples. To better understand annual patterns in airborne spore density, we collected spores samples one a month in 2014 at the same 12 sites for a total of 132 samples. To examine diurnal and nocturnal trends, 240 spore samples were collected. Each sample consisted of a microscope slide with a trace representing the particulate contents of 150 L of air. These slides were returned to the laboratory and stained with augmented Calberla's stain, which differentially stains pollen grains but not fungal spores (Fisher Scientific Co. LLC, Pittsburgh, Pennsylvania, USA). Spores were visualized and counted under a light microscope at 200× magnification. The particulate trace on each slide was first centered in the microscope light path by eye and then verified under 100× magnification; a field of view was then chosen haphazardly along the trace. From that starting point, a total of 10 adjacent fields of view were assessed per slide at 200× using Infinity Capture™ imaging software (Lumenera Corporation, Ottawa, Canada). All fungal spores were counted within each field of view and a digital image was captured for a total of 2400 images for the short-term study, 2160 for the wet season study, and 1320 for the year-long study. In order to calculate the total number of spores in a trace, the number of spores counted across 10 fields of view was multiplied by the total trace area (15.84 mm^2) and then divided by the total area for 10 fields of view (10.84 mm^2) under 200×. This value was divided by the volumetric flow rate of the air pump (0.150 m^3) per 10 min to obtain the total number of spores per cubic meter in a single trace (# spores m^{-3}) (Gilbert and Reynolds 2005).

Statistical Analyses

To examine how airborne spore abundance changed over a year in chaparral, mixed-evergreen, and redwood habitats, we fit a sine-cosine model to these data because spore densities showed marked periodicity (R Core Developer Team 2012). We fit linear models to our spore abundance data that was collected in the wet seasons. To determine if there were differences in airborne spore abundance and time of day, we calculated moving averages of spore densities found at each time interval within sites and then fit a sine-cosine model to these data. We plotted the residual spore counts from the sine-cosine model over 24 h to evaluate if the coastal prairie and mixed-evergreen forest differed in diurnal and nocturnal patterns. We used multiple linear regressions to evaluate the influence of meteorological factors on spore abundance separately for each vegetation type using the nlme package in the R statistical platform (https://cran.r-project.org/web/packages/nlme/). A forwards-backwards stepwise model selection procedure using AIC (Akaike's Information Criterion) was used to choose parameters to include for each model (Appendix 1C). Finally, to evaluate if vegetation type had an effect on airborne spore loads, we calculated the residual values for spore abundance from our fitted models and then evaluated the residuals as a function of vegetation type.

Results

Airborne fungal spore density changed seasonally, within seasons, and diurnally. Regardless of vegetation type, spores density peaked in the rainy season (November – April) with fewer spores during the drier summer months (June - August) (Figure 1.2, Appendix 1B). Within the rainy season, airborne spore density varied across weekly samples, but with trends differing between 2013 and 2014; spore abundance declined from January to March in 2013, but increased over the same period in 2014 (Figure 1.3). In the open coastal prairie habitat spore abundance was depressed at mid-day (11:00 h - 14:00 h) (Figure 1.4a, 1.4b), but this pattern was not seen in the closed-canopy mixed- evergreen forest (Figure 1.4c).

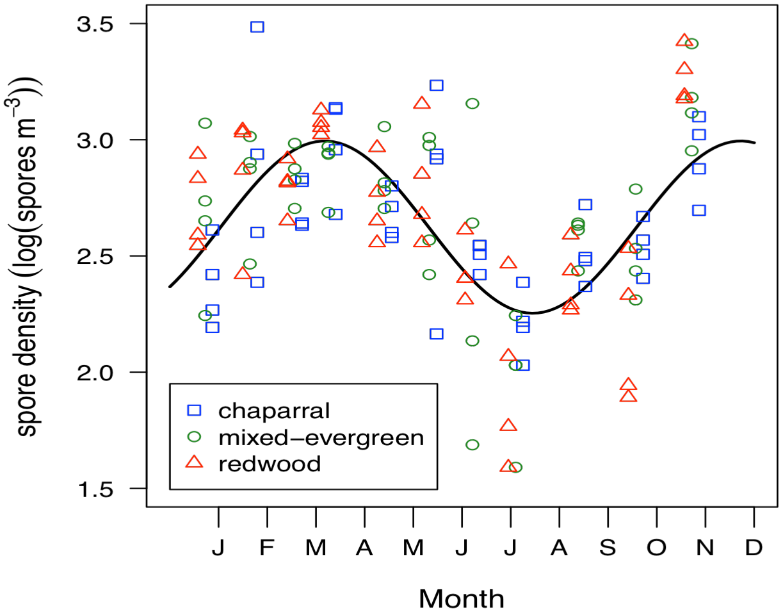

Figure 1.2. Average airborne fungal spores abundance found in maritime chaparral, mixed-evergreen forest, and redwood forest sites over one year. Samples were collected once a month from 12 field sites in 2014. Solid line denotes fitted sine-cosine model (Appendix 1C). Points are shown slightly offset from each sampling date to better see differences in spore density among vegetation type.

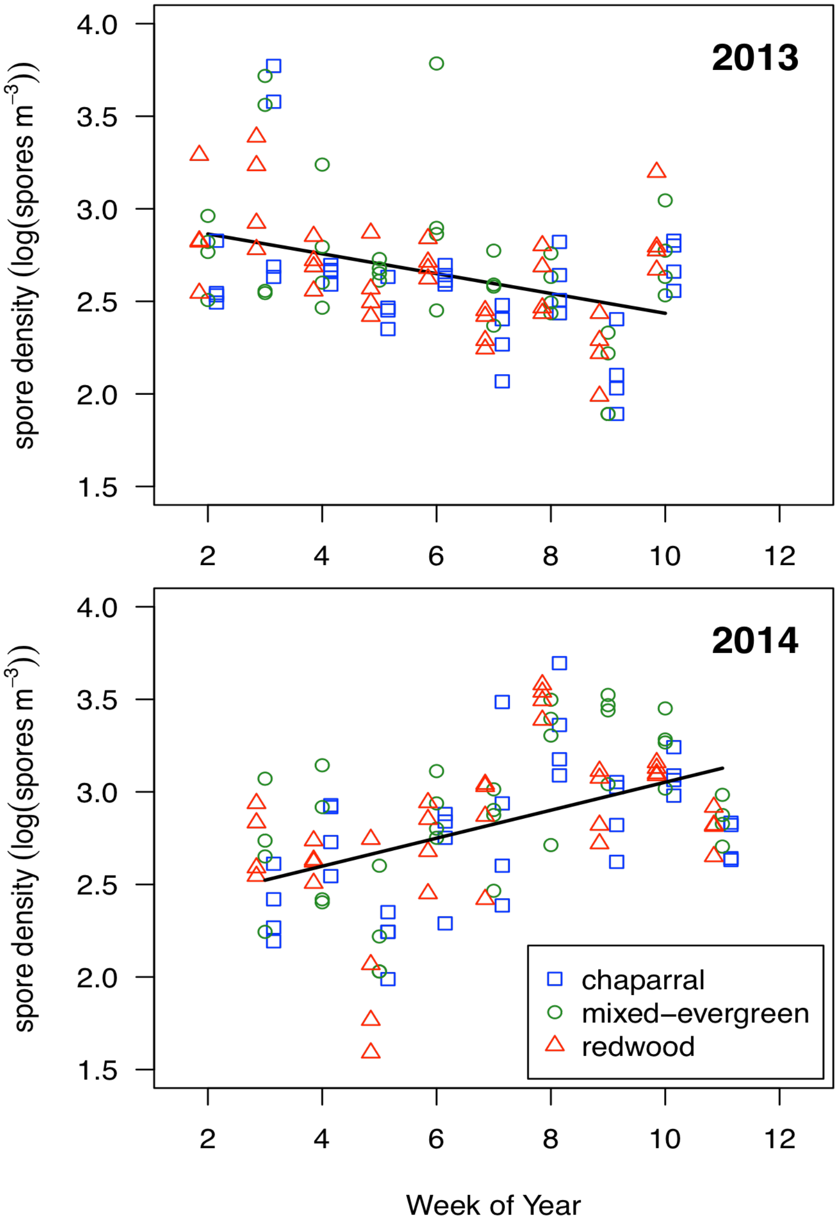

Figure 1.3. Average airborne fungal spore abundance in chaparral, mixed-evergreen forest, and redwood forest vegetation types across two wet seasons. Samples were collected over 9-wks in January - March in 2013 and 2014. Solid lines denote predicted model for spore density (Appendix 1C). Points are shown slightly offset to better see differences in spore density among vegetation types.

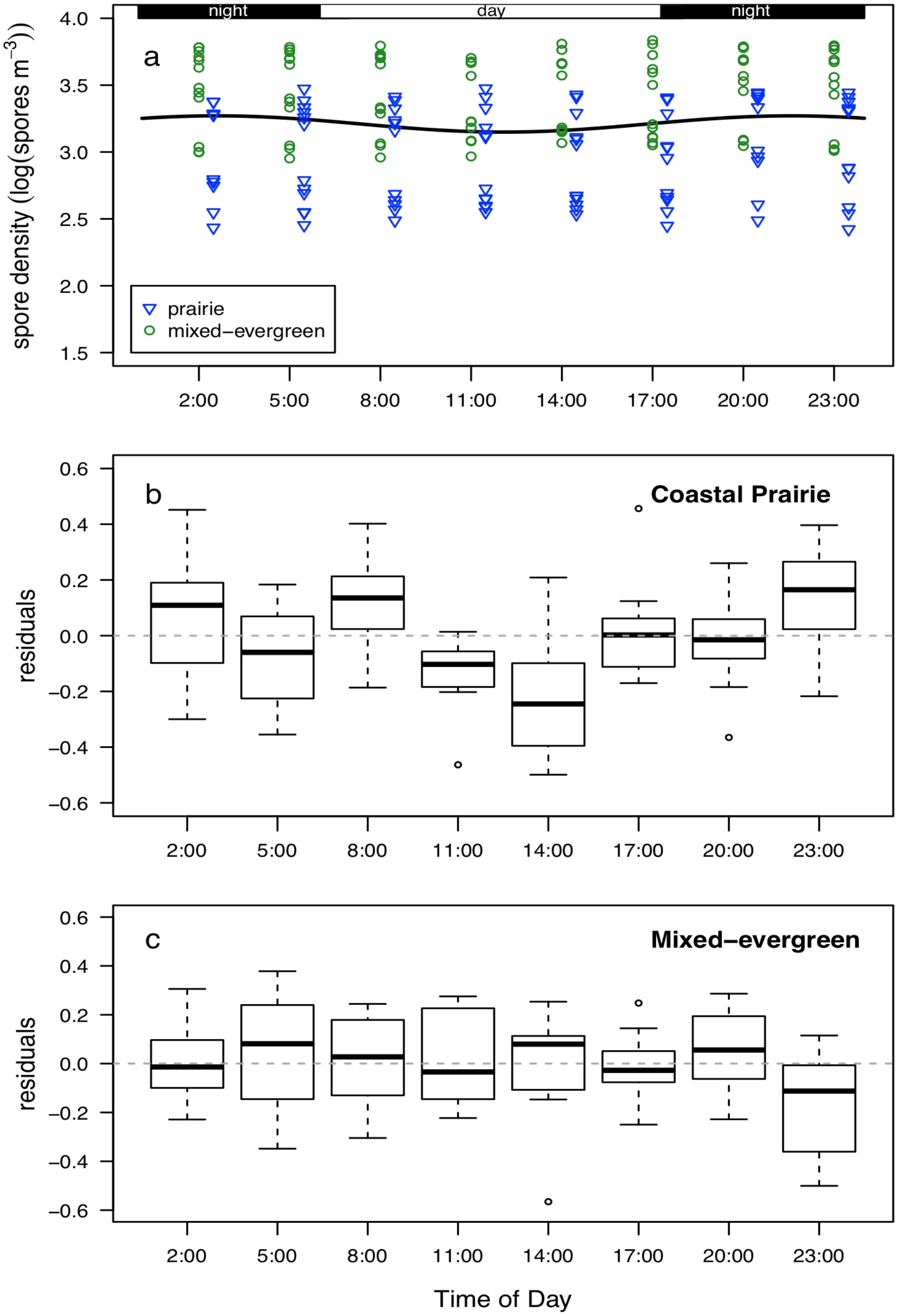

Figure 1.4. Airborne fungal spore density in a coastal prairie and mixed-evergreen forest a) as a function of time of day. Points are shown slightly offset to better see differences in spore density among vegetation types. Solid line denotes fitted sine-cosine model for all the spore density data. Airborne fungal spore samples were collected every 3 hours from January 7-12 in 2013. Boxplots show the median residual values (thick black horizontal line in each boxplot) versus time of day in a b) coastal prairie and c) mixed-evergreen forest.

Local meteorological conditions, particularly temperature and relative humidity, have strong effects on large-scale temporal and spatial patterns in airborne spore density. Across calendar year 2014, there were more fungal spores in the air during periods of high relative humidity and low air temperatures than during drier, warmer periods (Figure 1.5, Appendix 1D).

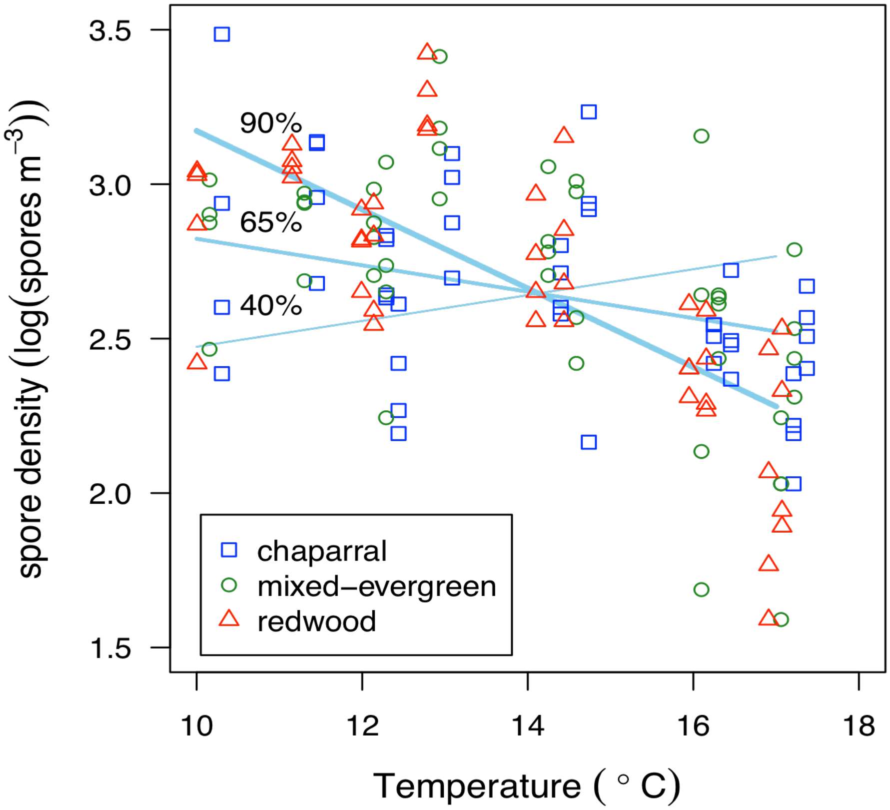

Figure 1.5. Average spore density as a function of air temperatures found across vegetation types over the calendar year 2014. Solid blue lines show spore density predicted from multiple regression model (Appendix 1C) at that relative humidity as a function of temperature (°C). The relative humidity values were selected to represent the range of values (approximately the minimum, median, and maximum values) observed across the year. Points are shown slightly offset to better see differences in spore density among vegetation types.

Relative humidity had the strongest relationship with spore density of any meteorological parameter at this temporal scale and spores decreased with relative humidity (Table 1.1). Soil moisture and temperature were also significantly associated with spore density - drier soil and warmer air temperatures were associated with reduced spore density (Table 1.1). Precipitation showed marginal significance for predicting airborne spore loads in a redwood forest, but not in the mixed-evergreen forest or maritime chaparral vegetation (Table 1.1).

From January to March in 2013 and 2014 (the peak season for spore density), the interaction between relative humidity and temperature was a better predictor for airborne spore density than each of these parameters alone (Table 1.1). The strength of effects of relative humidity and temperature on spore density was greater in 2014 than in 2013 (Table 1.1, Figure 1.6). This may be related to very different weather conditions in the two years, with 2013 cooler (4.6-11.6 °C) and wetter (70-90%) winter overall, than 2014 (7.0-14.4°C, 35-97%; temperatures and relative humidity are the range of daily averages measured from January to March in 2013 and 2014; Figure 1.6). There was a positive relationship between the amount of rainfall during the previous week and spore density (Table 1.1). Soil moisture is closely related to the amount of relative humidity and precipitation available in the environment. As soil moisture decreased during the 2013 wet season (Appendix 1E, Table 1.1), so did airborne spore density; as soil moisture increased between January and March in 2014, so did airborne spore density (Appendix 1E, Table 1.1).

Table 1.1. Multiple linear regression parameters, coefficients, and p values calculated for airborne spore densities.

	January - March 2013[a]		January - March 2014[b]		Year 2014[c]	
Parameter	Coeff.	p	Coeff.	p	Coeff.	p
Solar Radiation	**0.000**	**0.001**				
Temperature	**0.027**	**0.001**	-0.310	0.117	**-1.606**	**0.001**
Relative Humidity	**0.305**	**0.002**	-5.017	0.138	**-20.22**	**0.008**
Precipitation[d]	**-0.022**	**0.001**	**0.005**	**< 0.001**	-0.039	0.139
Leaf Moisture			**-0.030**	**0.009**	**-0.171**	**0.003**
Soil Temperature	**0.169**	**0.005**			**0.834**	**< 0.001**
Soil Moisture	**0.050**	**0.039**	**-1.102**	**0.022**	**4.459**	**0.050**
Mixed-evergreen Forest	0.115	0.058	**0.665**	**0.030**	0.741	0.144
Redwood Forest	0.083	0.170	**0.628**	**0.041**	**1.619**	**0.002**
Temperature × Relative Humidity	**-3.648**	**0.001**	**0.464**	**0.045**	**1.282**	**0.010**
Temperature × Mixed-evergreen					-0.047	0.153
Temperature × Redwood					**-0.107**	**0.001**
Relative Humidity × Precipitation					0.057	0.100
Relative Humidity × Mixed-evergreen			**-0.942**	**0.035**		
Precipitation × Mixed-evergreen					-0.001	0.350
Precipitation × Redwood					-0.002	0.057
Leaf Moisture × Mixed-evergreen			**0.028**	**0.005**		
Leaf Moisture × Redwood			0.012	0.228		

[a] $F = 6.917$, df = 9 and 98; [b] $F = 5.629$, df = 12 and 95; [c] $F = 4.311$, df = 14 and 117

[d] Precipitation was calculated as the total amount of rainfall for each month prior to each spore collection date in 2014 and the amount of total rainfall during the week prior to each spore collection date in the wet seasons 2013 and 2014.

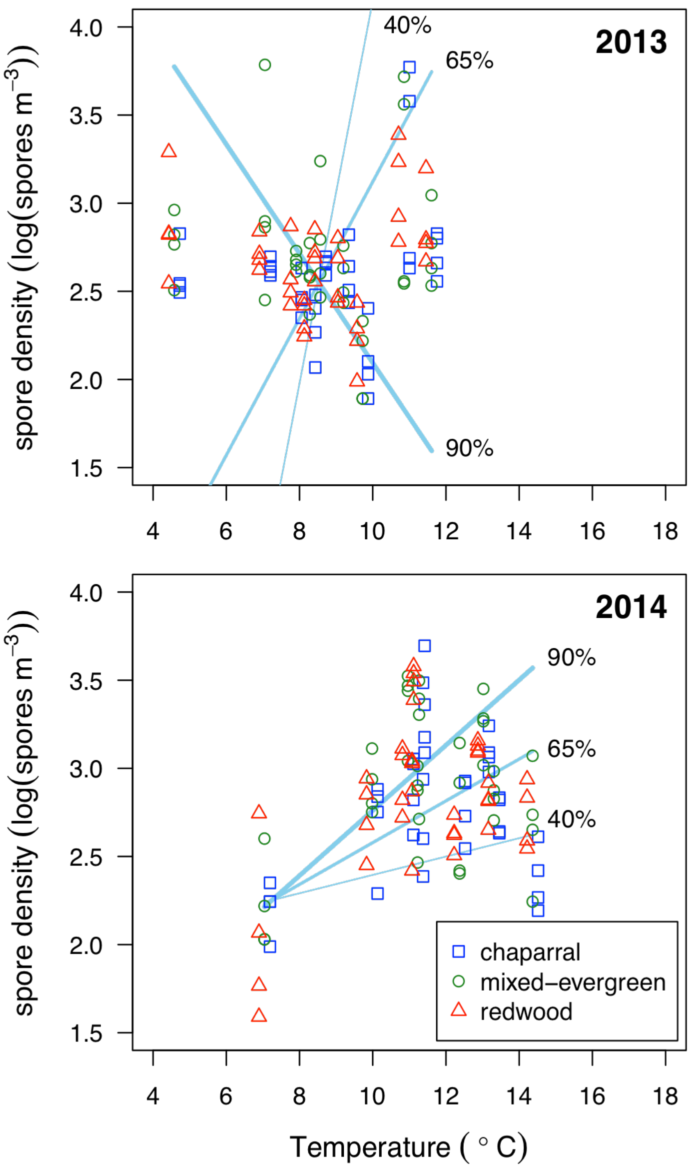

Figure 1.6. Average spore density as a function of air temperatures found across vegetation types during the wet seasons in January - March in 2013 and 2014. Solid blue lines show spore density predicted from multiple regression model (Appendix 1C) at that relative humidity as a function of temperature (°C). The relative humidity values were selected to represent the range of values (approximately the minimum, median, and maximum values) observed during each field collection period. Points are shown slightly offset to better see differences in spore density among vegetation types.

Airborne spore abundance was greater in forest than prairie vegetation (*F* = 65.06, df = 1 and 183, p = 0.0001) (Figure 1.7b). However, there were no differences among chaparral, mixed-evergreen, and redwood vegetation types during the wet seasons of 2014 (*F* = 1.067, df = 2 and 105, p = 0.348) (Figure 1.7c) or 2013 (*F* = 1.025, df = 2 and 105, p = 0.362) (Figure 1.7d). Similarly, there was no effect of the same vegetation types on airborne spore density across the full calendar year 2014 (*F* = 0.134, df = 2 and 129, p = 0.875) (Figure 1.7a).

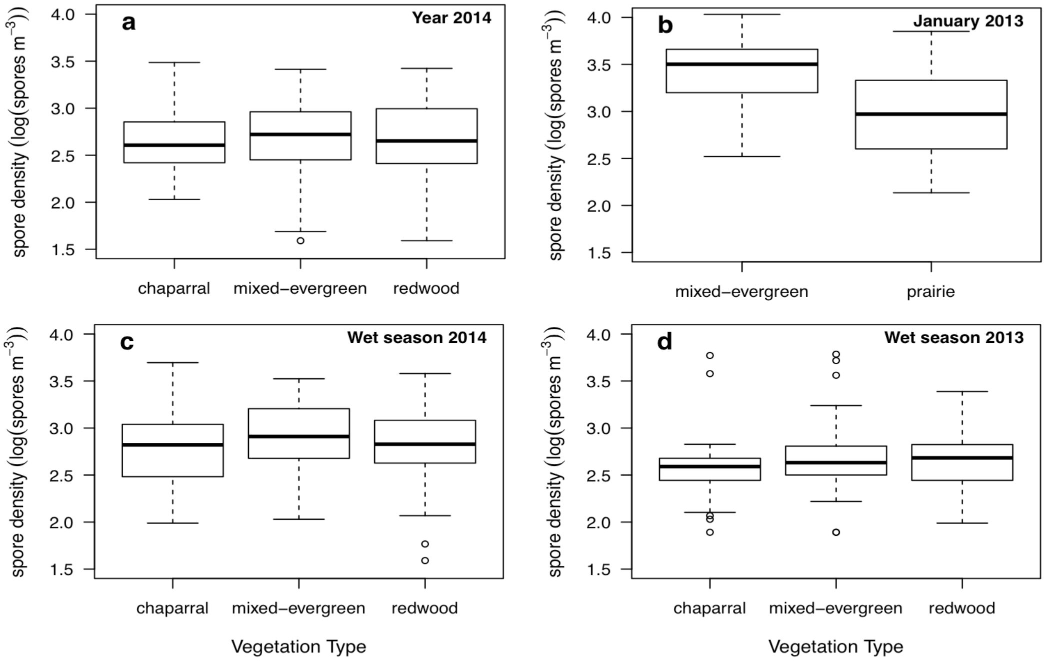

Figure 1.7. Average total airborne fungal spore density found across vegetation types at different temporal scales. The length of the rectangles within a boxplot is the interquartile range; the top and bottom lines of each box show the 3rd and 1st quartile range of the data respectively. The top whiskers show the maximum value plus 1.5 times the interquartile range and the bottom whiskers show the minimum value minus 1.5 times the interquartile range. The solid black horizontal line inside each boxplot is the median value for spore density. Open dots show outliers.

Discussion

Microclimate is a useful indicator of patterns in airborne fungal spore densities at time scales from hours to months. Relative humidity, temperature, and their interaction were the most important indicators of spore density across all time scales. Airborne fungal spore abundance was consistently higher when the air was cooler and wetter (Figure 1.5, 1.6), however, this is not surprising. Previous studies have long showed that relative humidity and temperature are important factors that cue fungal spore production (Gregory 1966, Meredith 1973), release (Lyon et al. 1984, Webster et al. 1989), and abundance in the air (Talley et al. 2002, Manstretta and Rossi 2015).

In tropical forest ecosystems, relative humidity rather than temperature drives high airborne spore densities, such as in the rainforests of Borneo, Malaysia and in the Amazon in Brazil (Gabey et al. 2010, Huffman et al. 2012). This is likely due to the reduced range of temperature variation in tropical regions, whereas moisture still varies dramatically seasonally and on diel scales. This research was conducted in a temperate Mediterranean climate region, where air temperature and relative humidity tend to consistently co-vary (Huffman et al. 2012).

There were fewer spores found in the air around mid-day in the coastal prairie (Figure 1.4b) compared to the mixed-evergreen forest (Figure 1.4c). The prairie experienced a larger diel range of temperature and relative humidity compared to the forest (Appendix 1F), primarily because mid-day temperatures were warmer in the open structured prairie than in the closed-canopy forest (Appendix 1F). The stratified understory and canopy vegetation in the forest may provide a structural buffer to extreme variability in microclimate (light, wind and fog in addition to air temperature and relative humidity), so the mid-day dip only appears in the prairie habitat (Figure 1.4b). Prairie habitats are similar structurally to agricultural systems (e.g., lack of woody shrubs, trees, thick duff layer) where temporal variation in airborne spore abundance has been previously studied (Couture and Sutton 1978, Fernando et al. 2000).

Still, others have found striking diurnal and nocturnal differences in airborne spore abundance in other ecosystems and climates. In tropical forests, more spores are produced at night than during the day, following the pattern of greater spore abundance under cooler, moister conditions (Graham et al. 2003, Gilbert and Reynolds 2005, Huffman et al. 2012). In contrast, however, concentrations of wind-dispersed spores can sometimes peak in the morning, because spores are produced at night during a period of high relative humidity and then released in the morning as spore-producing structures dry out (Quintero et al. 2010, Langenberg et al. 1977). The early morning can also be a time of windy conditions as surfaces warm and the air above the canopy becomes mixed, which could enhance sampled spore densities. In this regard, high airborne spore concentrations for the barley pathogen *Bipolaris sorokiniana* are found in the morning when leaves dry out after experiencing a wet night (Couture and Sutton 1978). Quintero and colleagues (2010) found an increase in outdoor fungal spore densities in the early morning after humid nights in Puerto Rico. Wind dispersed airborne spores that peak in the afternoon apparently respond to decreases in relative humidity (Savage et al. 2013, Hock et al. 1995). We were unable to directly measure wind speeds at our field sites, but wind should be included in future studies. Finally, larger scale weather events are important; I found spore loads declined in association with a cold front that moved into the region on the third of five days of sampling (Appendix 1F).

Rain events corresponded with an increase in spore density from January - March in 2014 but a decrease in spores for January - March of 2013 (Figure 1.3). This may be explained because the first rain fell 4-5 weeks later in 2014 than in 2013 (Appendix 1E). Because high levels of ambient moisture drive spore production and release, a shift in the timing of rainfall might change the direction of the effect. In contrast to our results, Pakpour and colleagues (2014) found that in New York and Toronto, airborne spore concentrations were greatest when there was little rain and during high temperatures in these urban environments. Fungal spores persist in the air during dry periods and rain "cleans" the air of spores. In the case of our study in forests of a Mediterranean-like climate, precipitation is a limiting factor for host-plant growth and fungal growth in general. Although our study was conducted during one of the longest and harshest droughts in California's recent history, we found, as expected from long-term regional weather data (Appendix 1B), that an increase in precipitation corresponds with an increase in airborne spore densities (Table 1.1). These results may not have been surprising given the patterns in long-term regional weather data (Appendix 1B). The contrasting patterns in urban and natural vegetation systems suggest that rainfall importantly provides moist conditions for spore production and removing fungal spores from the air (Pakpour et al. 2014). If our research was conducted in non-drought years, we might expect to find an order of magnitude higher spore loads during the wet seasons than we measured (Quintero et al. 2010). Regardless of the region's drought, little to no rain characterizes California’s Mediterranean climate in the summer months (Appendix 1B), however, summer fog could increase airborne spore densities (Dong et al. 2015). A shift in timing and duration of the rainy season (as seen in 2014) might have broader implications for when pathogenic fungi infect host-plants. Later rains, warmer temperatures, and higher airborne spore loads could increase the risk for plant disease incidence and severity in the region (Garrett et al. 2011).

Surprisingly, we found mixed evidence for differences in total average spore density across different vegetation types. There were no overall differences in spore abundance in coastal redwood, mixed-evergreen forest, and maritime chaparral habitats overall (Figures 1.7a, 1.7c, 1.7d) but we did find more spores on average in a mixed-evergreen forest compared to a coastal prairie in the five-day study (Figure 1.7b). These results suggest that airborne spore density may be driven more strongly by microclimate than the habitat (vegetation) type, provided there is adequate substrate for fungal growth and reproduction.

Differences in fungal spore physiology could explain why microclimate is a good predictor for spore abundance across time scales and vegetation types (Elbert et al. 2007, Stepalska et al. 2009). Fungi that respond to increases in relative humidity release functionally “wet spores” (e.g., *Ganoderma* spp.) and in contrast, those that respond to decreases in air moisture produce “dry spores” (e.g., *Alternaria* or *Botrytis* spp.) (Meredith 1973, Stepalska et al. 2009). Fungal physiology provides a compelling explanation for the decrease in mid-day airborne spores in the prairie. “Dry spores” may be produced in the mornings and throughout the day when temperatures are high and relative humidity is low. “Wet spore” types would be released in the evenings and throughout the night, triggered by an increase in relative humidity. Morphological traits, such as spore size or shape allow only certain types of spores to be released during the day versus night (Huffman et al. 2012). Graham and colleagues (2003) found smaller airborne fungal spores (2-10 µm) at night and larger spores (>20 µm) during the day in a tropical rainforest. Larger spores often possess thicker cell walls to deal with diurnal desiccation or are produced by fungi that are adapted to typically drier and warmer conditions (Nara 2009). In contrast, smaller spore types usually have thinner cell walls or are produced by fungi that are susceptible to drying out; these spores are readily able to germinate at night under moist conditions (Graham et al. 2003). We may expect to find wetter spore types during the rain events and throughout the rainy season.

An increase in wind speed may induce higher airborne spore concentrations. For example, for certain fungal pathogens, seasonality and timing of spore release are important for long distance spore dispersal when coupled with aerodynamic spore traits (Roper et al. 2008) and high wind speeds that launch spores into the near surface atmosphere (Brown and Hovmøller 2002, Savage et al. 2012, Glikson et al. 1995). Future research should examine the relationship between wind and airborne spore abundance across natural vegetation, manipulate drought effects by simulating rainfall to measure spore dynamics, and measure spore traits at different spatio-temporal scales.

Conclusion

Although fungi and their spores are ubiquitous, the abundance of airborne spores shows distinct temporal patterns that persist across a mosaic of natural vegetation. Peak spore loads were found in during the wet season compared to the dry season. Across spatio-temporal scales, microclimate is a stronger indicator of airborne spore concentration than is vegetation type. This research creates a baseline for understanding the timing of infection for plant and animal hosts, as well as understanding the phenology of other ecological processes that are important for ecosystem functioning such as decomposition. Our results suggest that across a matrix natural habitat types in the Mediterranean climate of coastal California, moisture and temperature drive the spore abundance in the air more than coastal vegetation type or structure.

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Chapter 2
Fungal spore diversity, community structure, and traits across a vegetation mosaic

Introduction

Understanding the patterns and processes that shape biodiversity can help us manage and conserve natural ecosystems (Loreau et al. 2001) and protect human health (Ostfeld and Keesing 2013, Wall et al. 2015). Fungi in particular are essential to ecosystems worldwide - they cause disease, decompose organic matter, and help provide nutrition to plants (Fisher et al. 2012, Brown and Hovmøller 2002, Daszak et al. 2000, Leake 1994, Bardgett and van der Putten 2014). Yet measuring the diversity and structure of fungal communities has challenged scientists for decades, which limits our ability to understand the processes that are driven by these communities (Parrent et al. 2010, Mueller and Schmit 2007). Most fungi are unculturable or possess cryptic morphologies, which renders taxonomic identification difficult (Hawksworth 2010, Blackwell 2011). Some fungi retain clandestine life histories underground or inside plant and animal hosts (Carroll 1988). Recent development of next-generation DNA sequencing, however, allows rapid identification of unculturable and culturable fungi from environmental samples (e.g., soil, water, roots, leaves, animal tissue) on the scale of entire communities and across spatial scales (Caporaso et al. 2010, Parrent et al. 2010, Metzer 2010).

Fungi are ubiquitous (Bisby 1943, Gregory 1952), but molecular research shows that fungi exhibit strong spatial structure and restricted geographic ranges (Meiser et al. 2013, Kivlin et al. 2011). For instance, the diversity of fungal leaf endophytes is highest in the tropics and tapers toward the polar regions (Arnold et al. 2007) whereas ectomycorrhizal fungal diversity peaks at temperate latitudes (Tedersoo et al. 2012). For a single tree species, fungal endophytic communities exhibit strong spatial structure along rainfall and temperature gradients (Zimmerman and Vitousek 2012). Habitats with similar climate, edaphic conditions, and vegetation (e.g., forest, grassland) share soil fungal communities (Tedersoo et al. 2014, Talbot et al. 2013, Pellissier et al. 2014). When taken together, these studies show that the structure of fungal communities at continental and landscape scales is driven by environmental factors and composition is tightly coupled with local host diversity and availability.

Fungi vary tremendously in how they respond to environmental conditions and these responses are governed by phenotypic traits (Aguilar-Trigueros et al. 2015). Phenotypic fungal traits have a genetic basis and are considered adaptive when they increase organismal survival or enhance reproductive fitness (Bell and Gonzalez 2009). Such traits are commonly used for taxonomic identification (Kumar et al. 2011), but trait values can also indicate how fungi may respond to different changes in environmental variables (e.g., moisture, temperature, pH) (Aguilar-Trigueros et al. 2015).

Quantifying how traits vary across geographic space can illuminate the ecological roles and functions of fungi (Parrent et al. 2010) and be used to predict the likelihood that fungi will thrive under different environmental conditions and disturbance regimes (Shipley 2006, Gilbert and Parker 2016, Koide et al. 2014).

Fungal traits are broadly classified as life history traits, morphological traits, and physiological or functional traits (Aguilar-Trigueros et al. 2015). Spores, the primary reproductive and dispersal structures for fungi (Halbwachs et al. 2015, Moore-Landecker 2011), possess traits that can elucidate fungal reproductive output (Hussein et al. 2013), dispersal (Roper et al. 2008, Lilleskov and Bruns 2005), propagule survival (Vellinga 2004), and persistence (Gange et al. 2011). Although generating species lists from molecular data to identify fungal communities is vital for documenting species diversity and distributions, spore trait measurements can provide ecological explanations for community structure and diversity. In this chapter, we combine metagenomic fungal diversity data with spore trait data to examine the diversity and structure of fungal communities collected from rainwater across a mosaic of natural vegetation types (redwood forest, mixed-evergreen forest, and chaparral) from (January - March) in coastal California.

Fungi show preferences for different hosts, substrates, and environmental conditions; therefore, we expect a higher diversity of fungi in more complex forested habitats than in structurally simpler and less diverse shrub-like habitats (Tedersoo et al. 2012). We expect fungal community composition to cluster spatially by vegetation type (Tedersoo et al. 2012, Pellissier et al. 2014). As such, we expect to see a shift in fungal spore composition during early in the rainy season (January) when conditions are wet and moist as oppose to later in the rainy season (March) when conditions are warm and dry (Crandall, Chapter 1, Appendix 1E, Peay and Bruns 2014). In addition to changes in species composition, we expect that the distribution of spore traits should differ between fungi from a drier, structurally more open environment (chaparral) than fungi from wet, shady environments (forests). Specifically, we expected that spores collected from chaparral would be larger because of the presence of thick spore walls that prevent desiccation (Dix and Webster 1995); larger spores typically contain more carbon nutrients to facilitate survival under-nutrient limited conditions (Hawker and Madelin 1976). We also expected spores collected from chaparral to be wider and more elliptical than from the forested habitats because these traits make spores more aerodynamic for dry air dispersal (Roper et al. 2008) and because chaparral habitats are structurally more open than forests.

To test these expectations we asked 1) are fungal communities in forests versus chaparral more diverse?, 2) does fungal spore composition shift temporally over the course of a wet season?, 3) do environmental factors, specifically moisture and temperature, correspond with fungal community diversity?, and 4) are spores significantly larger and wider in chaparral versus smaller and rounder in forested habitats?

Methods

Field Sites & Spore Trap Design

We collected airborne spores associated with natural vegetation on the central coast region of California (USA) at Wilder Ranch State Park and the University of California, Santa Cruz Campus Natural Reserve (UCSC CNR) (Chapter 1, Figure 1.1). The region experiences a Mediterranean-like climate where the total average annual precipitation (~ 745 mm) falls as rain from October to April (Gilbert et al. 2010, Chapter 1, Appendix 1B) and the remaining precipitation arrives as maritime fog from June to September (Johnston and Dawson 2009). The coastal vegetation forms a mosaic across the landscape that varies in plant composition and structure. Fungal spores were collected across locally dominant vegetation "alliances" (i.e., repeated patterns of plant associations across the landscape).

We visualized topographic maps and vegetation data obtained from reserve and state park managers as geospatial layers using ArcGIS (ESRI, version 9.0), and identified the three most common coastal vegetation alliances on the reserve and state park: redwood forest, mixed-evergreen forest, and maritime chaparral. These three habitats correspond to the established vegetation classification systems for California (Sawyer et al. 2009) as (1) Coastal Redwood forest (indicator species *Sequoia sempervirens),* (2) Douglas fir-tanoak forest (indicator species *Pseudotsuga menziesii* and *Notholithocarpus densiflorus*), and (3) Brittle leaf-Woolly leaf manzanita chaparral (indicator species *Arctostaphylos tomentosa* and *Ceanothus thyrsiflorus*), respectively.

These three alliances were selected because they were dominant vegetation types and they differed in both plant species composition and habitat structure. We established 4 replicate sampling sites for each of the 3 vegetation types. We established a total of 12 sites across the landscape, located so that were easily accessible by foot from hiking trails, were at least 200 m apart, and at least 10 m from an established trail or paved road to minimize any disturbance from human activity.

Sites were marked with a flag and GPS coordinates were recorded (Chapter 1, Figure 1.1, Appendix 1A).

Previous temporal sampling of fungal aerospora in this landscape indicates that the best time of year to trap fungal spores in coastal California is during the winter rainy season, when peak spore production and dispersal occurs (Crandall, Chapter 1, Peay and Bruns 2014). Rainwater spore traps were deployed and collected once a week across the 12 sites from 17 January 2013 to 14 March 2013, for a total of 108 rainwater samples over a nine-week period. We built rainwater spore traps that could be easily deployed and collected in the field and did not require electricity to operate (Peay and Bruns 2014). Glass Mason jars (1 L) were converted into rainwater spore traps by poking a hole in the lid, inserting the stem of a plastic funnel (diameter 20 cm), and covering the entire jar with duct tape to reduce sunlight penetration (which reduces evaporation, protects the spores, and reduces spore germination in the field). Before deployment into the field, we autoclaved the jars and lids and surface sterilized the funnel in 10% bleach for 5 min, then rinsed with sterile water. Meteorological data was downloaded from 12 weather stations and from the nearby UCSC Forest Ecology Research Plot which is part of the Smithsonian Institute Center for Tropical Forest Science / Global Earth Observatory network (CTFS/SIGEO) (Gilbert et al. 2010). We obtained mean daily measurements for meteorological variables expected to relate to patterns of fungal spore production and release: air temperature, relative humidity, soil moisture, soil temperature, and leaf moisture.

Daily precipitation and solar radiation were calculated by summing the total amount measured per day.

Rainwater Processing & Fungal DNA Extraction

To prepare spores collected in the spore traps for DNA extraction, we first filtered the rainwater from each Mason jar through a sterile 1-mm^2 Nylon mesh to remove any large particulates (e.g., leaves, dirt). Next, we separated fungal spores from the solution by pouring the rainwater through Whatman Qualitative Filter Paper ™ (pore size of 3 µm) into a vacuum flask using a Burkard funnel. Fungal spores that ranged from 3-20 µm in size were trapped on the filter. The filtered rainwater was discarded and the filter paper was placed in a sterile Petri plate, to which ~ 15 mL of sterile, autoclaved deionized H_20 was added to the top of the paper. This filtering procedure was repeated for each jar containing rainwater. All filtration equipment was sterilized in a 10% bleach bath (0.025% sodium hypochlorite) for 5 min between samples. When all the rainwater spore traps were emptied, 50 µL of the surfactant tween 80 (polyoxyethylene sorbitan mono-oleate) was added to each Petri plate to prevent spores from adhering to surfaces and clumping. Each filter paper was brushed ~ 20 times with a rubber policeperson (sterilizing between samples with 70% ethanol and then burning off the ethanol with the flame from alcohol burner). The water with the suspended spore particulates was added to a 15-mL falcon tube, then centrifuged at 12,000 g for 10 min. The supernatant was discarded and the resulting pellet was re-suspended in cetyl trimethylammonium bromide (CTAB). Samples were finally preserved in an -80 °C freezer to be used for later DNA extraction. We extracted fungal DNA from 108 samples (9 weeks x 12 field sites = 108 samples) and used a chloroform-isoamyl alcohol protocol (Method iii, Miller et al. 1999), with slight modifications to optimize the DNA yield (Kabir Peay, personal communication). Briefly, we chemically lysed the spore particulates with sodium dodecyl sulfate (SDS) and chloroform-isoamyl alcohol (24:1), bead-mill homogenized the sample, and then recovered and purified DNA using Sephadex G-200 columns.

Next-generation ITS marker sequencing and processing

Species identity of fungal spores was determined with Illumina DNA amplicon sequencing of the internal transcriber spacer (ITS 1 and ITS 2) regions of rDNA, which is a region genetically variable enough to distinguish between fungal genera or species (Gardes and Bruns 1993). We quantified nucleic acid content per DNA extraction with a Qubit® 2.0 Fluorometer (Life Technologies, Grand Island, NY, USA) to ensure enough DNA sequencing. DNA extractions were diluted if concentrations exceeded 0.1 ng/L (Caporaso et al. 2012). We amplified and sequenced ITS 1 and ITS 2 separately with fungal specific primers. ITS 1 was amplified with ITS 1-F (5'-CTTGGTCATTTAGAGGAAGTAA-3'; Gardes and Bruns 1993) and ITS 2 (5'- TCCGTAGGTGAACCTGCGG-3'; White et al. 1990). ITS 2 was amplified with ITS 3 (5'- GCATCGATGAAGAACGCAGC -3'; White et al. 1990) and ITS 4-B (5'-CAGGAGACTTGTACACGGTCCAG-3'; Gardes and Bruns 1993). Both sets of primers were outfitted with indexing primers (7-10 nucleotides) and Illumina adaptor stubs. The PCR product was visualized on a 1% agarose gel using UV light and normalized using a Sequal Prep Normalization Kit™

(Life Technologies), pooled, and dried down in a speed vacuum overnight, and then quantified again with a Qubit® 2.0 to ensure adequate concentrations (> 0.1 ng/L). The pooled samples were rehydrated with double distilled H_20 and then purified using with Agencourt Ampure XP magnetic beads (Beckman Coulter Inc., Brea, CA, USA) and a magnetic stand (Rohland and Reich 2012). Outer primers were added to the amplicons and libraries were amplified with an additional 20 cycles of PCR. Following PCR, we again purified reactions with the Agencourt Ampure XP magnetic bead, quantified with the Qubit® 2.0, and visualized on a 1% agarose gel. A qPCR reaction was conducted to ensure that the adapters and outer tags were annealed to amplicons. The amplicons were sequenced on an Illumina MiSeq platform at the University of California, Los Angeles (UCLA) Genotype and Sequencing Facility using a single lane flowcell.

Bioinformatics Pipeline

Raw sequences were demultiplexed with the publically available PYTHON script Splitaake (https://github.com/faircloth-lab/splitaake). A strict filter was used to exclude sequences that had a Hamming distance, or barcode mismatch, over one. Subsequent bioinformatics processing was done using Quantitative Insights in Microbial Ecology (QIIME; Caporaso et al. 2010), an integrated pipeline that allows sequence alignment and taxon-based analysis of operational taxonomic units (OTUs). First, paired-end sequences were concatenated wherever possible. We trimmed low quality base pairs (Phred score < 20), and removed sequences shorter than 100 bp, as well as sequences that matched adaptor sequences post-trimming. Next, OTUS were created as clusters of two or more sequences with a maximum of one mismatch using USEARCH v5.2.236 (Edgar 2010), and then matched against the UNITE database (Kõljalg et al. 2013) to create phylotypes using BLAST v2.2.22 (Altschul et al. 1990, 1997), with an e-value cut-off of 0.001. The UNITE database includes quality checked and curated fungal ITS sequences of known origin. Each OTU was assigned a taxonomic moniker based on their best hit to the UNITE database at greater than or equal to 97% sequence identity. Finally, we used UniFrac, a phylogenetic measurement tool which determined pairwise differences between fungal communities and external variables such as the habitat and time of samples collection (Bowers et al. 2013).

Meteorological Data

Meteorological data were obtained as averages from 12 Decagon™ model EM 50 weather stations (Decagon Devices, Pullman, Washington, USA) in the understory from the nearby University of California, Santa Cruz Forest Ecology Research Plot (FERP) (Gilbert et al. 2010, http://ferp.ucsc.edu). We took average hourly and daily measurements for seven meteorological variables: solar radiation (W m^{-2}), air temperature (°C), soil temperature (°C), relative humidity (%), precipitation (mm), leaf moisture hours (h), and soil moisture (%) (Chapter 1, Appendix 1E). Because the weather stations are distributed across 6 ha in a range of open and closed forest structure, the average measurements across all the stations provides a more integrated measure of temporal variation in weather patterns, but not highly localized microclimate conditions, near to the sampling locations.

Analysis of fungal spore traits

To measure the traits of airborne fungal spores, we collected spores in each of the three vegetation types using a Buck Bioslide™ model 1020 Sampling Pump (A.P. Buck, Inc., Orlando, Florida, USA) on 22 March 2015. To provide an adhesive surface for airborne spores to attach to while in the sampling pump, we used black, electron microscopy double-sided carbon tape (Electron Microscopy Sciences (EMS), Hatfield, Pennsylvania, USA); the dark color provided contrast between spores and the background area when viewed later under a microscope. We attached a strip of the carbon tape (75 mm x 25 mm) to a standard glass microscope slide (25 mm x 75 mm x 1 mm). We positioned the strip of tape on the microscope slide directly underneath the impaction slit opening located on the Buck Bioslide™. At each of our 12 field sites, slides were placed the sampling pump on a tripod 1 m above the ground. Air was pumped through the device for 10 min at a steady volumetric rate of 15 L min^{-1}. Air entered the pump through the slit and left an impact trace of spores and other particulates on the carbon tape. The procedure was repeated sequentially at each replicate site with a 15-20 min sampling time between each field location. We collected fungal spore samples from redwood, mixed-evergreen, and then chaparral sites sequentially in one day (Chapter 1, Appendix 1A).

We took digital images of the fungal spores using a scanning electron microscope (SEM) (FEI Quanta 3D FEG dual beam SEM/FIB™) at the W.M. Keck Center for Nanoscale Optofluidics at the Baskin School of Engineering at the

University of California, Santa Cruz. For each sample, we first found a point toward the bottom of the trace on the carbon tape and moved the field of view upward until a fungal spore was located. Spores were selected that 1) were turgid and 2) with as spore perimeter that was not occluded by other spores or particulates; these conditions allowed accurate measurements of spores. We measured geometric traits for 88 spores from the redwood forest, 90 spores from the mixed-evergreen forest, and 78 spores from chaparral. Images were taken at varying magnifications depending on the size of the spore (4000× - 12500× magnification). To measure spore traits, the digital images were imported into the open source image analysis software program ImageJ™ (http://imagej.nih.gov/ij/). For each image, we calibrated the scale bar to match the length of the scale located within the image and set the pixel-axis ratio to 1. With the polygon tool, we traced the outside boundary of the spore by hand to select and then measure a dozen standard geometric measures of each spore type (Table 2.1).

Table 2.1. Descriptions of twelve geometric traits of fungal spores that were measured using the ImageJ™ program.

Fungal Spore Trait	Description[a]
perimeter (µm)	The length of the outside boundary of the selected spore.
width (µm)	The shortest distance between two points located on the outside boundary of the selected spore.
height (µm)	The longest distance between two points located on the outside boundary of the selected spore.
major axis (µm)	The length of the primary axis of the best fitting ellipse for the selected spore.
minor axis (µm)	The length of the secondary axis of the best fitting ellipse for the selected spore.
Feret's diameter (µm)	The longest distance between any two points along the selection boundary of the spore; also known as the caliper length.
skewness	The third order moment about the mean of the pixels in the selection; the symmetry in the x and y coordinates of the image.
kurtosis	The fourth order moment about the mean of the pixels in the selection; the flatness in the x and y coordinates of an image. When the kurtosis value is = 0, the spatial distribution of values is normal. When kurtosis is < 0, the distribution is flatter, when kurtosis is > 0 it is more peaked, and when kurtosis is < -1.2, it is bimodal or multimodal.
circularity	$4\pi(\text{area}/\text{perimeter}^2)$. A value of 1.0 indicates a perfect circle. As the value approaches 0.0, it indicates an increasingly elongated polygon.
solidity	(area/convex area) with a value of 1.0 indicating a perfect circle. As the value approaches 0.0, it indicates an increasingly elongated spore shape.
AR	the aspect ratio of the spore's fitted ellipse, (major axis/minor axis).
roundness	$4(\text{area}) / \{\pi(\text{major axis})^2\}$ or the inverse of aspect ratio.

[a] descriptions are modified from the ImageJ™ User Guide (Ferreira and Rasband 2012).

Statistical Analyses

To examine how spore composition changes over time and among the three vegetation types, we conducted a nonmetric multidimensional scaling analysis (NMDS; k=2), using a dissimilarity matrix of Bray Curtis distances for species composition based on OTUs determined through Illumina sequencing (Holland 2008). We used a permutational analysis of variance (PERMANOVA) to determine if spore composition changed significantly over time (January - March) using the ADONIS function in R (R Core Developer Team 2012). We generated rarefied species-sample accumulation curves to compare diversity of fungal species associated with the different vegetation types. To understand which meteorological factors were associated with variation in spore composition, we overlaid environmental variables as vectors onto our ordinations using the ENVFIT library from the R Project (R Core Developer Team 2012). To determine whether fungal spore traits varied across vegetation type, we conducted a nested analysis of variance (ANOVA), where replicate field sites (random variable) were nested within vegetation type (fixed variable). We computed studentized range statistics (Tukey's Honest Significant Differences (HSD)) to compare trait means across habitats. We used a permutational analysis of variance (PERMANOVA) to determine if fungal spore traits changed significantly among redwood forest, mixed-evergreen forest, and chaparral using the ADONIS function in R (R Core Developer Team 2012).

Results

Fungal sequences from the spore traps grouped into 8650 operational taxonomic units (OTUs) based on fungal sequence matches greater than or equal to 97% sequence identity (Supplemental Information). When compared to the UNITE database, approximately 49% of OTUs were identified as Ascomycota, 25% as Basidiomycota, and considerably fewer Chytridiomycota (2%), Zygomycota (0.4%), and Glomeromycota (0.1%). Approximately 13% of the OTUs were classified as "unidentified" fungi and 11% of OTUs did not match any existing sequence in the database. The same abundant taxa were found in all three habitats (Figure 2.1); there was slightly higher OTU diversity in the mixed-evergreen forest than in either redwood forest or chaparral (Figures 2.2, 2.3).

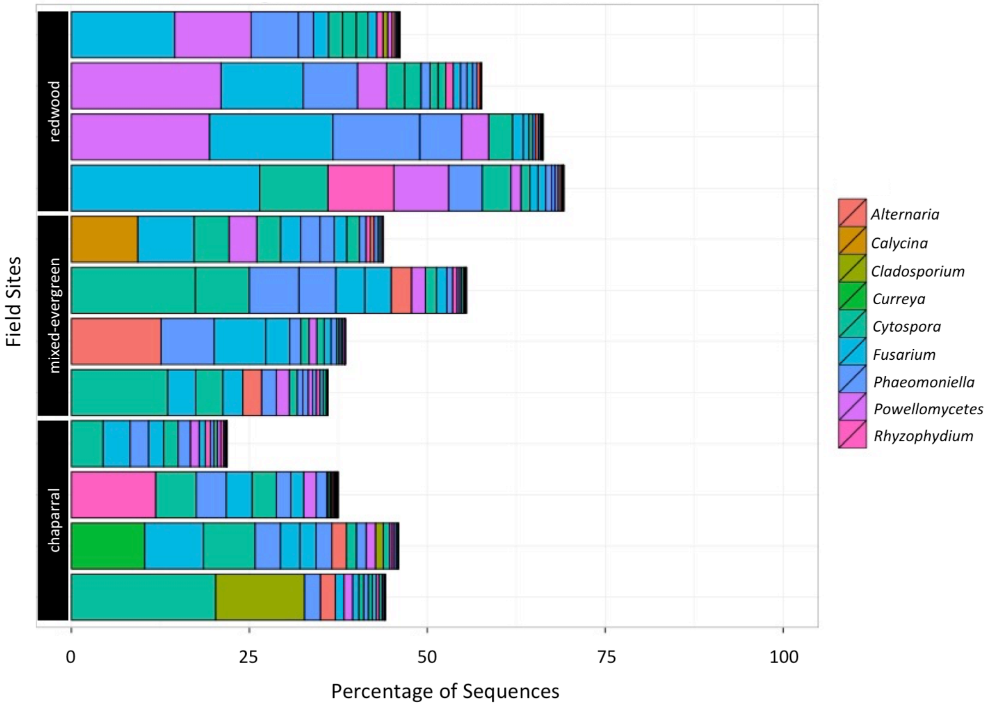

Figure 2.1. Fungal taxonomic composition associated with four sites in each of three habitats: coast redwood forest, mixed-evergreen forest, and maritime chaparral. Shown are taxa within the nine most abundant fungal genera found across all field sites for the three habitats.

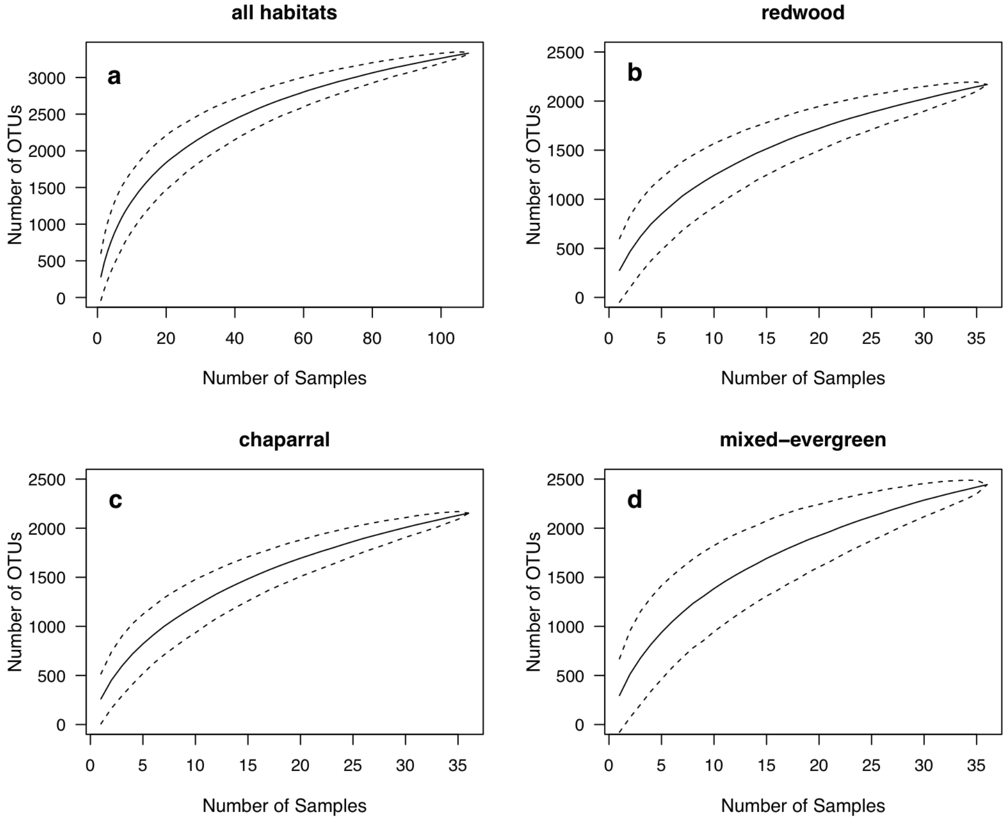

Figure 2.2. Species accumulation curves displaying the number of operational taxonomic units (OTUs) against the number of rainwater fungal spore trap samples for a) all habitat types combined, b) redwood forest, c) chaparral, and d) mixed evergreen forest. Solid lines for each curve show the expected mean species richness and the dotted lines represent 95% confidence intervals of the standard deviation around the mean. Each curve was calculated using subsampling without replacement by applying 1000 random data permutations.

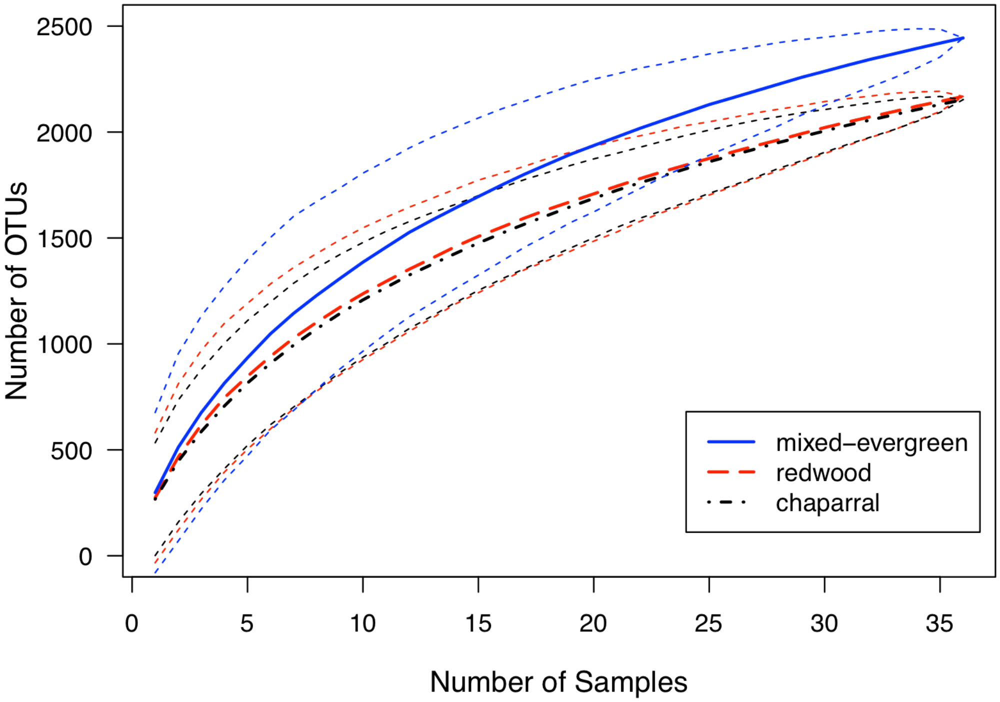

Figure 2.3. Species accumulation curves for three habitat types overlaid. Thicker lines depict the average number of operational taxonomic units (OTUs) and lighter dotted lines show 95% confidence intervals around each mean. Each curve was calculated using subsampling without replacement by applying 1000 random data permutations.

Fungal spore composition changed over time from January to March 2013 in redwood forest, mixed-evergreen forest, and chaparral. In each of the habitat types, fungal communities clustered temporally, with weeks 1 and 2 very similar, weeks 3 and 4 similar, and increasingly variable in later weeks (Figure 2.4; Appendix 2C).

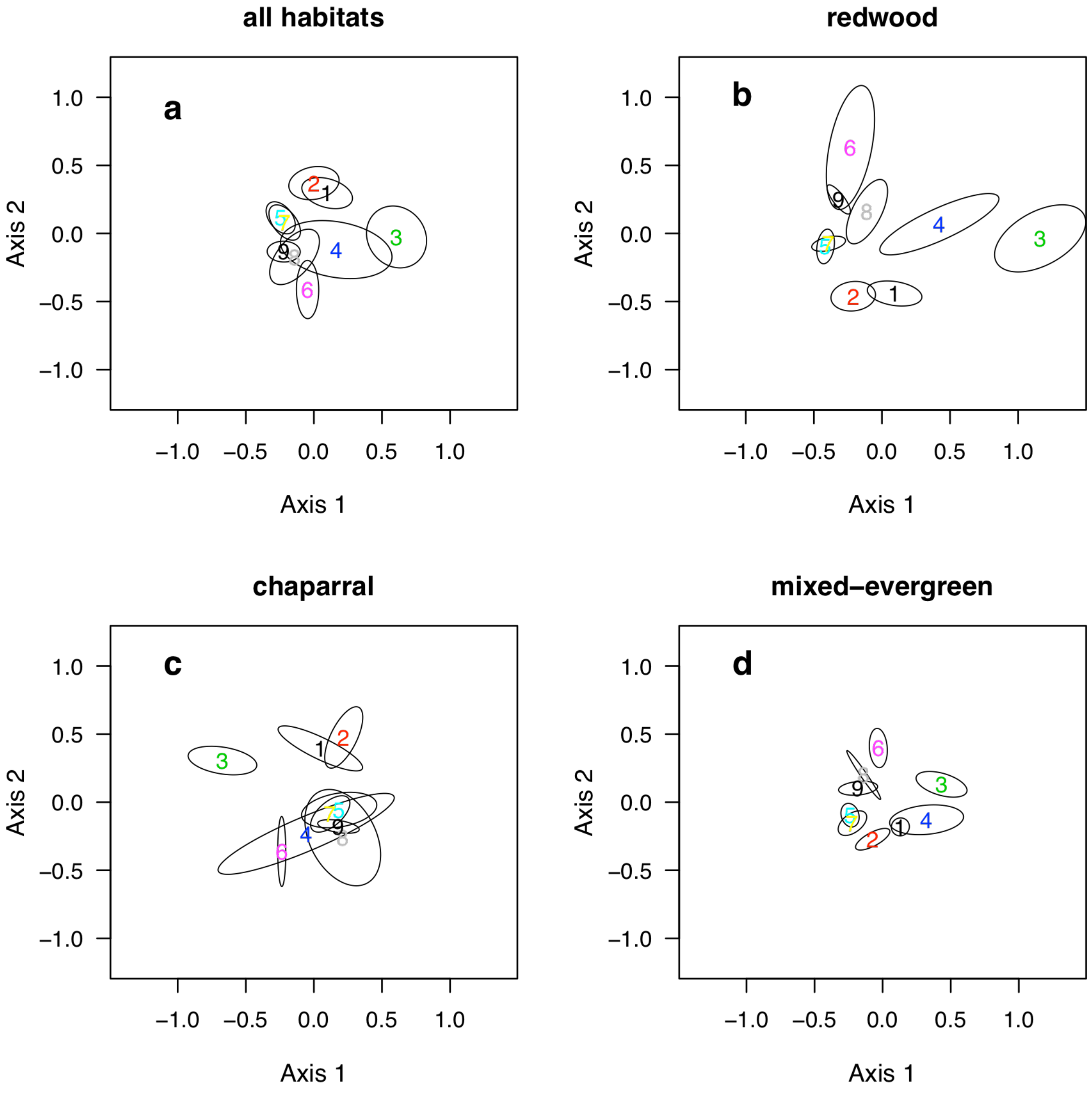

Figure 2.4. Nonmetric Multidimensional Scaling (NMDS) ordination plots of fungal communities based ITS OTUs from Illumina next-generation DNA sequencing over time; a dissimilarity matrix of Bray Curtis distances (k=2) was employed. Ellipses indicate groups of fungal communities: ellipses that are close together represent groups of samples with similar species compositions. The numbers in the ellipses indicate the week of the year when samples were collected from January - March 2013. For stress plots and scores, see Appendix 2A.

Fungal composition was similar among redwood, mixed-evergreen, and chaparral, however, there was some dissimilarity evident along Axis 1 of the NMDS ordination (i.e., see the extent of overlap in confidence ellipses below, Figure 2.5). Soil moisture, and to a lesser degree, relative humidity, soil temperature, and solar radiation were strongly correlated with fungal community composition (Figure 2.5).

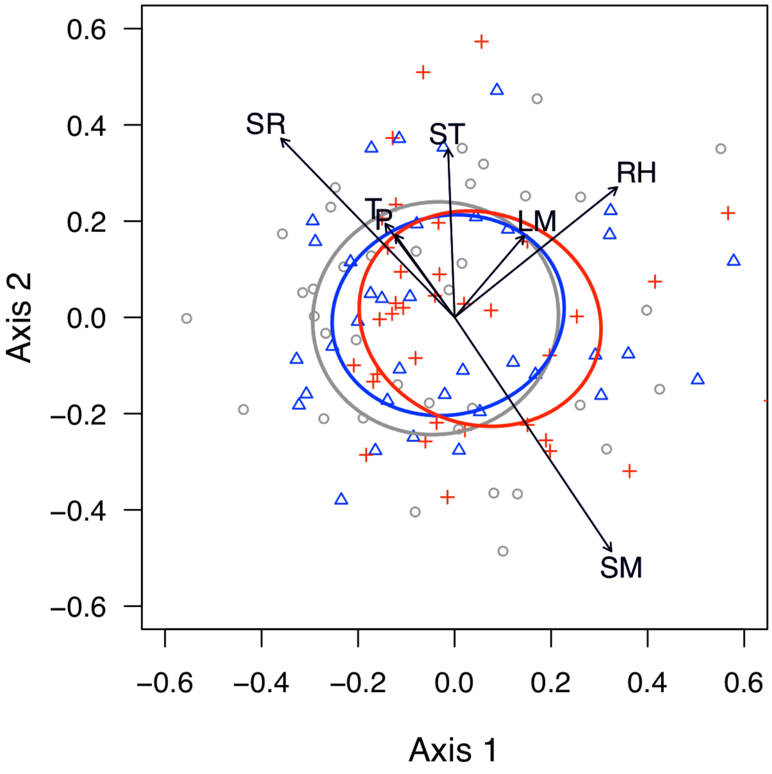

Figure 2.5. Nonmetric Multidimensional Scaling (NMDS) plot of fungal communities with environmental factors overlaid; a dissimilarity matrix was used of Bray Curtis distances (k=2) for species composition based on ITS OTUs from Illumina next-generation DNA sequencing. Points depict 108 samples collected across three coastal habitats: blue triangles = mixed-evergreen forest, gray dots = chaparral, and red crosses = redwood forest. Points that are closer together represent samples with similar fungal species compositions. Large colored circles for each habitat type (same color scheme as points) represent confidence ellipses drawn using the standard deviation of point scores. Environmental factors were fit as vectors onto the ordination (lines and arrows). The longer the line, the stronger the correlation between a meteorological variable and the ordination. Meteorological variables: SR = solar radiation, ST = soil temperature, T = air temperature, P = precipitation, LM = leaf moisture, RH = relative humidity, and SM = soil

When visualized under a scanning electron microscope, fungal spores showed a wide range of sizes, shapes, and ornamentation. Spores perimeters were (7.8 - 183.8 µm, mean = 38.1 µm) and had widths (2.2 - 58.3 µm, mean = 10.9 µm). Spores ranged in shape from spherical to oblong; some spores exhibited smooth outer walls while others had reticulate, spiny, or ridged ornamentation (Figure 2.6).

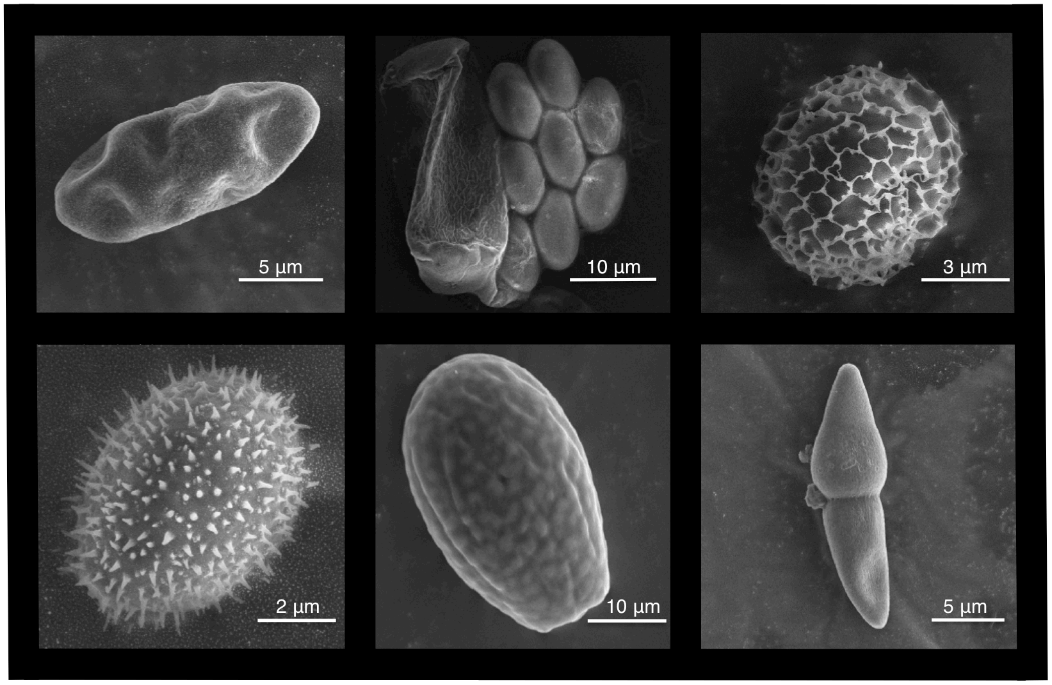

Figure 2.6. Example Scanning Electron Microscope (SEM) images of fungal spores showing various trait sizes, shapes, and ornamentations.

Fungal spores collected from different habitats differed for six of the twelve spore traits we measured: width, perimeter, major axis, minor axis, Feret's diameter, and kurtosis (Figures 2.7, 2.8; Appendix 2B, 2C). Spores collected from chaparral were significantly longer and wider and had a larger perimeter than spores collected in the redwood and mixed-evergreen forests.

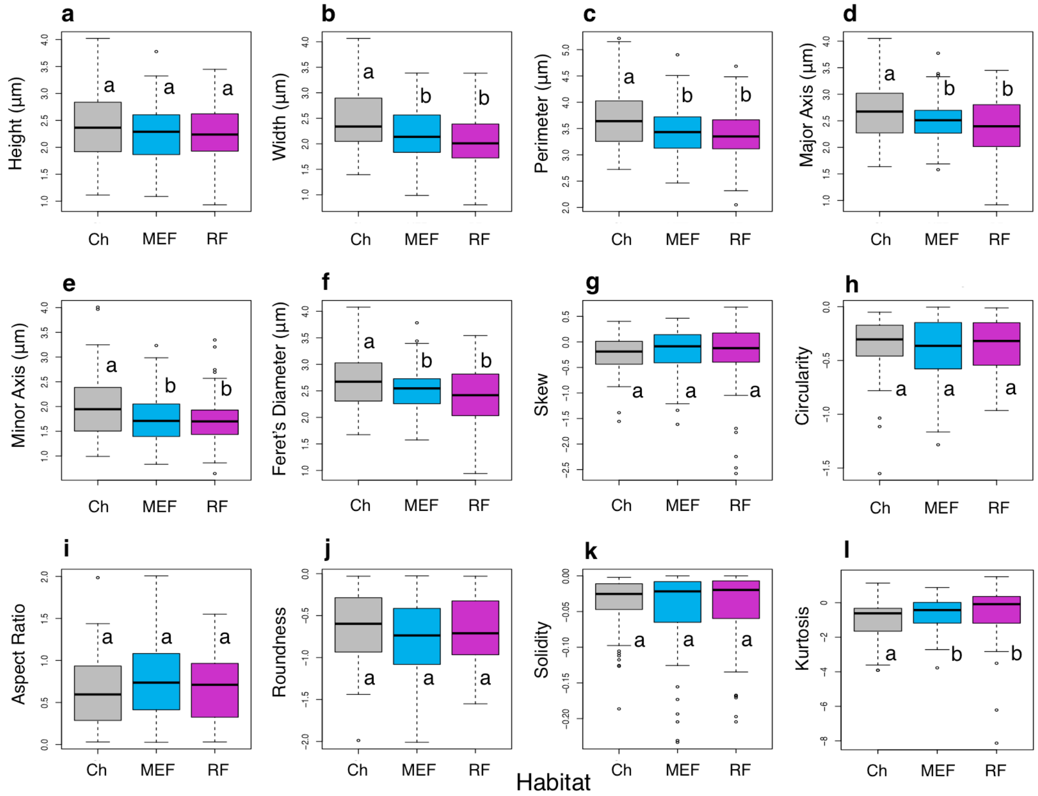

Figure 2.7. Boxplots for twelve fungal spore traits a) height, b) width, c) perimeter, d) major axis, e) minor axis, f) Feret's diameter, g) skew, h) circularity, i) aspect ratio, j) roundness, k) solidity, and l) kurtosis in three habitat types (Ch = chaparral, MEF = mixed-evergreen forest, and RF = redwood forest). The length of each rectangle within a boxplot is the interquartile range where the top and bottom lines of each box show the 3rd and 1st quartile range of the data respectively. The top whiskers show the maximum value plus 1.5 times the interquartile range and the bottom whiskers show the minimum value minus 1.5 times the interquartile range. Thick, solid black line inside each boxplot is the median value for the trait. Open dots show outliers. Letters (a,b,c) show significant and not significant results from the nested ANOVA Tukey HSD test (p values listed in Appendix 2C).

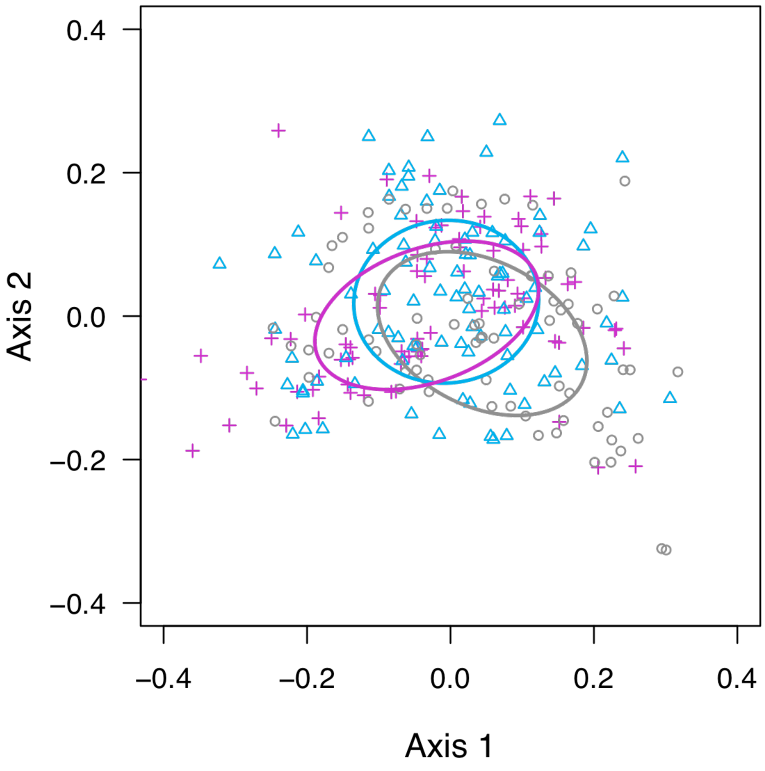

Figure 2.8. Nonmetric Multidimensional Scaling (NMDS) for fungal spore traits using the Bray Curtis distance method (k=2). Points depict a total of 256 fungal spores collected from three different habitats: gray dots = chaparral, magenta crosses = redwood forest, and sky blue triangles = mixed-evergreen forest. Large colored circles for each habitat type (same color scheme as points) represent confidence ellipses drawn using the standard deviation of point scores.

Discussion

Fungal community assemblages varied strongly over time and showed little spatial structure across a vegetation mosaic (Figure 2.4). Environmental factors such as soil moisture, soil temperature, relative humidity, and solar radiation may explain the temporal shift in fungal spore composition (Figure 2.5, Appendix 2B). From January to March in 2013, soil moisture decreased and soil temperature increased as the region transitioned from wet, cool conditions to dry, warm conditions (Crandall, Chapter 1, Appendix 1E). Over the same time period, local relative humidity decreased and the incidence of solar radiation increased (Crandall, Chapter 1, Appendix 1E). Others show that meteorological and edaphic factors can structure fungal communities over plant and fungal growing seasons (Taylor et al. 2010, Peay and Bruns 2014). For instance, Peay and Bruns (2014) found strong temporal and spatial structuring from autumn to spring of ecotomycorrizal fungi in coastal pine forests. Temporal shifts in fungal spore composition and abundance can also be driven by host plant phenology (e.g., leaf flush, flowering and fruiting time) (Diez et al. 2014, Büntgen et al. 2012). Bowers and colleagues (2013) found strong seasonality in microbial community structure (Fungi, Bacteria, Archaea) across land-use types and airborne fungal community abundance was highest in early spring to late summer (local plant growing season) compared to other times of year (Bowers et al. 2013). At finer scales, fungal ectomycorrhizal communities vary significantly by soil depth and over time. This may be due to the strong environmental gradients associated with vertical soil profiles, and soil heterogeneity, especially in soils that are highly stratified (Bahram et al. 2015). Our results suggest that when airborne fungal spores are measured at coarse spatial scales (2-4 km), meteorological factors are more important in shaping fungal reproductive timing (spore production and release) than above ground vegetation type. This result is important given that regional climate warming changes the composition and abundance of fungal communities across fungal functional groups (e.g., ectomycorrhizae, saprotrophs, pathogens) (Geml et al. 2016) and changes in fungal functional group composition and structure, may, in turn, influence ecosystem function (Talbot et al. 2013).

Fungal community diversity differed slightly across a vegetation mosaic; mixed-evergreen forest had significantly more OTUs than a redwood forest and chaparral (Figures 2.2, 2.3). Although not directly measured in this study, we know that coastal mixed-evergreen forests exhibit a higher diversity of plant species compared to coast redwood forest or maritime chaparral (Gilbert et al. 2010), and thus may provide fungal hosts, substrates, and nutrients. Others show that highly diverse fungal and bacterial assemblages can promote plant diversity and improve site productivity (van der Heijden et al. 2016).

Measuring phenotypic traits provides a compelling ecological explanation for how fungi respond to different environmental conditions (Aquilar-Trigueros et al. 2015) and, although not the focus of this chapter, can also illuminate the underlying processes that maintain biological diversity (Reich et al. 1999) and community assembly (Crowther et al. 2014, Ackerly et al. 2002, Cavender-Bares et al. 2004). One way to categorize how fungi respond to environmental change is by "response" and "effect" traits (Koide et al. 2013, Lavorel and Garnier 2002). Response traits influence how fungi respond to environmental factors and point to how fungi grow, disperse, and persist in a given habitat (e.g., spore size, shape, color, ornamentation) (Coleman et al. 1989, Lavorel and Garnier 2002) whereas effect traits are those that directly influence ecosystem function (e.g., decomposition rate) (Koide and Malcolm 2009).

We measured response traits for fungal reproduction and found that spores collected from chaparral habitats displayed significantly larger, longer, and wider spores than those collected in the redwood and mixed-evergreen forests (Figure 2.7, Appendices 2B, 2C). Large spores contain carbon nutrients that help fungi survive in nutrient-limited conditions (Hawker and Madelin 1976) and spores with thick cell walls prevent desiccation (Dix and Webster 1995) or help with long-term persistence in soil spore banks in fire-prone ecosystems (Glassman et al. 2016). Chaparral is a structurally open, water and nutrient-limited habitat type in Mediterranean-like climates that depends on periodic, low-density fires (Ackerly 2004). We also found that spores collected from chaparral were significantly wider and more elliptical than from the forested habitats, traits that make spores more aerodynamic for dry air dispersal (Roper et al. 2008). These results suggest that fungi in chaparral have spore traits that allow them to persist and disperse in harsh, dry, open conditions. Although there is scant research on fungal traits from chaparral habitat, Ackerly (2004) shows that chaparral plants possess leaf, stem, or seed traits that allow them to persist and survive in harsh environmental conditions and that suites of plant functional traits are found across ecological strategies in chaparral habitats (e.g. small seeds are found in both opportunistic and post-fire seeding plants). Future work is needed to measure fungal spore traits before and after ecological disturbance, such as fire or drought, which could further elucidate which traits allow different fungal species to persist and survive under varying environmental conditions (Shipley 2006, Gilbert and Parker 2016).

Conclusion

We asked how does fungal community diversity, structure, and reproductive traits vary in response to abiotic (weather) and biotic (vegetation) factors. We used next-generation genetic sequencing techniques (Illumina MiSeq) to identify fungal DNA collected from rainwater across a vegetation mosaic from January - March in 2013 and found that fungal spore composition varied strongly over time rather than vegetation type. Local meteorological (relative humidity, solar radiation) and edaphic factors (soil moisture, soil temperature) were strongly correlated with fungal community structure. The mixed-evergreen forest exhibited a higher diversity of fungi compared to coast redwood and chaparral, possibly due to a higher diversity of plant hosts and available substrate. Spores found in open, shrub-like habitat (chaparral) were significantly larger and longer than spores found in forests (redwood and mixed-evergreen), which suggests that fungi in chaparral have spore traits that allow survival dispersal in harsh, dry, open environments.

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Chapter 3
Ecosystem-based management of Special Forest Products: Willamette National Forest case study

Introduction

Ecosystem-based management was integrated into public land use policy and plans in the 1980s and 1990s as a way to improve natural resource management through landscape-scale assessment and collaborative multi-stakeholder participation for environmental planning. Environmental issues and potential impacts were assessed at the ecosystem level to incorporate information about large-scale ecological processes and to manage for multiple species, especially those with large ranges. To avoid political stalemates and litigation, collaboration between stakeholders (e.g., governmental agencies, non-governmental organizations, the public, Native American tribes) was used to incorporate a wide range of people's values and needs, in addition to ecological information, into the decision-making process. Today, many environmental institutions claim to use an ecosystem-based approach to manage natural resources. However, despite the requirement for landscape-scale assessment and collaborative planning on public land, some natural resource management projects depart from the ecosystem-based ideal; such departures depend on the natural resource in question, who uses it, the legal framework that allows access and use, and the socio-cultural context under which the resource is managed and harvested.

Special Forest Products (SFPs), sometimes called Non-timber Forest Products (NTFPs) or "biocultural resources", are natural resources valued and gathered for food, medicine, and/or commercial-use (e.g., mushrooms, berries, boughs). SFPs are harvested extensively in national forests in northern California, Oregon, and Washington. The Pacific Northwest Forest Plan (1994) was implemented two decades ago during the tumultuous "Timber Wars", a time when clear-cutting and other timber practices were degrading ecosystem health in the Pacific Northwest. The Plan was meant to improve forest resource management in national forests using an ecosystem-based management approach. In this chapter, I ask (1) how ecosystem-based management incorporates SFPs into forest planning in national forests under the Pacific Northwest Forest Plan, and (2) how landscape-scale and multi-stakeholder collaboration, two essential elements of ecosystem-based management, are incorporated into SFP management in the Willamette National Forest under the Pacific Northwest Forest Plan.

First, I define ecosystem-based management and describe landscape-scale assessment and collaborative planning. Then, I present the benefits and challenges of collaboration within the context of ecosystem-based management and review pertinent federal regulations and policies for SFP management in national forests as well as the rights of harvesters on public lands. Next, I present results from a survey on SFP management that I administered to USFS resource managers in the Pacific Northwest to query the current state of SFP programs in national forests that led to selection of the Willamette National Forest as a case study to examine collaborative activities between forest service staff and harvesters. Finally, I use the Willamette NF as a case study to evaluate existing hypotheses on collaboration over management of natural resources.

Ecosystem-based Management

Ecosystem-based Management Defined

Ecosystem-based management is an integrative approach for (1) managing species and ecological processes at the landscape scale (Forman 1995, Christensen et al. 1996), and that (2) requires multi-stakeholder collaboration for project planning and implementation (Innes and Booher 1999, Wondollek and Yaffee 2000). Ecological information, such as species habitat requirements, and stakeholder input are incorporated into different stages of the decision-making process to create a management regime that is adaptive, flexible, and open to unexpected ecological or social change (Stankey et al. 2005). In the United States, ecosystem-based management was incorporated into environmental planning in the 1980s and 1990s as a response to public regulations and policies that failed to protect the environment and address a full range of social values and needs. Today, ecosystem-based management has been adopted by governmental and non-governmental organizations worldwide and is still used to manage public land in the United States (Layzer 2013).

Landscape-scale assessment as an element of Ecosystem-Based Management

In the 1980s and 1990s, there was a growing consensus among scientists that landscape-scale environmental analysis and protection helped maintain populations of multiple species, ecosystem processes, and ultimately, long-term environmental health (Franklin et al. 1981, Pickett and Ostfelt 1995, Christensen et al. 1996, IEMTF

1996). Landscape-scale assessment was adopted after evidence that chief environmental regulations, such as the Endangered Species Act (ESA), resulted in fragmented landscapes that focused on the protection of single species and subsequently failed to recognized the complexity and connectivity of organisms and their ecological needs at larger scales (Layzer 2012, Franklin et al. 1981). However, in certain instances, the ESA can act as a unifying regulatory force in the face of other drivers that might fragment a landscape, as it did for protection of endangered Grizzly bears in Yellowstone National Park (Guercio and Duane 2010). The dominant notion in the early 20th century that ecosystems are closed systems with climax states, shifted in the second half of the century, to an understanding that ecosystems are open, dynamic systems where stochastic forces (e.g., natural or human disturbances) are important drivers of the ecology of landscapes (Franklin et al. 1981, Christensen et al. 1996). This shift in understanding led to the adoption of larger-scale ecological assessments for management of public land.

In addition to improved protection of habitat for species and ecosystems, landscape-scale assessment allows stakeholders, including federal agencies or private landowners, to view environmental problems at multiple scales and in relation to other stakeholders (Layzer 2008). For example, some ecosystem level processes affect different stakeholders in shared or differential ways (e.g., the impact of water pollution on entire watersheds rather than one river) (Layzer 2008). Examining the interconnected ecosystem processes rather than assessing resources in isolated habitats favors collaborative development of comprehensive environmental management plans that incorporate both ecological and social solutions (Christensen et al. 1996, Layzer 2008).

Collaborative Theory as an element of Ecosystem-Based Management

Collaborative theory was integrated into ecosystem-based management planning polices throughout the United States in the 1980s as a response to the failure of single-jurisdiction planning and management to protect species and public land against development and other special interests (e.g., timber) (Layzer 2013). A technocratic, top-down approach to resource management pervaded agencies charged with managing public lands and wildlife such as the USFS, the Bureau of Land Management (BLM), and the US Fish and Wildlife Service (USFWS) (Clark 1999). The traditional attitude toward environmental management was due, in part, to the impression that science and technology could solve land-use issues when implemented in an objective, rational manner. The result of traditional attitudes and land management approaches (dating from the Progressive Era, when most American land and resource management agencies were established) was the decoupling of human needs and values from the natural resource decision-making process. Decisions were made in a hierarchical, compartmentalized fashion were supposed to produce the most optimal result (Holling and Meffe 1996). However, traditional attitudes and approaches to environmental management ignored social values and needs, which contributed to often violent conflicts about how public land should be used and by whom (e.g., Grizzlies in Yellowstone, Timber Wars in the Pacific Northwest) (Clark et al. 1991, Layzer 2013). Thus, collaborative planning was integrated into many land management plans for public agencies within an ecosystem-based framework.

Collaborative Planning

Benefits of Collaborative Planning and Management

Collaborative planning, a process informed by collaborative theory, is a promising approach for successful environmental management (Wollendeck and Yaffee 2000, Beattie 1996, Innes and Booher 1999). Collaborative planning gained popularity in public and private sectors in the 1990s as a solution to the challenge of integrating social dimensions into natural resource management, and this planning approach has evolved into what is more broadly called collaborative governance (Koontz and Thomas 2006, Gerlak et al. 2013). Collaborative planning specifically allows participants to, "establish rules of engagement, define issues, design data collection and analysis, and help develop solutions" (Layzer 2008: 24). Collaborative planning brings various stakeholders together during the decision making process and opens a forum to find common ground, resolve complex issues, and create successful environmental outcomes. This approach finds its roots in the negotiation and planning literature (Susskind and Cruikshank 1987, Innes 1996) and possesses at its core the notion of consensus building. Issues or conflicts are first defined and then reframed during the consensus process. The parties involved outline and hone alternatives and then finally agree on the best solution (Clark 2002). To streamline the conversation, a facilitator is often present (Innes 1996). One of the main requirements for consensus building is equitable access to information by all parties. Moreover, for true collaborative planning to occur, each stakeholder in the community should be involved at each step of the process (Duane 1997). Equal participation can allow people to feel empowered to participate and see the process through. Duane (1997) emphasizes the role of community in collaborative planning, where communities can be linked together by place, identify with common issues, and share an interest in the planning outcome (Duane 1997).

Some purported benefits of collaborative planning are to create trust and understanding between people with disparate backgrounds, views, and motivations (Conrad and Hilchey 2011, Wollendeck and Yaffee 2000, Voege and Wagner 1997). This may occur through transparency and information sharing during the decision making process. Participants are given a voice throughout the process to raise concerns that allows all stakeholders the opportunity to learn from a spectrum of ideas. Stakeholder collaboration also encourages a sense of "fairness and legitimacy" because multiple parties participate and provide input during the management plan's development. This should, in turn, allow for a smooth implementation of the plan (Layzer 2008). Finally, the shared nature of collaborative planning encourages joint research and the mobilization of resources (e.g., sharing, pooling of administrative resources) across different agencies and groups for a common goal (Wollendeck and Yaffee 2000).

An example of a successful collaborative planning effort in forest management is of the Inimim Forest near the Yuba River in California (Duane 1997). In this case, the Bureau of Land Management wanted to cut timber on land adjacent to the San Juan Ridge Community. The community members were concerned that the proposed timber practices would degrade the local soil and water quality. Through a collaborative planning effort between the community and a public agency, a multiple use and sustained yield timber harvest plan was created. Old growth forest was set aside for preservation and the timber production in other areas increased local jobs. Beyond enabling equal participation in the decision-making process, this case also exemplifies the importance of fostering a sense of equitable project ownership between stakeholders to produce a successful forest management outcome. The Inimim Forest case involved only a small land area, however, and scaling that experience to larger landscapes is likely to involve more spillover effects that will require the involvement of more stakeholders—which may limit collaborative efforts (Duane 1997).

Challenges of Collaborative Planning and Management

Despite the rise in popularity of collaborative planning for ecosystem-based management projects over the past 30 years, some are skeptical about whether this approach actually addresses social concerns and improves ecological functioning (Duane 2007, Layzer 2008). Conley and Moote (2003) suggest that an "idealized narrative" has risen around collaboration: an assumption that all stakeholders are invited to the table, they all contribute equally, and that reason prevails over politics to produce improved ecological outcomes (Duane 2007).

Challenges during the collaborative planning process include the influence of regulations on stakeholder negotiation, the effect of power dynamics on planning outcomes, and the difficulty of simultaneously developing environmental and economic during the initial planning phases. Collaboration theory recognizes that the Best Alternative to a Negotiated Agreement (BATNA) for each stakeholder can affect project planning and management (Fisher and Ury 1981). For instance, the presence of environmental regulations can make each party's BATNA unattractive, therefore leaving collaboration as a key for success. Legislation such as the Endangered Species Act (ESA) can act as a formidable force, providing incentive for stakeholders to collaborate or else face the penalties of non-compliance through fines or lawsuits (Duane 1997, Guercio and Duane 2010). However, power dynamics outside of the negotiation room can also structure the relationships among the stakeholders inside the room. Asymmetric power dynamics between stakeholder groups, for example, may lead to adoption of an alternative/s that may not be in the best interest of each stakeholder or may not lead to improved environmental outcomes (Layzer 2008).

One of the biggest barriers to collaboration occurs when environmental and economic goals are simultaneously designed. In Duane's (2007), “Good Politics Before Good Science?", stalemates and failed consensus occur when ecological goals are too specific early in the decision making process and political concerns and issues are not included, or if they are, are incorporated too late in the process. Duane offers a solution for dealing with political issues: include them early in the discussion and keep the environmental goals vague earlier on to dissipate arguments on the specifics of management (Duane 2007, ELI 2003).

Social and Institutional Scales of Collaborative Planning and Management

Stakeholder cooperation and coordination, a requirement for collaborative planning, encourages the interaction of social communities - from groups of concerned citizens to governmental agency or corporate representatives (Wollendeck and Yaffee 2000). Duane (1997) defines three types of stakeholder communities who share social values, interests, or both - those that (1) are united by geography or place, (e.g., local landowners); (2) share a common identity (e.g., cultural, historical), or (3) have a common interest (e.g., park recreationists, commercial interests). Collaborative planning requires that people meet face-to-face to reach consensus on a plan; they can meet in neutral, public space such as library or cafe. In order for collaborative planning to succeed, however, all stakeholders from all three of these communities should be present and should contribute through out the process (Duane 1997). In the case of the Quincy Library Group's collaborative effort for sustainable forest harvesting in California, certain communities of identity and interest were excluded from the planning process. The USFS, a key institutional player, was minimally included during the collaborative process although the management projects that were proposed were on land managed by the USFS. Other institutional players, such as non-local environmentalist groups (e.g., The Wilderness Society) and non-governmental organizations (NGOs) (e.g., Natural Resources Defense Council (NRDC)) were not given a voice during the Quincy Library Group collaboration.

In theory, collaborative planning allows for more regular consultations of representatives from within and between institutions than when a collaborative approach is not used. In time, face-to-face meetings can also establish trust among strangers or former political foes (Danaher et al. 2007). Furthermore, the combination of expert scientific knowledge from different institutions and local knowledge from individuals about ecosystem processes can lead to a plan that is feasible and more likely to meet original management goals and objectives during project implementation (Anderson 2005, Layzer 2008).

Special Forest Products

Study Region: social conflict and the emergence of Ecosystem-Based Management

The Pacific Northwest spans the states of Washington, Oregon, and northern California in the United States. In the 1980s and early 1990s, controversy erupted about how old growth forests should be harvested and managed in the region (Yaffee 1994, Danaher et al. 2007, Layzer 2012). Concern over how timber practices endangered the northern spotted owl (*Strix occidentalis caurina*) led to measures to protect the owl on federal land (Yaffee 1994, Franklin et al. 1981). However, it became increasingly clear that protections and policies were inadequate and failed to incorporate ecological information about the owl, broader ecosystem health, and stakeholders' needs (e.g., timber companies, governmental agencies, conservation groups, private landowners) (Layzer 2012). In an effort to address a situation which turned into a heated national crisis (Andre and Velasquez 2015), the Clinton Administration in 1994 proposed a solution for the region's national forests: The Pacific Northwest Forest Plan was created as a comprehensive ecosystem management strategy to provide standards and guidelines for landscape scale and multi-species management while also acknowledging the importance of a flexible management approach and stakeholder involvement for decision-making (ROD 1994).

The Pacific Northwest Forest Plan (hereafter the Plan) is the overarching document that provides standards and guidelines for managing approximately 24 million acres of federal land spanning Washington, Oregon and northern California (USFS Regions 5 and 6) (ROD 1994). Today, the USFS divides management of national forests in the area along state boundaries: the Pacific Northwest Region 6 (OR, WA) and the Pacific Southwest Region 5 (CA). Within the Pacific Northwest Region 6, the USFS is charged with managing 17 national forests (Figure 3.1).

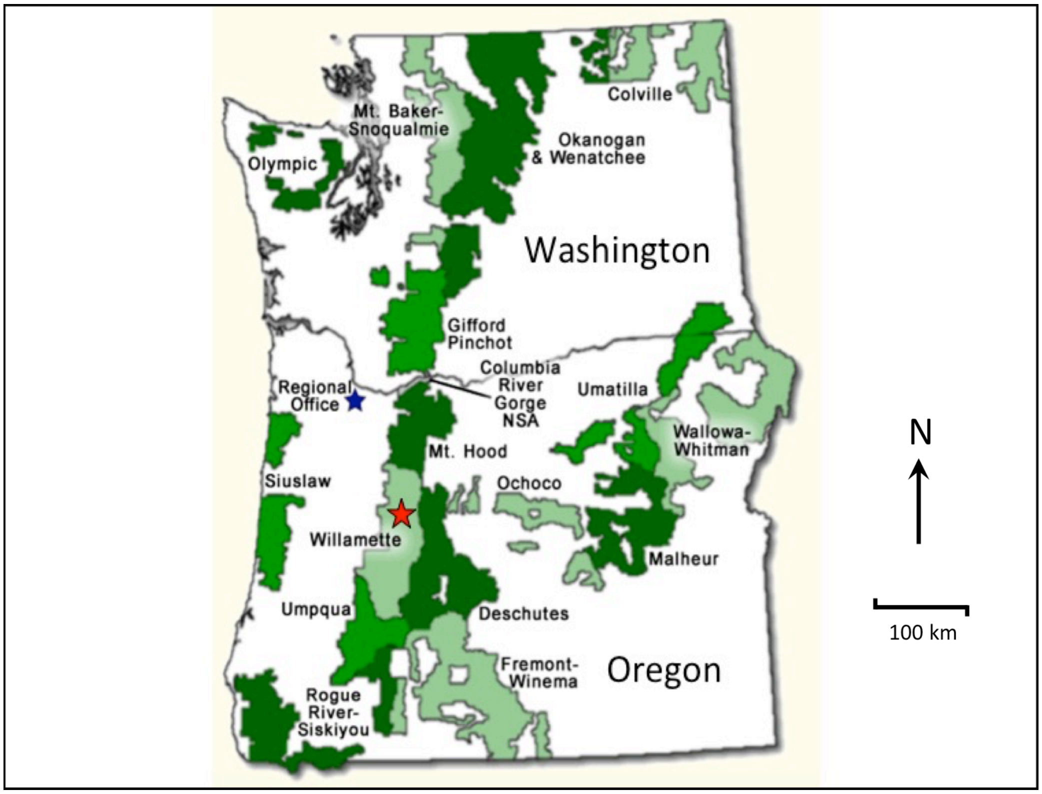

Figure 3.1. Map of national forests (green) in the Pacific Northwest (USFS Region 6) located in Oregon and Washington. The red star indicates the case study site, the Willamette National Forest, and the blue star indicates the USFS Pacific Northwest Regional Office. (Source map modified from: www.fs.usda.gov/detail/r6/passes-permits/recreation).

Approximately 30% of the land managed under the Plan was set aside by Congress and designed as Congressionally Reserved Areas (CRAs) in the Plan to conserve and protect habitat for endangered species such as the northern spotted owl and the marbled murrelet (*Brachyramphus marmoratus*). CRAs include areas such as Wilderness Areas, National Parks and Monuments and National Wildlife Refuges (ROD 1994). The remaining land was allocated into other categories under the Plan: Late Successional Reserves (30%), Matrix or land that was within the range of the northern spotted owl (16%), Riparian Reserves (11%), Managed Late Successional Areas (1%), and Administratively Withdraw Areas (6%). Finally, ten Adaptive Management Areas (AMAs) were set aside which comprised approximately 6% of the total area managed under the plan (1,521,800 acres), "to develop and test new management approaches to integrate and achieve ecological, economic, and other social and community objectives. The Forest Service and BLM will work with other organizations, government entities and private landowners in accomplishing those objectives." (ROD 1994: 6).

The Importance of Special Forest Products in the Pacific Northwest Forest Plan

The Plan focuses on forest management practices for timber in national forests within the range of the northern spotted owl. SFPs are barely mentioned in the Plan under "Standards and Guidelines for Multiple-Use Activities Other Than Silviculture" for management in Late Successional Reserves and Managed Late Successional Areas:

> Special forest products include but are not limited to posts, poles, rails, landscape transplants, yew bark, shakes, seed cones, Christmas trees, boughs, mushrooms, fruits, berries, hardwoods, forest greens (e.g., ferns, huckleberry, salal, beargrass, Oregon grape, and mosses), and medicinal forest products. In all cases, evaluate whether activities have adverse effects on Late-Successional Reserve objectives. Sales will ensure resource sustainability and protection of other resource values such as special status plant or animal species. Where these activities are extensive (e.g., collection of Pacific Yew bark or fungi), it will be appropriate to evaluate whether they have significant effects on late successional habitat. Restrictions may be appropriate in some cases. (ROD Attachment A 1994: Standards & Guidelines: C-18).

The Plan mentions monitoring of Special Forests Products such as "mushrooms, boughs, and ferns." Evaluation should occur specific to Native American tribes as to whether they have "access to and use of forest species, resources, and places important for cultural, subsistence, or economic reasons, particularly those identified in treaties" (ROD Attachment A 1994: Implementation: E-9).

Despite sparse direction and guidance for SFP management in the Plan, there is a need to critically evaluate collaborative planning efforts for SFP management projects in Region 6 to understand the differential ecological and social outcomes of these projects over time, especially in the wake of incorporating ecosystem based management into the Pacific Northwest Forest Plan of 1994. Collaborative planning efforts, in theory, should provide a voice and platform for stakeholder communities to incorporate their interests and needs into the federal environmental management process. Moreover, public participation of citizens, such as SFP harvesters, is a central idea for democratic governance of public lands and property in the United

States (McLain and Jones 2005). Public participation is required during the decision making process under the National Environmental Policy Act (NEPA) and involvement and consultation of federally recognized sovereign nations is required under the American Indian Religious Freedom Act (AIRFA) and other tribal laws (detailed in the next section). At the same time, federal resource managers are overstretched for financial resources and time to engage in-depth evaluations of their own natural resource programs. This vacuum offers the space and opportunity for researchers from other organizations, such as universities, to conduct outside assessments of federal natural resource management programs and practices.

Special Forest Product management is understudied in the United States - yet there is a growing socio-economic demand for SFPs in the United States (McLain and Jones 2002). Common SFPs harvested in national forests include mushrooms, berries, cedar bark, Christmas trees, and boughs for making holiday wreaths and decorations (McLain and Jones 2005, Pojar and Mackinnon 1994). In the Pacific Northwest, SFP harvesting occurs by diverse communities of harvesters in national forests (McLain and Jones 2005, Charnley et al. 2008) and understanding the demographics of these harvesters and their needs is useful to inform management of SFPs (Love and Jones 1997, Anderson 2005, Anderson 2009). SFP monitoring programs and collaborative activities data are sparse (McLain and Jones 2005, Lynch et al. 2004); the last nationwide SFP program survey was administered to USFS managers a decade ago and information about SFP management practices today can shed light on the current state of SFP programs to determine which forests are collaborating with harvesters for various products. In national forests in the Pacific Northwest, federal managers must comply with regulations, regional, and local policies and contract agreements (e.g., AIRFA 1978, Farm Bill 2008, the Plan, WNF Plan, Memorandums of Agreement (MOUs)) and should allow harvesters, including federally recognized tribes access to traditional products such as SFPs. Although USFS collaborative partnerships with tribes occur, examining the nature of these partnerships and whether they succeed in meeting both social and ecological management goals (Vinyetta and Lynn 2015) can inform sustainable collaborative management of SFPs in national forests today and into the future (McLain and Jones 2005).

Influential Laws & Policies for Special Forest Product Management

National Environmental Policy Act (NEPA)

The National Environmental Policy Act (NEPA) of 1970 establishes specific environmental goals and procedures for the protection and maintenance of the environment and identifies how to implement these goals into federal policy and management (NEPA 1970). NEPA directly affects the federal agency management of SFPs by mandating the project-scoping process and environmental analyses prior to starting federal projects that may have a significant environmental impact on public land. For example, the USFS routinely conducts Environmental Assessments (EAs) for timber projects or prescribed burns which includes assessing the environmental impact of harvesting and collecting SFPs. In the case of Willamette National Forest in Oregon and other national forests in the Pacific Northwest and Alaska, EAs may detail the potential impact of allowing harvesters to access burned areas to collect morels (*Morchella* spp.) (Pilz et al. 2007, Wurtz et al. 2005). EAs may also outline how boughs are collected after thinning noble fir (*Abies procera*) or detail potential bough sales. Certain ranger districts ask for a Categorical Exclusion (CE) when there is no significant overall environmental impact for a particular project, such as the "hand gathering of a variety of special forest products within 150 feet or roads open to public access" (Willamette National Forest 2014). Finally, NEPA mandates public participation, especially during the initial scoping process. There is the potential for SFP harvesters to provide input about their needs and concerns through this process (McLain and Jones 2002).

National Forest Management Act (NFMA)

The National Forest Management Act (NFMA) of 1976 outlines how the USFS should administer and govern national forests and is an amendment to The Forest and Rangeland Renewable Resources Planning Act (RPA) of 1974. Where RPA requires periodic reports and analyses on the current and projected status of natural resources in national forests and grasslands (USDA USFS 2012), NFMA outlines the forest planning and decision-making (USDA 1990). Specifically, NFMA details land and resource management planning and implementation, a process that follows three major phases: plan promulgation, judicial appeals, and plan administration. The first phase involves forest plan promulgation where Environmental Impact Statements (EISs) are drafted, plans are reviewed and public hearings are held. Public comments are incorporated into the plan and the proposal is approved. The second phase involves plan appeals and judicial review of decisions.

The third phase, plan implementation and administration, includes monitoring, evaluation, and further judicial review if necessary, and subsequent plan revision (Gippert and DeWitte 1990).

Although SFPs are not specifically cited in NFMA, "renewable resources" are mentioned which, if broadly interpreted, includes non-timber forest products in addition to timber resources (NFMA 1976, Antypas et al. 2002). During phase one of the planning process, there is room for SFP harvesters to provide input and voice their concerns and needs during public hearings. Inventorying and monitoring of renewable resources occurs during phase three of the planning process, which includes documentation of plant and animal biodiversity within the multiple-use mandate for national forests (NFMA Sec.14). Although there is no direct language to manage SFPs in the law (e.g., access, harvest), these products are still managed by national forests (Antypas et al. 2002) due to their long-standing economic and cultural importance (McLain and Jones 2002).

Endangered Species Act (ESA)

The Endangered Species Act (ESA) of 1973 protects plant, wildlife, and fish species whose populations are at risk for extinction by formally categorizing them as either threatened or endangered (Antypas et al. 2002, Peyton 2013). The ESA allows for the protection of critical habitat: the geographical areas occupied by a species, or physical or biological features that are essential for its conservation, and can include the area that may lay outside the species range that may be needed for special protection and species management (ESA.Sec.3.5.A.). The ESA defines the term “plant” as separate from “wildlife” (ESA.Sec.3.C.8; ESA.Sec.3.C.14) which has indirectly influenced SFPs because plant conservation laws and funding mechanisms to support research and conservation have lagged behind those for animals (Bean and Rowland 1997; Stein and Graveur 2008).

The ESA directly influences SFP policy by allowing federal agencies the authority to protect forest species from extinction and to conserve critical habitat. This law protects SFPs habitat that may be at risk from exploitation by unsustainable harvesting methods, over harvesting, and habitat degradation. It specifically prohibits the unauthorized removal or take of species which means “to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct” (ESA.Sec.3.19). However, critics view ESA as a barrier to access SFPs because policies made in reaction to a real or perceived threat of overharvest are often made in the absence of socio-cultural information and an understanding of the drivers of harvest, such as the motivations of harvesters (Emery and McLean 2001).

Federal Regulations for SFP Management

The Lacey Act applies to the movement of SFPs across state and international boundaries while other regulations, such as AIRFA establish the rights of federally recognized Native American tribes to access and use SFPs on public land; and other laws (discussed below) establish rules for the federal government-tribal government consultation on projects that may include SFP management.

The Lacey Act of 1900 was the first legislative effort to protect wildlife against illegal trade. Initially, it was enacted to curtail the commercial exploitation and transport of animals in the U.S. in the early twentieth century (Dunlap 1989). Amendments to the Lacey Act in 1981 expanded the law to include plants that are taken, transported or sold in violation of any state or federal law. Amendments made in the 2008 Farm Bill (Public Law 110-246, 122 Stat. 1651) broadened the purview of the Lacey Act to include plants and plant products obtained in violation of foreign laws and regulations such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (APHIS Illustrative List of Taxa 2014, Bean and Rowland 1997, FWS 2014). Thus, SFPs that are listed under any state laws or listed in the CITES Appendices are protected under the Lacey Act. The Lacey Act has been successfully used to prosecute violations involving SFPs, such as American ginseng, which is listed in CITES and protected under state laws (FWS 2014). The Animal and Plant Health Inspection Service (APHIS) is responsible for enforcing the Lacey Act and deals with violations pertaining to plants and plant products. Special permits are required to move plants and their products and a product declaration is necessary to transport plants across domestic and international borders. Similarly, the US Fish and Wildlife Service (USFW) oversees the transport of wildlife parts and products, including animals, fish, birds and their products that may come from US forests or forests abroad. For further discussion of Lacey Act prohibitions related to plants, including violations of U.S. or Tribal law and violations of state or foreign laws, see USCRS (2014).

The American Indian Religious Freedom Act (AIRFA) of 1978 was one of the first laws to establish the rights of federally recognized groups who self identify as

Native Americans, Native Alaskans, and Native Hawaiians to harvest plants that are used for religious purposes on public land. In the 1990s, two other major pieces of legislation gave federally recognized tribes the ability to access and harvest plants the (1) National Indian Forest Resources Management Act (NIFRM) (1990, 25 U.S.C. § 3103(3)), which allowed land management activities on Indian forest land (including land where title is held by the US in trust for non-federally recognized tribes), either directly or through contracts, cooperative agreements, or grants under the Indian Self-Determination and Education Assistance Act (1975), and (2) American Indian Agricultural Resources Management Act (1993) which allowed tribes the rights of access to SFPs as an "agricultural product." These products could include crops, livestock, forage and feed, grains, and any other marketable or traditionally used materials. Moreover, Executive Order 12898 was created in 1994 specifically to “address environmental justice in minority populations and low-income populations (59 FR 7629, February 16, 1994). This Order includes Native Americans and their right to traditional items, including food. The Tribal Forest Protection Act (TFPA, 2004; Public Law 108-278) allows the USFS, BLM, and federally recognized tribes to enter into contracts for harvesting traditional products from national forests, including special consideration stewardship contracting. The TFPA therefore allowed for the harvest of traditional forest products beyond plants (e.g., honey, animals, fungi). For an in-depth review and analysis of tribal consultation on federal lands that goes beyond the scope of this chapter, see Vinyeta and Lynn (2015).

SFP Management under the Northwest Forest Plan

Pacific Northwest Forest Plan & Adaptive Management Areas

The Central Cascades Adaptive Management Area (CCAMA) is one of the ten adaptive management areas under the Plan (ROD 1994, Stankey et al. 2005). The Plan set aside Adaptive Management Areas as places where new approaches to forest management could be tested and where collaboration between stakeholders should be a priority (ROD 1994, Stankey et al. 2005). The CCAMA comprises 155,700 acres of land that is jointly owned and managed by the USFS and BLM. The specified research and development emphasis for the CCAMA under the Plan were ecosystem landscape processes and forest management practices. In contrast, other AMAs had other emphases, such as forest management in the Adaptive Management Area (AAMA), intensive timber production in the Little River Adaptive Management Area (LRAMA), and marbled murrelet management in the Northern Coast Adaptive Management Areas (NCAMA) (Donoghue et al. 2006). The Willamette National Forest (WNF) is charged with managing the CCAMA together with the local BLM office (headquartered in Eugene).

The WNF comprises 1,678,031 acres of land. The WNF first developed a plan for forest management called the Willamette National Forest Land and Resource Management Plan in 1990 and was amended in 1994 once the Plan was passed. Annual Forest Plan Monitoring and Evaluation Reports are generated (1999 - present) to document monitoring activities and outputs in the forest. These reports document the implementation of monitoring activities on the forest since the original forest plan was executed in 1990. The reports synthesize information on monitoring categorized by physical resources, biological resources, resources and services to people, and social and economic resource management (WNF Monitoring Report 2013).

Methods: survey and history of previous survey of agency staff

We administered a Special Forest Products (SFP) Survey in March-April of 2014. The survey was given to USFS personnel in Region 6 (OR, WA) as part of a longitudinal study on non-timber forest products policy and management on National Forests. We administered the survey as part of a this dissertation research at the University of California, Santa Cruz (UCSC), Environmental Studies Department and through guidance from the Institute for Culture and Ecology (ICE) and the United States Forest Service (USFS). This was the third time a survey was given to USFS staff, with earlier versions that were distributed in 2000 and 2003. The results from previous surveys informed natural resource management for several ranger districts as well as various publications and books (McLain and Jones 2005). The goals of the 2014 survey were to report on the significant SFPs in the region, aggregate information on current SFP management (e.g., SFP inventorying and monitoring), better understand harvesting on districts, and provide feedback to the USFS on staff concerns and barriers for effective SFP management.

The rationale and administrative methods for the 2014 survey differed slightly from previous surveys. First, the 2014 SFP survey was given electronically rather than through a mass hard copy mailing effort through the US Postal Service. This decision was made in response to the difficulties that researchers experienced in gathering hard copy responses for the 2003 SFP Survey (McLain and Jones 2005). We concluded that an electronic version would also minimize the time it would take for survey participants to answer questions as well as expedite electronic data collection and analysis. Second, we obtained specific permission to administer this survey from both USFS Headquarters in Washington, DC as well as the Regional Forester (Kent Connaughton), who agreed to send the survey electronically to his personnel. The rationale for distributing the survey electronically was twofold: (1) to increase the questionnaire response rate from the 2003 survey since the regional office would encourage its staff to report data through the survey; and (2) to reach a broader group of respondents beyond district rangers who may be involved in SFP management (e.g., SFP Coordinators, Forestry Technicians, Forest Supervisors). Third, only a subset of national forests was surveyed (Region 6) compared to all Regions in the 2003. This was done, in part, to delve deeper into the SFP management in a particular region rather than gathering data from a broad survey from all US Regions.

Important SFPs that are Harvested in National Forests in the Pacific Northwest

Survey respondents indicated six types of SFPs that they considered important (i.e., demand and sales for product was high) within the national forests where they worked: firewood, boughs, mushrooms, beargrass, Christmas trees, and floral greens (Figure 3.2). Firewood was used for heating homes and campfires and was ranked as the single most important SFP in the region. Boughs (tree branches) were salvaged from Noble fir, Douglas fir, and red cedar trees after thinning forest stands or after large windstorms during the fall and winter to sell for holiday decoration and wreathes. Within the mushroom SFP category, commonly listed species included chanterelles (*Cantharellus* spp.), lobsters (*Hypomyces lactifluorum*), bear's head (*Hericium americanum*), king boletes (*Boletus edulis*), oysters (*Pleurotus ostreatus*), morels (*Morchella elata*), chicken of the woods (*Laetiporus sulphureus*), puffballs (*Lycoperdon* spp.), trumpets (*Craterellus* sp.), and matsutakes (*Tricholoma magnivelare*) (Figure 3.3). Harvesting permits are required for mushroom, beargrass, and floral green collection in national forests. For reporting on sales for SFPs in the Pacific Northwest, see McLain and Jones (2005).

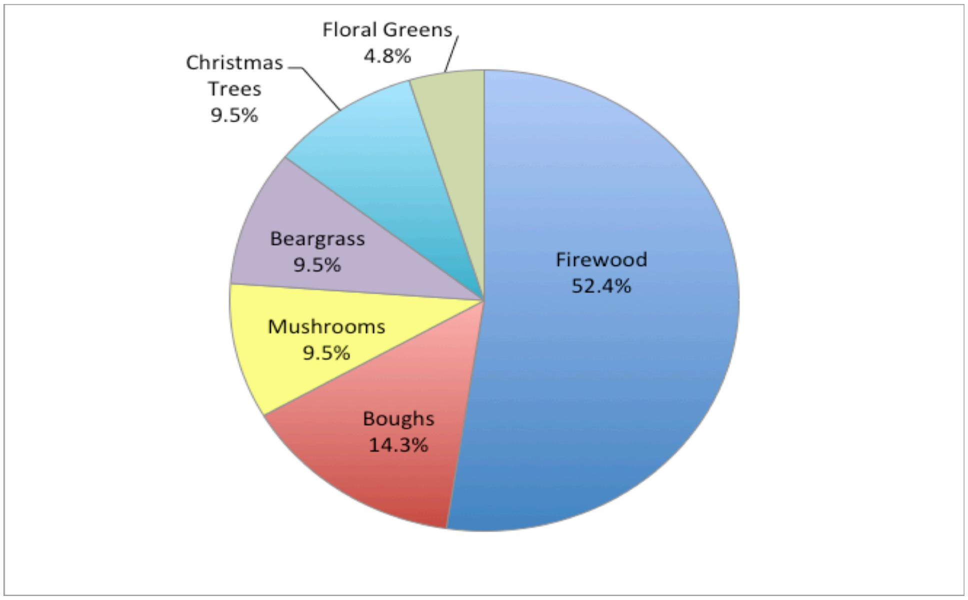

Figure 3.2. Important SFPs harvested in national forests in the Pacific Northwest (USFS Region 6). SFPs that are commonly harvested in national forests in the Pacific Northwest that are considered to be the "most important" products by survey respondents. Respondents were asked to write and rank the most significant and/or important SFPs harvested in their forest on a scale of 1 to 5, (where 1 was the most important and 5 the least important). The chart above shows the 6 types of products that were consistently ranked as number 1; percentages correspond with the proportion of responses that indicated each product as most important.

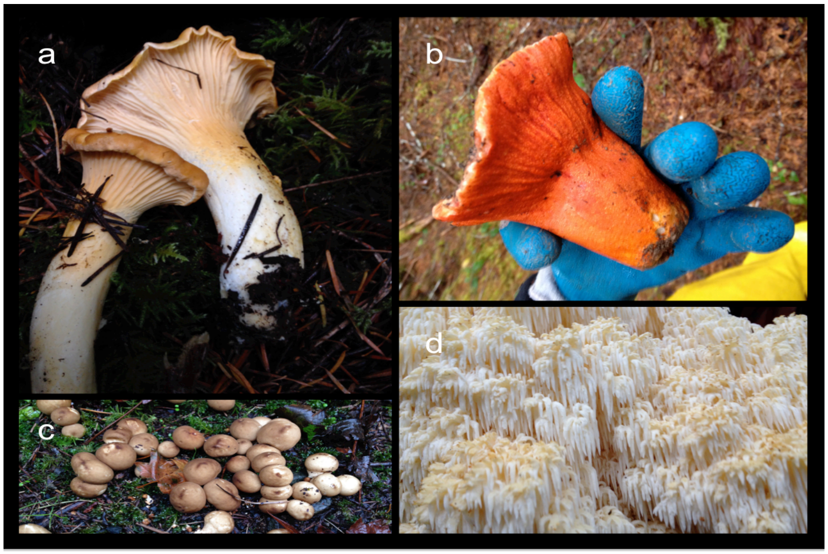

Figure 3.3. Examples of mushrooms that are harvested in Pacific Northwest national forests. a) white chanterelles, b) lobster mushroom, c) puffballs, d) bear's head mushroom. These mushrooms need personal or commercial permits for collection. Photo credit: S.G. Crandall.

SFP Management Planning

Resource managers overwhelmingly cited forest plans and environmental assessments as key SFP planning and data gathering documents; to a lessor extent, they cited environmental impact statements, watershed analyses, and landscape analyses. The NWFP was cited by only one respondent (Figure 3.4).

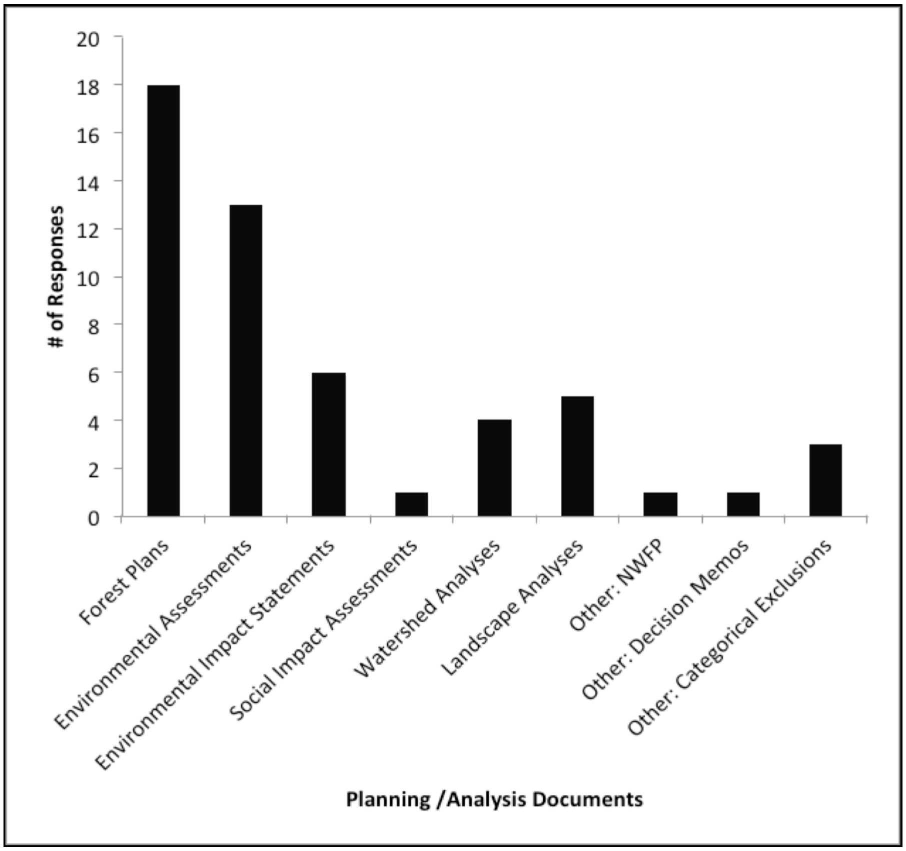

Figure 3.4. Forest planning documents & data gathering management processes that include SFPs. Inclusion of SFPs in planning documents and data gathering processes across national forests in Region 6. Forest plans specifically refer to national forest level plans, not region wide Northwest Forest Plan (NWFP), which is categorized under Other: NWFP.

SFP Management Practices

Two-thirds of resource managers indicated a SFP coordinator was present in their national forest and more than half stated there was a forest-specific SFP law enforcement program that prevented SFP theft and enforced the use of collection permits for personal and commercial harvesting (Figure 3.4). SFPs are monitored more consistently than inventoried and fewer than half of the respondents said there were collaborative activities with SFP harvesters in their forests (Figure 3.5).

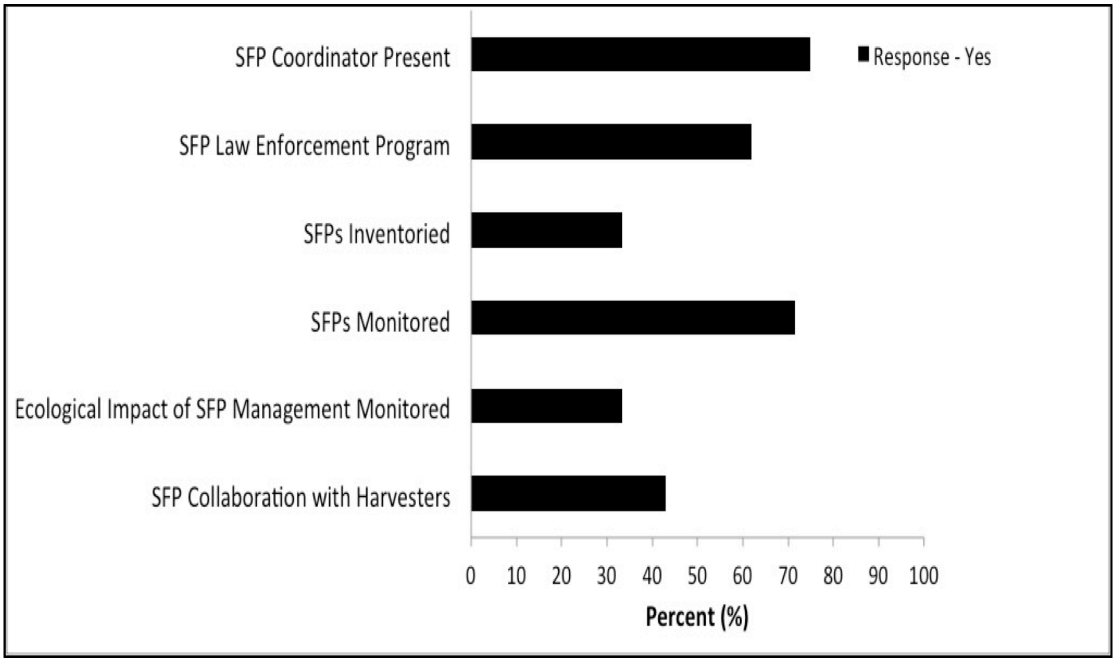

Figure 3.5. Special Forest Product (SFP) management practices in national forests in the Pacific Northwest. Percentage of survey responses from resource managers who indicated yes to the presence of experts such as SFP Coordinators, whether law enforcement programs were in place, inventorying and monitoring activities, and collaborative projects with harvesters.

Common Barriers for Inventorying & Monitoring SFPs

Collecting and recording biotic data (e.g., species identity, distributions) and abiotic data (e.g., weather, edaphic conditions) is ecological field inventorying whereas field monitoring involves repeated inventories over time. Inventory and monitoring data can help foresters manage species and site conditions. The top three barriers for inventorying and monitoring SFPs were inadequate federal funds to conduct these activities (62% of respondents), lack of personnel and help with fieldwork (43% of respondents), and time (29% of respondents) (Figure 3.5). Some respondents commented that USFS management made SFP inventorying and monitoring a low priority and consistently considered timber a higher management priority than non-timber product management. In some forests, there was low demand

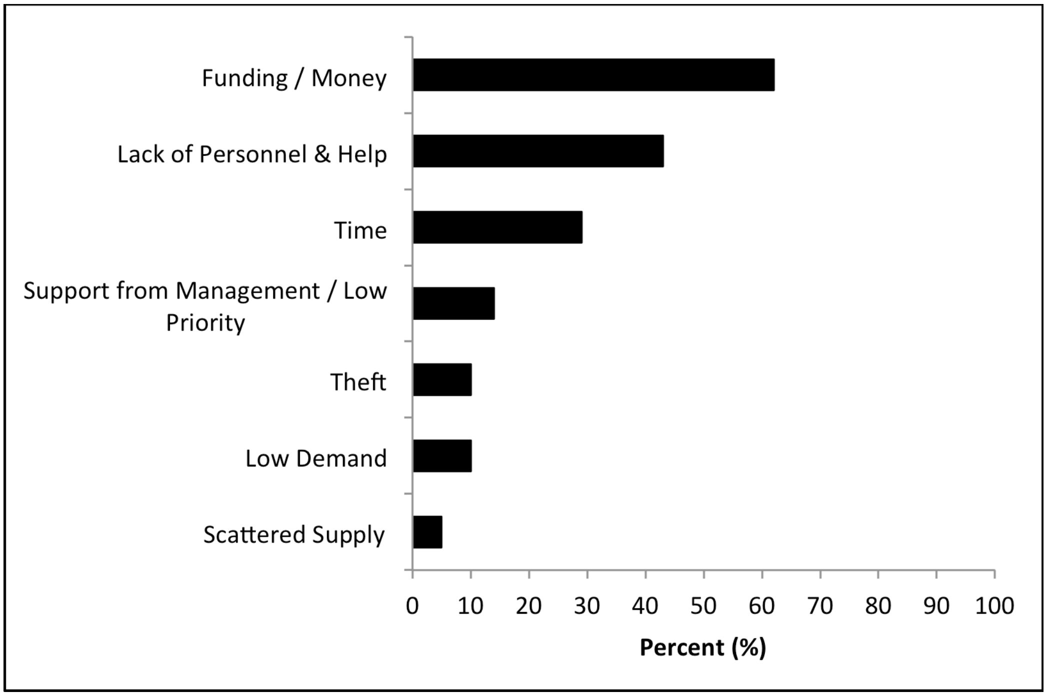

Figure 3.6. Common barriers for inventorying and monitoring SFPs in national forests according to survey respondents. Comments from all forests were consolidated into the seven categories from the most common to the least common barrier (top to bottom of chart). Bars indicate the number of times a category was mentioned once by each respondent compared to the total number of respondents who commented (shown as a percentage of total responses).

for SFP products. Others cited a scattered supply of SFPs in the field as a barrier for inventorying and monitoring products and that theft (the take of SFP without permits) was a persistent problem, despite law enforcement efforts (Figure 3.6).

SFP Collaborative Activities in National Forests

Resource managers from six national forests (Willamette, Rogue River-Siskiyou, Mt. Baker-Snoqualmie, Gifford Pinchot, Umatilla, and Mt. Hood) provided detailed comments about collaborative activities with harvesters in their forests. Various USFS partners were mentioned, such as Native American Tribes, local watershed councils, timber and fire officials, and groups that represented the interests of forest workers and harvesters (Table 3.1). Of the collaborative projects that were cited, managing huckleberries was considered a major collaborative activity in at least three national forests (Willamette, Mt. Baker-Snoqualmie, and Gifford Pinchot) in the Pacific Northwest (Table 3.1). Because the Willamette National Forest indicated the most detailed account of collaborative activities with harvesters, this forest was selected as a case study to further examine ecosystem-based management and collaborative partnerships for this dissertation (Table 3.1).

Table 3.1. Special Forest Product collaborative activities in national forests in the Pacific Northwest. Comments on SFP collaborative projects and activities that occur in national forests and harvester partners.

SFP Collaborative Projects & Activities	USFS Partners identified as "Harvesters"
Willamette National Forest	
Camas Restoration	Tribes
Huckleberry Enhancement	Tribes
Beargrass Harvesting	Tribes
Cedar bark, cedar boards for longhouses, first foods	Tribes
Breitenbush Collaborative - watershed health	North Santiam Watershed Council
South Santiam All Lands Collaborative - boughs, biomass for biochar	Unidentified
Administering Contracts, Law Enforcement	Unidentified
Rogue River-Siskiyou National Forest	
Botany, Fish, Wildlife	Unidentified
Firewood	Timber & Fire Officials
Mt Baker-Snoqualmie National Forest	
Huckleberry production, maintenance, improvement	Tribes
Gifford Pinchot National Forest	
Huckleberry monitoring of harvest areas, harvester educational outreach	Alliance of Forest Workers and Harvesters
Umatilla National Forest	
Collaboration to a minor degree, incorporated into larger projects	Unidentified
Mt. Hood National Forest	
Minimal	Unidentified

The Case of SFP Management in the Willamette National Forest

SFP Collaborative Activities: Contracts & Projects

The WNF, much like other national forests in the Pacific Northwest, had a forest-wide SFP Program, staff within each ranger district were responsible for both district and forest-wide management of SFPs. There were formal and informal SFP collaborative activities in the WNF that involved coordination and cooperation with SFP stakeholders, especially with local, federally recognized tribes. These collaborative activities took the form of contracts and projects. Memoranda of Understanding (MOUs) were formal contracts that created a framework for government-government consultation and coordination on forest policies and management (e.g., forest plans, proposals). The WNF established MOUs with (1) The Confederated Tribes of Siletz Indians of Oregon (CTSI), (2) The Confederated Tribes of the Grand Ronde Community of Oregon (CTGR), (3) The Confederated Tribes of the Warm Springs Reservation of Oregon (CTWS), and a Memorandum of Agreement (MOA) with (4) the Klamath Tribes (KT). Collaborative projects included restoration, vegetation enhancement and harvesting projects (Table 3.1).

Rationale for a Case Study of the Willamette National Forest

Based on results from the 2014 SFP Survey that we administered across Region 6, WNF natural resource managers indicated that SFPs were important products in their district and that collaboration over SFPs with harvesters, and specifically with federally recognized tribes, was ongoing. In addition, survey respondents from the WNF gave the most in-depth comments and responses to the SFP survey compared to other forests, which indicated a willingness to talk to researchers about best practices and challenges for collaboration in their forest. Finally, the WNF overlaps geographically with the Central Cascades Adaptive Management Area, making this national forest unit an ideal candidate for examining collaborative planning process in an area originally designated by the USFS in the 1994 Northwest Forest Plan to adopt an EBM approach. A working paper put forth by the Ecosystem Workforce Program from the University of Oregon assessed collaborative opportunities in the WNF and encouraged further, in-depth analysis of collaborative activities for SFPs (Davis and Moseley 2012).

Methods: Document Analysis and Key Informant Interviews

We used a mixed-methods approach to answer our research questions. Collaborative activities (e.g., formal or informal SFP management projects) were first identified from our region-wide SFP survey. Next, semi-structured interviews were conducted with 18 natural resource managers from the WNF in the fall of 2014 and in the summer and fall of 2015. Although there were many SFP collaborative activities that were present in the WNF, we chose to focus our analysis on those activities that were considered "successful" endeavors between the USFS and tribes by key informants (Wondolleck and Yaffee 2000) because these data can provide best practices and a useful model of collaboration for other national forests. We also collected information on collaborative activities (e.g., SFP monitoring, prescribed burns to enhance SFP habitat) using participant observation for monitoring activities such as prescribed burns and sowing native plant seeds (Bernard 2006). Moreover, we examined the WNF Annual Forest Plan Monitoring and Evaluation Reports, which are public documents that must report on activities as per the Plan. We also placed our research findings within the broader collaborative planning and ecosystem-based management literature to determine whether our case departs from or agrees with current theories and hypotheses on collaboration (Innes and Booher 1999).

Camas, Huckleberry, and Beargrass Monitoring Projects

The WNF engaged The Confederated Tribes of Siletz Indians of Oregon (CTSI), The Confederated Tribes of the Grand Ronde Community of Oregon (CTGR), and The Confederated Tribes of the Warm Springs Reservation of Oregon (CTWS) in three major SFP "biocultural resource tending" and monitoring projects (MOUs, Anderson 2005, Anderson 2009). The first was the restoration of a Cascadian meadow for camas lily (*Camassia quamash*) and other biocultural resources such as hazel (*Corylus cornuta*), oceanspray (*Holodiscus discolor*), wild rose (*Rosa nutkana*), tarweed (*Madia gracilis*) and the removal of invasive species such as Himalayan blackberry (*Rubus armeniacus).* The second project was for huckleberry (*Vaccinium* sp.) pruning and enhancement, and the third project was for gathering beargrass (*Xerophyllum tenax*) (Hummel et al. 2012, Pojar and MacKinnon 2004, WNF Interviewees 7, 11, 13).

The WNF acquired an approximately 14-acre patch of land in 1994 and began a Cascadian wet prairie restoration project in 1998. The project goals were to remove invasive plant species and to enhance native plant biodiversity. Initially, forest managers surveyed the site and found meadow indicator native species in addition to camas lily, such as Oregon checkermallow (*Sidalcea virgata*) and hyacinth brodiaea (*Triteleia hyacinthina*). However, the area was overgrown by invasive species such as Himalayan blackberry, Scotch broom (*Cytisus scoparius*), Oregon Ash (*Fraxinus latifolia*) and Queen Anne's lace (*Daucus carota*) (USDA NRCS 2016). The invasive plants would have to be removed if the prairie was to be restored to enhance native plant growth and survival (WNF Interviewee 7). "The ash and blackberry were taking over," remembers one forest manager. They recalled that they would need a lot of time and resources to clear the area (WNF Interviewee 7).

According to WNF forest interviewees, forest managers consulted tribal partners to see if they were interested in restoring the prairie together with forest personnel (WNF Interviewee 5, WNF Interviewee 1, WNF Interviewee 7). The Confederated Tribes of Siletz Indians and the Confederated Tribes of Grand Ronde Indians showed interest and became involved in the early decision-making process for how to restore the site and determined which biocultural resources to restore. (WNF Interviewee 7). Together, the federal resource managers and tribal representatives decided to use low-intensity fire in the late summer / early fall, a traditional method used to clear invasive species and promote the growth of native plants that are considered tribal cultural resources. According to one forest manger that was present at the start of the project, the tribes were instrumental in devising the long-term goals of the restoration project and tribal members worked side-by-side foresters to clear invasive weeds and conduct the burns (WNF Interviewee 5). Project goals were created from the start, but they were "loose and flexible" remembers one resource manager (WNF Interviewee 5). Since 1998, the land has been burned every two years and prescribed burns are still implemented today to manage invasive species and promote the growth of plants such as camas lily (Figure 3.6).

Figure 3.7. Prescribed burn of a wetland prairie site to restore camas lily and other biocultural resources. a) Camas lily stalk in the foreground growing in a sea of invasive grasses and forbes, b) low-intensity prescribed burn in 2015, c) site one day after the burn; the ground is cleared of most invasive plants, d) camas lily seeds were sown after the burn. Photo credit: S.G. Crandall.

Forest resource mangers and tribal representatives jointly monitor plants and tend the prairie. Today, the camas lily population has doubled since the project was implemented and there are half as many invasive species found on site as there were at the beginning of the restoration project. One forest manager said that the project goals were flexible from the start, and evolved over time to include cultural resource management techniques and tribal needs, "restoration is not complete until the cultural function has resumed." Native plant seeds are collected and sown after the burns by forest managers, tribal members, and public volunteers (e.g., local community college students, Girl and Boy scouts); tribes also take periodic community field trips to the area to teach youth about tending camas and other Native American traditional plant resources (WNF Interviewee 5, WNF Interviewee 7, WNF Interviewee 14).

WNF forest managers work closely with tribal partners to increase access to SFPs that are valued as important tribal resources (e.g., huckleberry, beargrass) (WNF Interviewee 14, WNF Interviewee 8), (Figure 3.8). According to WNF

Figure 3.8. Special forest products that were tended and harvested during tribal-federal collaborative activities in the WNF. a) huckleberries were pruned and harvested as a first food, b) beargrass was harvested for weaving, c) red cedar bark was harvested for traditional clothing, and d) digging stick and basket full of camas bulbs used as a first food. Photo credit: S.G. Crandall.

interviewees, tribal representatives initially approached WNF forest managers to inquire about gathering huckleberries in the forest and to manage huckleberry patches (< 1-2 acres) for tribal use. During huckleberry harvest season in the early fall, forest managers and tribal members engaged in annual "work parties" to coordinate pruning patches of huckleberries for "huckleberry enhancement" (WNF Interviewee 14). During these events, managers and their families joined tribal resource managers and their families, and over the years, they had the opportunity to get to know each other through physically working together on huckleberry enhancement (WNF Interviewee 1, WNF Interviewee 5, WNF Interviewee 7). WNF works closely with tribes to protect the location of these sites from others who may exploit important traditional first food resources (WNF Interviewee 5, WNF Interviewee 14). Moreover, SFP program staff direct public harvesters with harvesting permits to field sites that are designated for public use only; tribal members access and tend designated huckleberry harvesting sites as protected under MOU contract agreements and other legislative mandates (e.g., AIRFA, NIFRM, AIARMA) (WNF Interviewee 2, WNF Interviewee 14).

Beargrass is an important plant used by Native Americans tribes throughout Northern California and Oregon for weaving baskets and other crafts as well as in ceremonial dances, such as the summer solstice feather dance of the Confederated Tribes of Siletz Indians (Hummel et al. 2012, Anderson 2005, Juntunen et al. 2005, Wilkinson 2010, WNF Interviewee 10, WNF Interviewee 5). The WNF worked with tribal partners to increase access for beargrass and other traditional plant resources:

"Tribes asked for easier access to SFPs such as hazel, beargrass, and oceanspray, so the USFS planted them along roadsides with a dual purpose: good for a fuel break and to make the area more fire resistant as well as tribal gathering area. It was a win-win." (WNF Interviewee 14). Other products were harvested in the WNF by tribes include Western red cedar (*Thuja plicata*) cedar boards for longhouses and bark for traditional clothing (WNF Interviewee 5), (Figure 3.8).

Although not the focus of this research, the WNF continues to conduct and propose collaborative activities with various stakeholders that indirectly involve SFPs. The Cool Soda Project was a vegetation restoration project that did some SFP enhancement in the Sweet Home Ranger District. There are some future large-scale initiatives in development: the Breitenbush Collaborative and Southern Willamette Forest Collaborative seek to protect and improve watershed health, and the Santiam All Lands Collaborative aims to collaboratively manage SFPs such as boughs and biomass for biochar (WNF Interviewees 1, 8, 9).

On-the-ground: A Departure from Ecosystem-system based Management Goals

Recall that ecosystem-based management was integrated into the NWFP in the 1990s as a way to improve natural resource management in national forests in the Pacific Northwest with two goals: (1) use landscape-scale assessment and planning for natural resource management, and (2) use collaborative multi-stakeholder participation during environmental planning. Our case study, however, suggest a departure from the original ecosystem-based management goals outlined in the Plan. Below, we discuss two major findings: first, we found small-scale collaboration rather than large-scale collaborative management for SFPs, and second, bi-lateral stakeholder exchanges were more prevalent than multi-stakeholder interactions.

Small-scale versus Landscape-scale Collaborative Management

Collaborative SFP management projects in the WNF occurred at small scales (< 20 acres). We suspect three factors contribute to this result: (1) Many SFPs exist in small, fragmented habitats, (2) plant and mushroom distributions are inherently patchy or unknown, making these products difficult to manage across federal jurisdictions, and (3) lack of federal funding and resources to manage SFP projects.

First, land-use history played an instrumental role in shaping the distribution of SFPs in north-central Oregon. Less than 2% (~1000 acres) of Cascadian wetland prairie remains in the Willamette Valley region because of wetland conversion to ranches, farms, and urbanization which started in the 1850s (Krueger et al. 2014). These wet prairies contain many biocultural plant resources that are important to Oregon tribes in antiquity and today. For instance at least 50 wet prairie plants are considered important to the Kalapuyans (Juntunen et al. 2005, Krueger et al. 2014). Wetland prairies exist as islands in a matrix of forest or other public and private land-use types; which makes coordinated efforts to access or manage these products difficult (Krueger et al. 2014, WNF Interviewees 1, 14).

Second, many plants and mushrooms inherently possess restricted geographic ranges (McLain and Jones 2005, Peay et al. 2010) and some species ranges are yet to be delineated (Pilz et al. 2007, Krueger et al. 2014). Still other forest products, such as bark from red cedar or Pacific yew (*Taxus brevifolia*) come from trees that grow in uneven forest stands across coastal and central Pacific Northwest (McLain and Jones 2015). WNF resource managers know where to find SFPs within their jurisdictions, or as one manager put it, "their backyard" (WNF Interviewee 2), rather than throughout unfamiliar territory in other districts or forests regionally (WNF Interviewees 2, 3, 7, 11, 17). There is some evidence for dialogue and coordination across ranger districts in the WNF. Key informants confirmed that SFP coordinators from across WNF districts meet periodically to discuss the current state of SFPs in their jurisdictions and to share forestry challenges and best practices. However, inter-district coordination does not occur on a regular basis since most products grow and are harvested in the Sweet Home and McKenzie ranger districts, with a lessor amount of SFP management in the Detroit and Middle Folk districts (WNF Interviewees 1, 2, 4, 8, 17).

Third, forest managers frequently cited scant funding and resources to conduct SFP inventorying and monitoring (Figure 3.6, WNF Interviewees 2, 3, 6, 7, 13). Although SFP Coordinators exist in some ranger districts, they might be hired part-time or have little to no personnel to help with field monitoring, conducting sales, or the daily ins-and-outs of managing SFP project administration (e.g., permitting, reporting, pruning and planting, helping law enforcement prevent SFP theft and vandalism) (WNF Interviewees 2, 4). Notably, multiple informants indicated that collaborative projects for SFPs that were small in scope (i.e., small area to manage, needed few resources) were logistically feasible and built trust with stakeholders because there were fewer people involved to make on-the-ground decisions (WNF Interviewee 1, 2, 5, 15).

Ansell and Gash (2008) show that for collaborative governance to be successful, "small wins" driven by stakeholder incentives and leadership are essential to create "a virtuous cycle of collaboration." We found three factors that contribute to the small-scale nature of collaborative projects; the first two factors - fragmented landscapes and restricted and unknown species distributions - are inherent to the land-use history, ecology of the products, and institutional design of national forests which manage SFPs by jurisdiction, i.e. ranger district. However, the third factor, lack of federal funding and resources, we argue, compelled a focus on "small wins" in the WNF. Initially, lack of funding and staff for SFP management provided an incentive for federal resource managers to reach out to stakeholders, namely local tribes, to help them restore a wetland prairie beyond an opportunity for cultural restoration of the site (WNF Interviewees 1, 5, 7). Moreover, federal resource managers (e.g., anthropologists, archeologists, federal-tribal liaisons) who had interdisciplinary training in socio-cultural issues and forest science helped other Forest Service personnel understand the tribal perspective for increasing access and use of cultural resources, such as SFPs, on federal land (WNF Interviewees 1, 5, 7, 14). The leadership and presence of these experts during the early decision-making process for each collaborative activity, in turn, facilitated understanding and trust between federal resource managers and local tribal members involved in the SFP projects (Wondolleck & Yaffee 2000). Specifically, co-management of the camas restoration site (e.g., weeding, prescribed burns, native seeding and planting, inventorying and monitoring), and later, joint tending of huckleberries and beargrass on an annual or biannual basis, perpetuated the virtuous cycle of collaboration in the WNF (Ansell and Gash 2008).

Still, ecosystem-based approaches call for large-scale conservation planning and management, especially for species that have large ranges, such as grizzlies or wolves (Layzer 2008, 2012). At first glance, it may seem that large-scale projects might not be feasible for SFPs, given their growth and persistence in fragmented habitats and patchy or unknown species distributions. However, Duane (2007) showed that in some cases, good politics can outweigh good science to produce successful environmental outcomes, especially if ecological and social goals are somewhat nebulous and flexible at the start of the collaborative planning process. This was the case with each of the SFP collaborative activities in the WNF. While not perfect, positive relations between local federally recognized tribes and the WNF developed over the years because restoration goals were simple, yet adaptive (Stankey et al. 2005). If sustained, these government-to-government relationships could contribute to successful large-scale collaborative initiatives where social and ecological outputs and outcomes are improved (Layzer 2008), despite lacking data for entire SFP species distributions, ranges, and population biology (Duane 2007).

There is US legislation in place that enables federally recognized tribes access to SFPs that have cultural importance on federal land (AIRFA, NIFRM, AIRMA, TFPA). Certain policies mandate federal-tribal consultation that require federally recognized tribes to be invited to the planning table (Vinyeta & Lynn 2015). However, a long-standing history of broken treaties and promises between the federal government and tribes in Oregon (Wilkinson 2010) must be acknowledged and addressed by federal agencies when working with tribes. Historical and current asymmetries in political power could influence whether federal-tribal collaborations succeed in the long-term regardless of project scale (Wondolleck & Yaffee 2000, Anderson 2005, Anderson 2009, Vinyetta and Lynn 2015).

Bi-lateral versus Multi-lateral Stakeholder Interactions

Bi-lateral, rather than multi-lateral interactions were the norm, for SFP collaborative activities in the WNF. This may be for two reasons: (1) it was difficult for some stakeholders to participate in WNF collaborative activities because of geography, and (2) it took years to build federal-tribal relationships because most Forest Service personnel were unaware of legal obligations toward federally recognized tribes and the socio-cultural importance of SFPs.

First, according to key informants, certain tribes, notably The Confederated Tribes of Siletz Indians and the Confederated Tribes of Grand Ronde Indians, became more involved in collaboratively managing SFPs than other tribes because of where the sites were located relative to how far tribal members had to travel from their homes (either on or off reservations) to engage in meetings and on-the-ground projects (WNF Interviewees 1, 5, 7, 12). Although the WNF has MOUs with the Confederated Tribes of the Warm Springs Reservation of Oregon and the Klamath Tribes, the Warm Springs Tribal headquarters, for instance, is located over a hundred miles east of many federal-tribal collaborative sites that are in the western part of the national forest. WNF resource managers claim that although multiple tribes were consulted for tending SFPs, it was hard for certain tribal members to attend pruning work parties, prescribed burns, or other harvesting and SFP centered events simply because they lived too far away, and that they expressed this concern to Forest Service personnel (WNF Interviewees 1, 5, 12, 14). Moreover, these tribes were more willing to work closely with national forest personnel in forests where harvesting would be geographically closer (WNF Interviewees 2, 5, 14). This is an example where stakeholders that belong to similar communities of interest (SFP harvesting) participate in collaborative activities in a smaller capacity than other stakeholders due to geography (Duane 1997).

Second, it took more than 15 years to build trust between Forest Service personnel and stakeholders to establish bi-lateral collaborations for SFP management. In the 1990s, there were very few Forest Service experts who had training in the social dimensions of natural resource management in the WNF (WNF Interviewees 2, 5, 7, 14). Although these individuals, over time, helped raise awareness about stakeholders needs and values, including those of historically disenfranchised groups such as Native American Tribes (Wilkinson 2010), the change within the Forest Service culture occurred at a glacial pace in the WNF, especially among higher ranked personnel whose management priorities revolved around timber rather than non-timber products (WNF Interviewees 8, 9, 14). According to key informants, tribal-federal conflicts would arise periodically when Forest Service employees failed to consult with tribes about projects, or simply informed "the public" and failed to uphold their government-to-government obligation to consult tribes separately (WNF Interviewees 1, 5, 14). Certain Forest Service positions were created in the past decade with specific tasks and responsibilities to coordinate tribal-federal relationships; these personnel run law, policy, and cultural training presentations and workshops in national forests to increase awareness and socio-cultural understanding among fellow Forest Service personnel, as well as with tribal resource mangers and tribal council representatives from multiple local tribes (WNF Interviewees 5, 14).

The WNF does have some large-scale, multi-lateral collaborative natural resource proposals underway that seek to engage various stakeholders across WNF ranger districts to address ecosystem health and management (e.g., Breitenbush Collaborative and Southern Willamette Forest Collaborative, South Santiam All Lands Collaborative). In the wake of federal funding and budget cuts, it is critical that any collaborative projects for the WNF and other forests in the Pacific Northwest, keep expert Forest Service positions for personnel who are trained in forest policy and social science (e.g., federal-tribal liaisons, archeologists, anthropologists, SFP coordinators) to lead successful multi-lateral collaboration.

Finally, there is growing evidence for a shift in the harvester landscape from the time the Plan was enacted in the 1990s till today (Charnley et al. 2008, Langdon 2013). Key informants noted repeatedly that the demographics of who harvests mushrooms and applies for collection permits has changed in the past 20 years (WNF Interviewees 1, 2, 5). Initially, predominately Caucasian residents and Native

Americans harvested SFPs; but today, East and South Asians and Hispanic groups pick mushrooms and other SFPs for cultural, religious, and commercial purposes (Tsing 2009, Charnley et al. 2008). Although some US legislation protects the rights of federally recognized tribes to access and harvest SFPs on federal land (Vinyeta & Lynn 2015), no formal policies exist that represent the diverse needs and values of other SFP harvester groups, Native Americans from tribes that are not federally recognized (Charnley et al. 2008, Lynch et al. 2004). Should the needs and values of harvester groups not be recognized, this could be problematic for encouraging multi-stakeholder participation in large, federal, ecosystem-scale projects in the future that will also manage for SFPs (Lynch et al. 2004, Stumpff 2001, Stuart and Martine 2005).

Conclusions

Collaboration is used to help diverse stakeholders (e.g., governmental agencies, non-governmental organizations, federally recognized tribes, and the public) incorporate people's values and needs, in addition to ecological information, into the decision-making process. Although ecosystem-based management, which is informed by collaboration theory, was incorporated into the Northwest Forest Plan in the 1990s to improve ecological and social outcomes for natural resource management, Special Forest Management in the Willamette National Forest departs from the original ideals in two ways: (1) collaborative activities occurred at small scales, and (2) collaboration occurred primarily through bilateral rather than multi-lateral stakeholder interactions. Moreover, collaborative SFP management was driven by legal obligations to tribes and the presence of key personnel that served as leaders and facilitators who increased policy and cultural awareness within the WNF helped cultivate federal-tribal relationships. Further research is needed to document the perspectives and needs of harvesters, including federally recognized tribes and other groups of harvesters (e.g., ethnic groups, recreational, commercial) (Lynch et al. 2004, Love and Jones 1997), should large-scale, multi-lateral collaborative projects be initiated by the Forest Service.

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Supplementary File Information

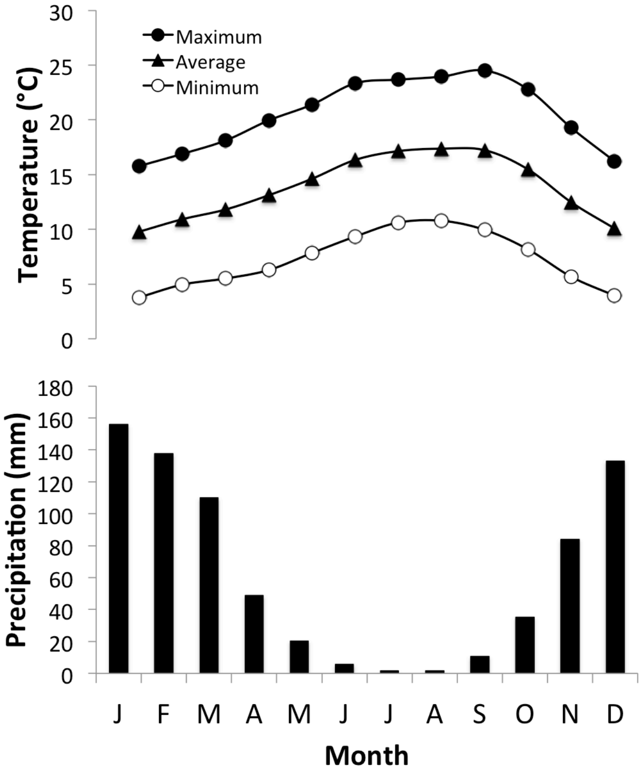
Description: Fungal diversity found in rainwater across a coastal vegetation mosaic in California, USA.
File Name: Crandall_2016_OTU_fungal_consensus_lineages.xlsx

Appendices

Appendix 1A. Global Positioning System (GPS) coordinates of field sites where airborne spore samples were collected at different vegetation types and temporal scales.

Vegetation Type	Site	GPS Coordinates	Temporal Scale
coastal redwood forest	1	36°58'43"N, 121°59'3"W	Year / January - March
coastal redwood forest	2	36°58'46"N, 122°1'11"W	Year / January - March
coastal redwood forest	3	37°2'59"N, 122°2'21"W	Year / January - March
coastal redwood forest	4	37°3'9"N, 122°2'54"W	Year / January - March
maritime chaparral	1	36°58'4"N, 122°1'25"W	Year / January - March
maritime chaparral	2	36°40'52"N, 121°47'6"W	Year / January - March
maritime chaparral	3	37°2'2"N, 121°59'57"W	Year / January - March
maritime chaparral	4	37°3'11"N, 122°2'12"W	Year / January - March
mixed-evergreen forest	1	36°58'42"N, 121°59'16"W	Year / January - March
mixed-evergreen forest	2	36°58'47"N, 122°1'56"W	Year / January - March
mixed-evergreen forest	3	37°3'34"N, 122°1'30"W	Year / January - March
mixed-evergreen forest	4	37°3'9"N, 122°1'39"W	Year / January - March
coastal prairie[a]	1	37°1'16"N, 122°4'21"W	Diurnal / Nocturnal
mixed-evergreen forest[a]	2	37°2'45"N, 122°4'21"W	Diurnal / Nocturnal

[a] For diurnal and nocturnal airborne spore collection, GPS coordinates were measured in the center of an equilateral triangle (perimeter of 30 m) and samples were collected at each apex.

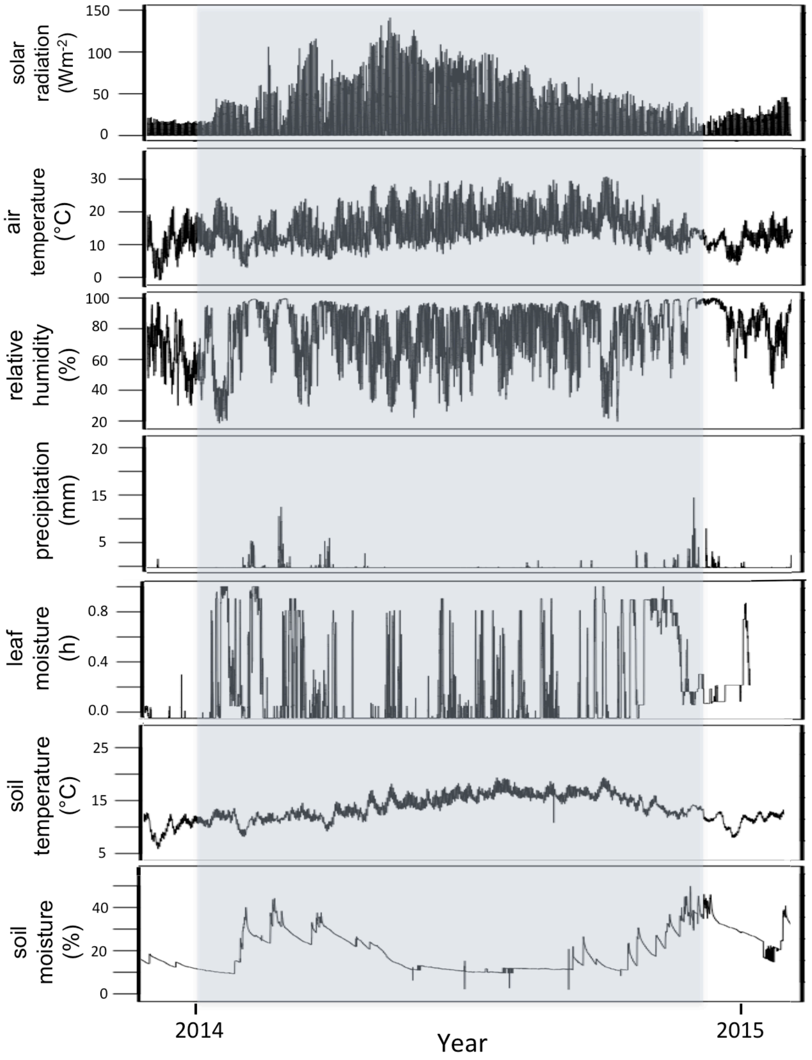


Appendix 1B. Weather patterns for Santa Cruz, California. Shown are monthly maximum, average, minimum temperatures and total precipitation from 1893 - 2015. Data source is from the National Oceanic and Atmospheric Administration (NOAA) Western Regional Climate Center and Santa Cruz weather station number 047916 (wrcc@dri.edu).

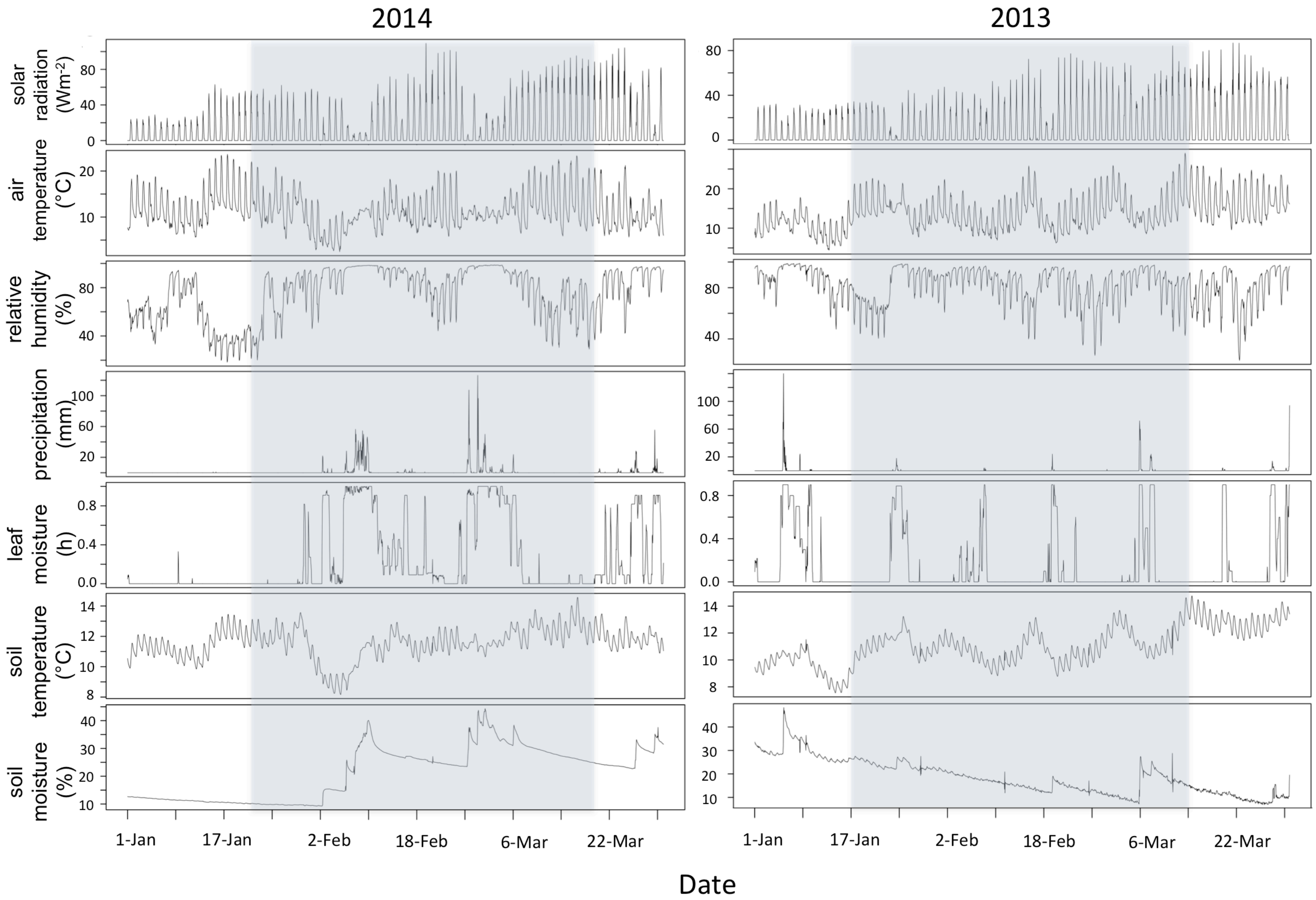
Appendix 1C. Multiple linear regression models for different time scales. The best model is the result from the stepwise selection (both directions) and the model with the lowest Akaike Information Criterion (AIC) score.

Model	Description	Best Model Selection[a]	AIC
1	Year 2014	residuals ~ {temperature + relative humidity + precipitation + soil moisture + soil temperature + leaf moisture + habitat + (temperature × relative humidity) + (relative humidity × precipitation) + (temperature × habitat) + (precipitation × habitat)}	-361.19
2	Wet season 2014	residuals ~ {temperature + relative humidity + precipitation + soil moisture + leaf moisture + habitat + (temperature × relative humidity) + (relative humidity × habitat) + (leaf moisture × habitat)}	-295.97
3	Wet season 2013	residuals ~ {temperature + relative humidity + precipitation + soil moisture + leaf moisture + solar radiation + habitat + (temperature × relative humidity)}	-7007.09

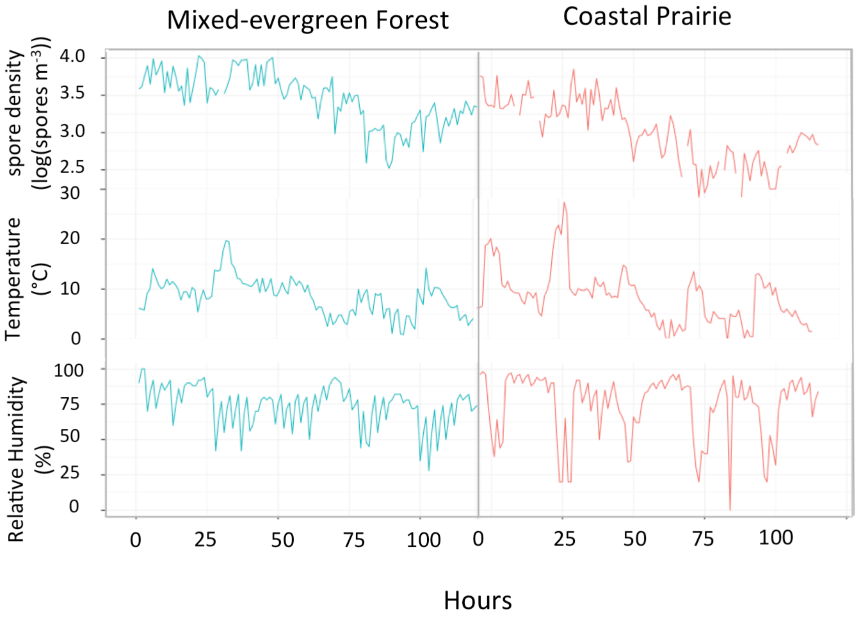
[a] Initial model used for all multiple linear regressions: residuals ~ (temperature * relative humidity * precipitation * soil moisture * soil temperature * leaf moisture * solar radiation * habitat).



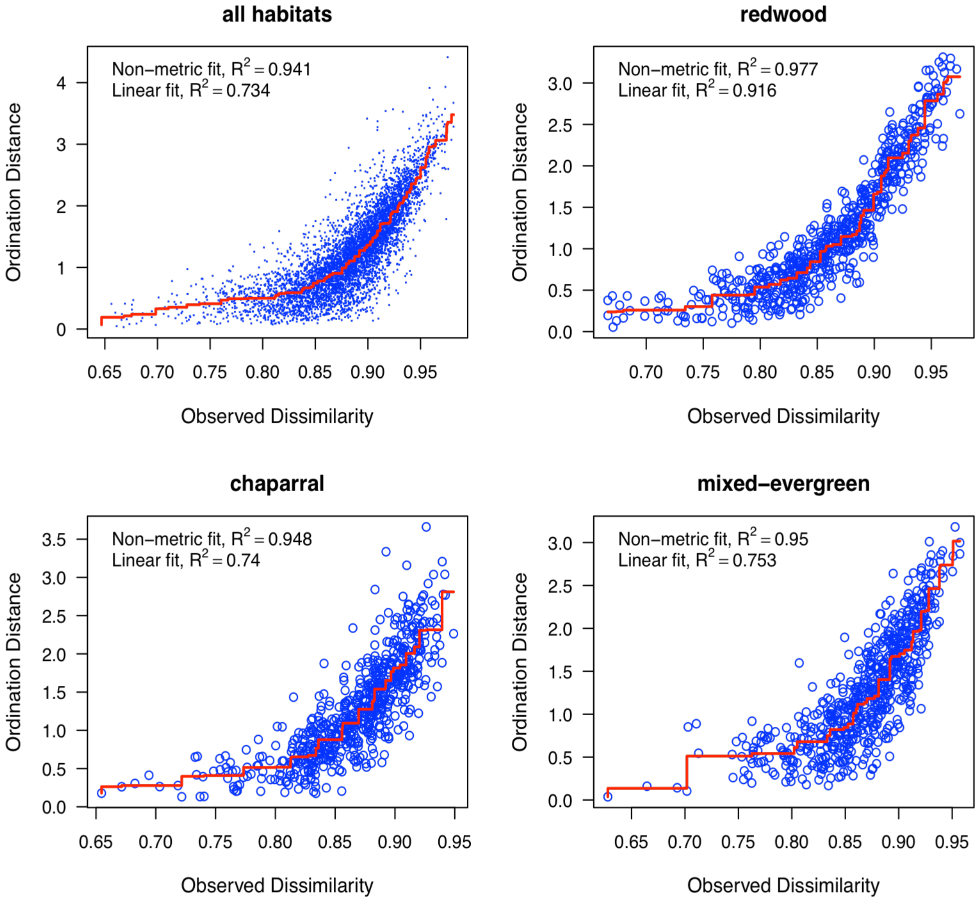
Appendix 1D. Weather data obtained as daily averages from 12 Decagon™ model EM 50 weather stations (decagon.com) from the University of California, Santa Cruz Forest Ecology Research Plot (Gilbert et al. 2010, http://ferp.ucsc.edu). Shown are measurements from January - November in 2014 for seven meteorological variables: solar radiation (W m^{-2}), air temperature (°C), soil temperature (°C), relative humidity (%), precipitation (mm), leaf moisture (h), and soil moisture (%). Shaded area shows when airborne spores were collected in the field.



Appendix 1E. Weather data obtained as daily averages from 12 Decagon™ model EM 50 weather stations (decagon.com) from the University of California, Santa Cruz Forest Ecology Research Plot (Gilbert et al. 2010, http://ferp.ucsc.edu). Shown are measurements from January - March in 2014 and 2013 for seven meteorological variables: solar radiation (W m^{-2}), air temperature (°C), soil temperature (°C), relative humidity (%), precipitation (mm), leaf moisture (h), and soil moisture (%). Shaded areas were when airborne spores were collected in the field.



Appendix 1F. Airborne spore density, air temperature, and relative humidity measured in a mixed-evergreen forest and coastal prairie over a 120 h period in January 2013.



Appendix 2A. Stress plots of ordination distance versus observed dissimilarity for each NMDS ordination for fungal community diversity.

Appendix 2B. Permutational Analysis of Variance (PERMANOVA) results to determine if there was a significant effect of sampling week on fungal diversity using next-generation DNA sequencing (Illumina) (top row); to determine if spore traits differed significantly among redwood forest, mixed-evergreen forest, and chaparral (bottom row).

PERMANOVA	**p**	***F***	**r^2**	**df**
Fungal diversity	0.005	1.323	0.158	16
Fungal spore traits	0.005	4.769	0.036	2

Appendix 2C. Tukey HSD Test results as part of the Nested Analysis of Variance (ANOVA) for fungal spore trait parameters and between habitats; adjusted p-values are shown from left to right for mixed-evergreen and chaparral, redwood forest and chaparral, and redwood forest and mixed-evergreen forest.

Spore Trait	**mixed-evergreen - chaparral** p	**redwood - chaparral** p	**redwood - mixed-evergreen** p
Height	0.196	0.156	0.990
Width	**< 0.001**	**< 0.001**	0.400
Perimeter	**0.012**	**< 0.001**	0.656
Major Axis	**0.040**	**0.002**	0.524
Minor Axis	**0.002**	**0.001**	0.980
Feret's Diameter	**0.044**	**0.002**	0.489
Skew	0.886	0.923	0.996
Circularity	0.684	0.998	0.632
Aspect Ratio (AR)	0.207	0.763	0.559
Roundness	0.207	0.763	0.560
Solidity	0.575	0.907	0.821
Kurtosis	**0.043**	**0.018**	0.936